COWRIE – BEN – 03 – 2002

Predicting the displacement of common scoter *Melanitta nigra* from benthic feeding areas due to offshore windfarms

Centre for Applied Marine Sciences, School of Ocean Sciences, University of Wales, BANGOR

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Final report – Executive Summary

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Acknowledgements

This project was supported by COWRIE funding under BEN-03-2002. The overflight data used in this study was funded jointly by the Countryside Council for Wales, English Nature, The Crown Estate, BHP and the developers of the offshore windfarms in Liverpool Bay and was compiled by Peter Cranswick of The Wildfowl & Wetlands Trust, Slimbridge. We are grateful to the following people for the provision of data or help with sourcing data: Peter Cranswick The Wildfowl & Wetlands Trust, Tony Fox NERI, Victoria Copley English Nature, James Dargie Countryside Council for Wales, Andy Webb Joint Nature Conservation Committee. Ship disturbance data was compiled by Mike Cain Anatec Ltd from the COASTS database under a subcontract. The compilation of the 1 km x 1 km gridded bathymetry for the Irish Sea, Celtic Sea and North Channel was funded by the Department of Transport and the Regions (DETR), and the Ministry of Agriculture Fisheries and Food (MAFF). (Brown, J., Joyce, A.E., Aldridge, J.N., Young, E.F., Fernand, L. and P.A. Gurbutt, 1999. Further Identification and Acquisition of Bathymetric Data for Irish Sea Modelling. DETR research contract CW075.). Thanks to the following; field assistants, Robin Chittenden, Alexander Lees, Ilya Maclean and Simon Woodhouse.

Executive summary

i Introduction

The environmental impact assessments of most offshore windfarm proposals raise the potential effects on birds as an important issue. Offshore windfarms may affect birds in a number of different ways including mortality due to direct collisions of birds while in flight and mortality induced by habitat loss due to the avoidance by foraging birds of such conspicuous structures. Birds that may be affected by displacement from foraging areas within close proximity to windfarms are likely to be those such as common scoter and common eiders that feed on sedentary or slow-moving bottom-dwelling organisms such as bivalve molluscs and fish-eating birds such as grebes, terns, auks and divers. This present study used field observations and surveys combined with an individuals-based modelling approach to predict the change in over-winter mortality rates of common scoter that would result from the displacement of birds from potential feeding habitat through the avoidance of windfarms in Liverpool Bay. The model code is, however, not specific to Liverpool Bay and can be utilised for other areas provided that suitable data are collected.

ii Project Structure

The project included the following tasks:

- A description of the physical habitat utilised by common scoter
- Quantification of the spatial and temporal variability in prey
- Observation of the behaviour of birds at sea and their response to disturbance
- Quantification of other forms of disturbance relevant to common scoter
- A review of the diving duck literature
- Development of a behavioural model to predict responses to windfarms
- Calibration and validation of the behavioural model
- Predicting the consequences of offshore windfarm developments
- Making recommendations for future research requirements

iii Project findings

The key points relating to each of these tasks are outlined in the following sections

iv A description of the physical habitat utilised by common scoter

A tidal model of the Irish and Celtic Seas was developed with a grid resolution of approximately 3.7 x 3.35 km to simulate the tidal elevations and currents throughout Liverpool Bay. The predictions of this tidal model were used to simulate the spatial and temporal variation in water depth throughout the study area covered by the individuals-based model of common scoter' behaviour.

The tidal model was also used to predict the tidal elevations and currents at the locations and times when common scoter were observed during aerial and land-based surveys. It was then possible to calculate the depth of water beneath each bird at the time of observation and the speed of drift at the sea surface.

A histogram of observed duck numbers as a function of the mean water depth showed an approximately domed distribution with most of the birds concentrated around depths of 10-12m with a range of from 2-22m. When the depths were tidally corrected, however, the histogram became more ramp-like with a relatively rapid decline in numbers where the depth was greater than 18 m. This is consistent with the literature concerning common scoter diving depths and with the diving sub-model within the behavioural model.

The area of habitat that is available to common scoter i.e. water depth les than *circa* 20m can be reduced by approximately a third when comparing low water and high water spring tide conditions. The sea bed stress due to waves was estimated to be an order of magnitude larger than that associated with the tidal motion in the relatively shallow region along the Lancashire coastline and this probably has a strong influence on the depth zone in which the highest biomass of prey types (bivalve molluscs) and hence common scoter are found.

v Quantification of the spatial and temporal variability in prey

An extensive survey of the potential benthic prey of common scoter was conducted in August 2003. This involved sampling 81 stations off the Lancashire coast and a further 88 stations off the North Wales coast. Analysis of the samples was used to define the spatial variation in the abundance of the principle food resources (i.e. benthic bivalves) throughout the study area covered by the individuals-based model of common scoter behaviour.

The highest numbers of common scoter observed on over flights coincided with sites that had a high abundance and biomass of bivalve prey species, and bivalve biomass was among the strongest predictors of numbers of common scoter observed during over flight surveys.

Off the sheltered North Wales coastline the peak in biomass occurred at a shallow depth of 8 m whereas off the Lancashire coastline the peak occurred in deeper water at 14 m. Thus birds that remain to feed off the Lancashire coastline have to dive deeper and expend more energy to acquire their food. If windfarm developments dissipate wave energy this could have implications for the depth zone in which the highest biomass of prey are found (i.e. the peak biomass could move inshore into shallower water).

The distribution of bivalve prey species was extremely patchy even when these were grouped into ‘prey-types’ according to their morphological features i.e. brittle-shelled oval prey, hard-shelled oval prey, elongate prey. One important implication for future Environmental Impact Assessments related to windfarms is that it will not be possible to use an ‘indicator species’ to represent bivalve prey as the distribution of one species on its own has little or no resemblance to the distribution of the entire bivalve assemblage.

Inter-annual variation in bivalve abundance was much lower than spatial variation in their abundance for a four year period between 2001 and 2004. Thus, while the abundance of individual species may vary from one year to the next the number of species of bivalve in Liverpool Bay means that there is usually likely to be a sufficient abundance of some species to meet the energetic requirements of the common scoter.

Repeat surveys of the benthos at 24 sites in December 2003 and April 2004 were used to quantify the seasonal change in the abundance of benthic bivalves. Analysis of the data from stations where common scoter were scarce was used to define the rate of change in the abundance of resources in the individuals-based model of common scoter behaviour

vi Observation of the behaviour of birds at sea and their response to disturbance

A programme of land-based and ship-based observations of the behaviour of over-wintering common scoter were made in Liverpool Bay. These observations included determination of: sex ratios in common scoter flocks, flush distances in response to ships, dive durations, orientation on the sea surface and flight directions and distribution in fair and inclement weather. Little is known of the behaviour of common scoter other than on their breeding grounds. The results reported in the current study are a unique addition to our knowledge of this species.

Differential arrival times were apparent for males and females, with the latter arriving in mid to late winter. Thus, activities in Liverpool Bay will affect different components of the population at different times of the year.

Common scoter tend to face into the current or the wind depending upon which has the greatest influence on their position at any particular time. Severe weather does not appear to change the utilisation of particular areas, and sheltered areas such as Conwy Bay were not used to any greater degree during severe weather conditions.

Common scoter often dive to the seabed in groups and remain submerged for periods of c. 30 – 50 seconds. They spend more time submerged in deeper water. This, coupled with the association between water depth and benthic bivalve abundance means that water depth will clearly be a key factor that influences the energetic costs and benefits of feeding in any given location.

Common scoter are sensitive to disturbance by moving vessels. Observations from a 390 t (35 m long) vessel indicated that large flocks of common scoter were put to flight at a distance of 2 km from the vessel, while smaller flocks were less sensitive and only put to flight at a distance of 1 km. Vessels larger than that used in the study would be expected to have a larger flushing distance. The study did not have a remit to determine disturbance from other boat users (recreational fishing, yachting, jet-skis) or disturbance generated by low flying aircraft.

vii Quantification of other forms of disturbance relevant to common scoter

Commercial shipping activities are considered one of the major forms of disturbance that may affect common scoter distribution. Analysis of a database of commercial shipping activity revealed that there is little seasonal fluctuation in this activity but considerable spatial variation. This information, coupled with data on avoidance distances, was used to characterise the spatial variation in the disturbance caused by shipping throughout the study area covered by the individuals-based model of common scoter behaviour.

The great majority of birds observed in Liverpool Bay do not coincide with the areas of heaviest commercial shipping traffic (vessels > 300 t). Thus, common scoter would appear to be excluded from areas of the seabed that coincide with these activities at present. It is possible that if forced to utilise such areas the birds may be able to habituate or tolerate these activities. This is however entirely subjective.

Direct observations of fishing activities indicate that these are concentrated in areas deeper than 20 m depth and they do not interfere with common scoter in Liverpool Bay other than those encountered on the outbound and inbound journey.

Commercial helicopter activities are another form of disturbance that may affect common scoter distribution. Analysis of a database of commercial helicopter activity revealed that helicopter traffic tends to occur along clearly defined flight paths. There is, therefore, considerable spatial variation in this activity. The frequency of helicopter traffic is, however, very low in comparison with shipping traffic. Nonetheless, this information was used to characterise the spatial variation in the disturbance caused by helicopter traffic throughout the study area covered by the individuals-based model of common scoter behaviour.

viii A review of the diving duck literature

A review of the literature was undertaken to gather information required to parameterise the behavioural ecology model. In the course of the literature review in excess of 100 scientific papers and reports concerning the physiology, diet, energetics, foraging ecology and general behaviour of diving ducks were collated. This served four main purposes: i) to build up knowledge of the way in which diving ducks forage ii) to derive reasonable assumptions on which the model could be based iii) to derive values for the many parameters that the model would need and iv) to derive independent empirical data against which model outputs could be validated.

During the literature review approximately 1,500 notes were made of points or parameter values that may have proven relevant to the final model. These were entered into an Excel database. All of the relevant notes are presented in a series of appendices to this report.

Although many of the entries in the database refer directly to common scoter, the majority do not. This reflects the inaccessible nature of the habitat in which the birds live during the winter months. Thus, in meeting each of the four principal objectives of the literature review it was necessary to utilise information derived from studies of other species of diving duck. Although this is not ideal, it is the only option where data for common scoter did not exist in the literature.

ix Development of a behavioural model to predict responses to windfarms

At the start of the project a computer code existed for an individuals-based model which had, hitherto been applied to predict the response of waders and geese feeding in intertidal and terrestrial habitats to environmental change. It had never been applied in the context of either offshore areas or sea ducks. During this project a new version of the model code was developed which, by virtue of being entirely generic and free of any biological detail, is flexible enough to be applied to a very wide range of consumer-resource systems including sea ducks foraging in offshore habitats.

The model is based on fundamental ecological principles such as fitness maximisation by individual animals which will apply under any change to environmental circumstances. The purpose of the behavioural modelling was to predict the change in the over-winter mortality of the common scoter population of Liverpool Bay that might result from the displacement of birds from feeding grounds in close proximity to offshore wind farms, based on the assumption that common scoter will avoid using areas of sea either within the boundaries of an array of turbines or within some wider area around such arrays.

The model predicts how each individual bird in the population would redistribute its foraging effort in space and time under the novel circumstances and whether these behavioural responses would enable them to survive the winter or not. It is the combination of the survival consequences of each of these individual decisions that enables the model to generate the predicted population-level mortality under any novel environmental circumstance.

In total, one hundred and eighty runs of the model MORPH, exploring 36 different ‘scenarios’, were conducted in the course of producing the results which are presented here. Principally, these address the consequences for the common scoter population of Liverpool Bay of a number of different windfarm scenarios and whether these consequences might vary depending upon various uncertainties in model parameterisation. Additional simulations explore the consequences of removing what appear in the model to be the most profitable feeding areas within Liverpool Bay and also the sensitivity of model outputs to variation in its key parameters.

x Calibration and validation of the behavioural model

Initial runs with the model to simulate the current day environment, as experienced by common scoter in Liverpool Bay, predicted that the common scoter population would be widely scattered throughout the study area. Most of the areas predicted by the model to be used by common scoter do hold common scoter in reality. However, two areas of the bay that are rich in benthic bivalve resources and were accordingly heavily used by birds in the model are seldom used by birds in daylight in reality. These two areas were excluded from the majority of model runs, although the significance of birds’ ability to utilise these areas in response to certain windfarm developments was explored.

The outputs of the model, when run to simulate the current environmental conditions in Liverpool Bay, were compared with independent empirical data concerning: the proportion of daylight hours spent feeding by birds, their daily rate of food consumption, daily rate of energy expenditure, seasonal variation in body mass, distribution (across 99 tidal grid cells) and over-winter mortality. In every case, the model output was in close agreement with independent data. In particular, the range (minimum to maximum) of over-winter mortality predicted by the model was between 5.4% and 8.8% of the common scoter in Liverpool Bay for the baseline conditions (Liverpool Bay with the existing North Hoyle windfarm). This estimate accorded well with the estimated real over-winter mortality (6.4%) of the common scoter population in Liverpool Bay, a value that was computed from published observations of common scoter mortality in the field and the known sex ratio of common scoter in Liverpool Bay (see section 7.2.16 and Appendix 20).

The model did not produce an absolutely perfect fit to the distribution of common scoter across the bay. In particular, several grid cells on Shell Flat that hold birds in reality were seldom or never used by model birds. This reflected the very low quality of the bivalve resources available in these areas and raises the question as to the usefulness of empirical over-flight distribution data in identifying common scoter feeding grounds.

Overall, there was, however, good quantitative agreement between model outputs and a variety of independent empirical data. This provides a basis on which to use the model to predict the likely consequences of novel environmental circumstances following the construction of windfarms in Liverpool Bay.

xi Predicting the consequences of offshore windfarm developments

The model was used to simulate a variety of combinations of existing (North Hoyle), consented (Rhyl Flats and Burbo Bank) and proposed (Gwynt-y-Mor and Shell Flat) windfarms. The model deals only with the predicted effects of the displacement of birds from an area of sea with either a 0km or a 2km radius around these windfarms. It does not deal with any other possible mechanism by which the construction, presence or servicing of offshore windfarms might affect common scoter.

The common scoter population was assumed to number 30,000 birds. Core simulations assumed access to a core of 99 tidal grid cells that encompass all those that are used by common scoter in reality plus twice as many again that are seldom or never used. They also assumed that common scoter only feed during daylight and used the best estimate of benthic resource abundance based on the results of the benthic survey. Additional simulations explored the sensitivity of the model’s predictions to varying these baseline conditions/ assumptions.

The following is a summary of the predicted effects of existing/ consented and proposed windfarms.

North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor: The displacement of common scoter from areas of the sea around windfarms at Rhyl Flats, Burbo Bank and at Gwynt-y-Mor, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality. This conclusion holds regardless of the assumed radius of the buffer zone around the physical perimeter of the windfarms (up to a limit of 2km) and regardless of the sampling error inherent in the benthic resource database.

North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor + Shell Flat: The displacement of common scoter from areas of the sea around windfarms at Rhyl Flats, Burbo Bank, Gwynt-y-Mor and Shell Flat, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality if there is no buffer zone around the physical perimeter of the windfarms. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor + Shell Flat: The displacement of common scoter from areas of the sea around windfarms at Rhyl Flats, Burbo Bank, Gwynt-y-Mor and at Shell Flat, in addition to that at North Hoyle, is predicted to have a significant adverse effect on common scoter mortality if the buffer zone around the physical perimeter of the windfarms extends to a radius of 2km. In this scenario the median mortality of common scoter increased to 11.7% (range 11% to 12.2%) compared with the baseline condition (Liverpool Bay with North Hoyle) which resulted in a median mortality of 7.3% (range 5.5% to 8.8%). This conclusion holds regardless of the sampling error inherent in the benthic resource database.

It is the presence of a windfarm on Shell Flat which, in combination with the others, and on the assumption that the radius of the buffer zone around them all extends to 2km, leads to increased common scoter mortality. This reflects that the fact that only in the scenarios in which a 2km buffer zone around the Shell Flat windfarm was included did the model predict that common scoter would be excluded from a number of grid cells in which the model predicted they would otherwise feed heavily. The magnitude of this effect may be underestimated by the model, **but nonetheless, a significant effect is predicted.** However, this cumulative adverse effect may be negated if: i) the radius of the buffer zone is smaller than 2km, ii) common scoter redistribute to currently unused but apparently profitable feeding areas within Liverpool Bay such as Burbo Bank or iii) common scoter feed during the hours of darkness as well as during daylight.

xii Recommendations for future research requirements

The following recommendations for future research requirements are made:

- i) Re-examine the validity of over flight data as a means of identifying common scoter preferred feeding grounds
- ii) Conduct direct observations of common scoter foraging/resting activity throughout the tidal cycle,
- iii) Investigate night time movements and feeding activity. Quantify the extent to which common scoter feed during darkness and where they do so and whether this habit varies seasonally.
- iv) Identify the environmental factors that may exclude birds from feeding on areas that are apparently rich in profitable, benthic bivalve food supplies.
- v) Confirm that birds feed at sites off Lancashire.
- vi) Investigate the spatial distribution of different age and sex classes within the common scoter population.
- vii) Undertake observations of common scoter responses to small ship traffic (e.g. fishing vessels) and recreational boat user activities. Quantify the spatial and temporal variation in these activities across the bay.
- viii) Implement more detailed study of disturbance effects of smaller vessels.
- ix) Conduct detailed monitoring of the exclusion/ avoidance distances exhibited by sea ducks around all existing offshore windfarms. Establish whether birds habituate to such static structures over time.
- x) Run Wave Amplitude Model for higher resolution calculations of physical forcing on the seabed.
- xi) Run wave climate change model to predict changes in wave erosion in the future.
- xii) Model the effects of windfarm arrays on dissipation of wave energy.
- xiii) Fund desk based study to ascertain future risk of prey resource collapse with changes in sea temperature and possible extractive fishing activities.

xiii Project Achievements

Hitherto, one of the principal techniques employed in assessing the potential impact of offshore windfarms on bird populations due to avoidance displacement has been the use of ‘proportional distribution maps’ of aerial survey results. However, this technique leaves the key question of the ecological consequences of such displacement still outstanding. With this approach the corresponding population impact *(of a displacement)* can only be determined by **assigning** an associated mortality rate. In contrast, this project **provides** all of those concerned with predicting the ecological consequences of offshore windfarms in Liverpool Bay with

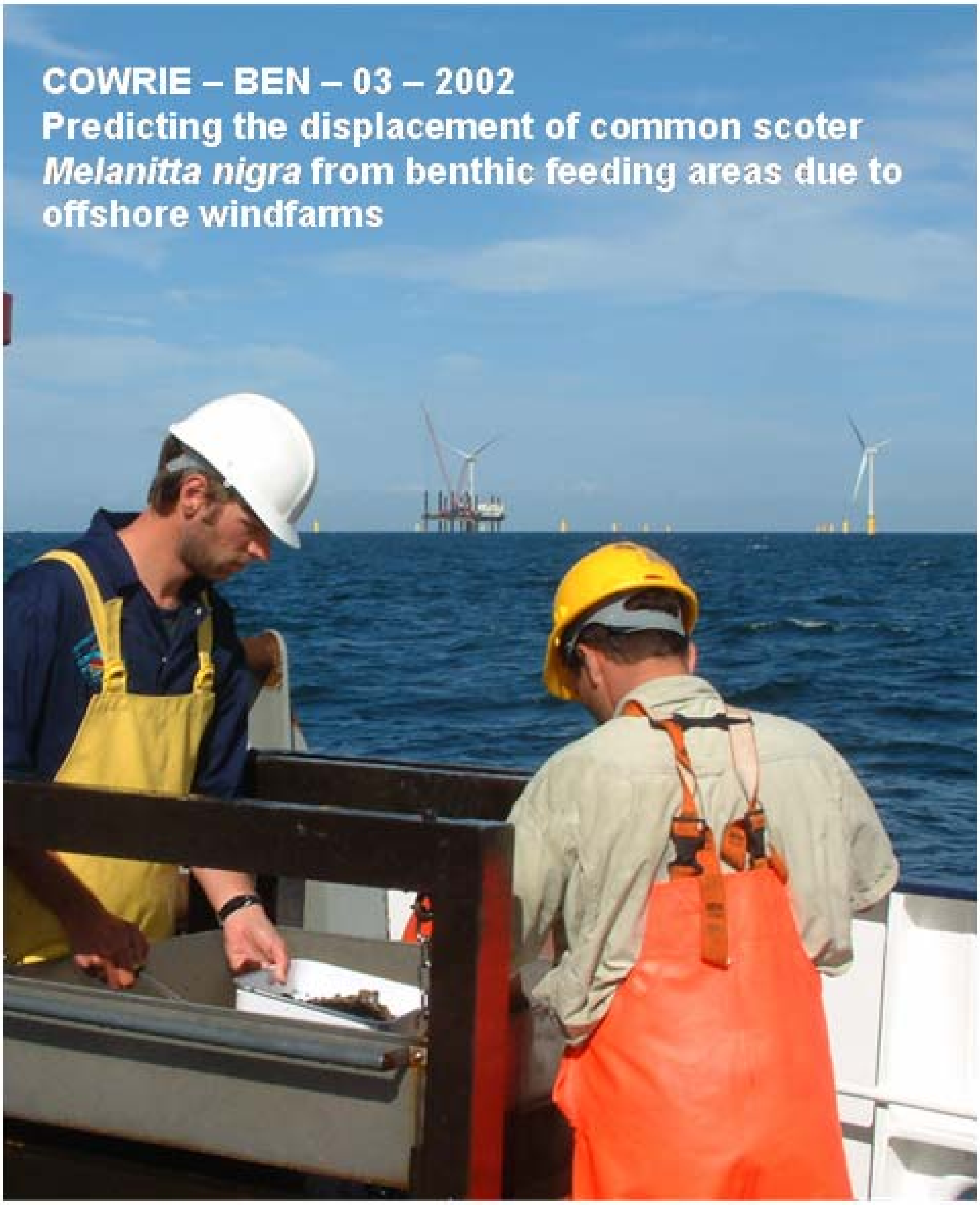
precisely such quantitative predictions of mortality. This is the principal achievement of this project. However, the behavioural model is generic and hence, provided that empirical data are available for other areas, it is applicable to other situations.

This project has provided the **first quantitative predictions of the change in overwinter mortality rate of the common scoter population of Liverpool Bay** under various alternative windfarm scenarios. It is predicted that the displacement of common scoter from areas of sea around wind farms at Rhyl Flats, Burbo Bank and Gwynt-y-Mor, in addition to that at North Hoyle, will not cause any increase in over-winter mortality. These predictions hold irrespective of the assumed radius of the exclusion zone, the sampling error inherent in the benthic database and regardless of whether common scoter feed at night or not or whether they can or cannot relocate to currently unused areas of Liverpool Bay. Thus, the project has provided unequivocal quantitative predictions concerning the effect of four of the five existing/ consented/ proposed windfarm locations within Liverpool Bay.

Only in the case of the proposed wind farm at Shell Flat is the predicted change in common scoter mortality subject to uncertainty dependent upon the radius of the exclusion zone and whether common scoter will respond by feeding at night or by redistributing to apparently suitable but currently unused parts of Liverpool Bay. The uncertainty concerning these issues is not a failing of this study. Rather, the uncertainty reflects the current lack of knowledge in the wider scientific community concerning: i) the nocturnal behaviour of sea ducks in general and common scoter in particular, ii) the avoidance of offshore windfarms exhibited by sea ducks in general and common scoter in particular and iii) the total number and relative importance of environmental factors (other than food abundance/ availability/ quality) that influence the distribution of foraging birds. Even so, the ability to make quantitative predictions of mortality under alternative assumptions has allowed exploration of the significance of these areas of uncertainty and highlighting of the key issues that must be the focus of future research in order to increase certainty in the predicted effects of a wind farm on Shell Flat.

All approaches to predicting how populations of animals will respond to environmental change depend upon making assumptions. The individuals-based modelling approach upon which this project is founded is relatively complex and relies upon detailed information about the biology of the species concerned and its environment. The presentation in this report of all the information gathered during this project allows the reader to identify the uncertainties and assumptions. This transparency does not mean that the approach is any less credible than any other. The apparent simplicity of simple models often hides a very complex suite of un-stated assumptions. The open approach adopted has the advantage of making clear where further research should be focussed in order to continually improve the predictive power of such ecological models.

In conclusion, this study has resulted in the development of a new tool which enables the quantitative prediction of the population-level impacts of offshore windfarm development on over-wintering common scoter populations. This is a major advance on any previous approach applied in this field of research. It has indicated that the displacement of common scoter from the areas around four out of five existing/ consented/ proposed windfarms within Liverpool Bay will have no adverse effect on the over-winter mortality of the population. In contrast, it has indicated that the displacement of common scoter from an area around a wind-farm on Shell Flat, given the current best estimates of how these birds behave, will have an adverse effect on the over-winter mortality of the population. However, uncertainty concerning various aspects of the biology of this elusive species means that this prediction may not hold. This highlights the further research that is needed in order to improve the predictive power of future model applications.



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A programme of land-based and ship-based observations of the behaviour of over-wintering common scoter were made in Liverpool Bay. These observations included determination of: sex ratios in common scoter flocks, flush distances in response to ships, dive durations, orientation on the sea surface and flight directions and distribution in fair and inclement weather. Little is known of the behaviour of common scoter other than on their breeding grounds. The results reported in the current study are a unique addition to our knowledge of this species.

Differential arrival times were apparent for males and females, with the latter arriving in mid to late winter. Thus, activities in Liverpool Bay will affect different components of the population at different times of the year.

Common scoter tend to face into the current or the wind depending upon which has the greatest influence on their position at any particular time. Severe weather does not appear to change the utilisation of particular areas, and sheltered areas such as Conwy Bay were not used to any greater degree during severe weather conditions.

Common scoter often dive to the seabed in groups and remain submerged for periods of c. 30 – 50 seconds. They spend more time submerged in deeper water. This, coupled with the association between water depth and benthic bivalve abundance means that water depth will clearly be a key factor that influences the energetic costs and benefits of feeding in any given location.

Common scoter are sensitive to disturbance by moving vessels. Observations from a 390 t (35 m long) vessel indicated that large flocks of common scoter were put to flight at a distance of 2 km from the vessel, while smaller flocks were less sensitive and only put to flight at a distance of 1 km. Vessels larger than that used in the study would be expected to have a larger flushing distance. The study did not have a remit to determine disturbance from other boat users (recreational fishing, yachting, jet-skis) or disturbance generated by low flying aircraft.

vii Quantification of other forms of disturbance relevant to common scoter

Commercial shipping activities are considered one of the major forms of disturbance that may affect common scoter distribution. Analysis of a database of commercial shipping activity revealed that there is little seasonal fluctuation in this activity but considerable spatial variation. This information, coupled with data on avoidance distances, was used to characterise the spatial variation in the disturbance caused by shipping throughout the study area covered by the individuals-based model of common scoter behaviour.

The great majority of birds observed in Liverpool Bay do not coincide with the areas of heaviest commercial shipping traffic (vessels > 300 t). Thus, common scoter would appear to be excluded from areas of the seabed that coincide with these activities at present. It is possible that if forced to utilise such areas the birds may be able to habituate or tolerate these activities. This is however entirely subjective.

Direct observations of fishing activities indicate that these are concentrated in areas deeper than 20 m depth and they do not interfere with common scoter in Liverpool Bay other than those encountered on the outbound and inbound journey.

Commercial helicopter activities are another form of disturbance that may affect common scoter distribution. Analysis of a database of commercial helicopter activity revealed that helicopter traffic tends to occur along clearly defined flight paths. There is, therefore, considerable spatial variation in this activity. The frequency of helicopter traffic is, however, very low in comparison with shipping traffic. Nonetheless, this information was used to characterise the spatial variation in the disturbance caused by helicopter traffic throughout the study area covered by the individuals-based model of common scoter behaviour.

viii A review of the diving duck literature

A review of the literature was undertaken to gather information required to parameterise the behavioural ecology model. In the course of the literature review in excess of 100 scientific papers and reports concerning the physiology, diet, energetics, foraging ecology and general behaviour of diving ducks were collated. This served four main purposes: i) to build up knowledge of the way in which diving ducks forage ii) to derive reasonable assumptions on which the model could be based iii) to derive values for the many parameters that the model would need and iv) to derive independent empirical data against which model outputs could be validated.

During the literature review approximately 1,500 notes were made of points or parameter values that may have proven relevant to the final model. These were entered into an Excel database. All of the relevant notes are presented in a series of appendices to this report.

Although many of the entries in the database refer directly to common scoter, the majority do not. This reflects the inaccessible nature of the habitat in which the birds live during the winter months. Thus, in meeting each of the four principal objectives of the literature review it was necessary to utilise information derived from studies of other species of diving duck. Although this is not ideal, it is the only option where data for common scoter did not exist in the literature.

ix Development of a behavioural model to predict responses to windfarms

At the start of the project a computer code existed for an individuals-based model which had, hitherto been applied to predict the response of waders and geese feeding in intertidal and terrestrial habitats to environmental change. It had never been applied in the context of either offshore areas or sea ducks. During this project a new version of the model code was developed which, by virtue of being entirely generic and free of any biological detail, is flexible enough to be applied to a very wide range of consumer-resource systems including sea ducks foraging in offshore habitats.

The model is based on fundamental ecological principles such as fitness maximisation by individual animals which will apply under any change to environmental circumstances. The purpose of the behavioural modelling was to predict the change in the over-winter mortality of the common scoter population of Liverpool Bay that might result from the displacement of birds from feeding grounds in close proximity to offshore wind farms, based on the assumption that common scoter will avoid using areas of sea either within the boundaries of an array of turbines or within some wider area around such arrays.

The model predicts how each individual bird in the population would redistribute its foraging effort in space and time under the novel circumstances and whether these behavioural responses would enable them to survive the winter or not. It is the combination of the survival consequences of each of these individual decisions that enables the model to generate the predicted population-level mortality under any novel environmental circumstance.

In total, one hundred and eighty runs of the model MORPH, exploring 36 different 'scenarios', were conducted in the course of producing the results which are presented here. Principally, these address the consequences for the common scoter population of Liverpool Bay of a number of different windfarm scenarios and whether these consequences might vary depending upon various uncertainties in model parameterisation. Additional simulations explore the consequences of removing what appear in the model to be the most profitable feeding areas within Liverpool Bay and also the sensitivity of model outputs to variation in its key parameters.

x Calibration and validation of the behavioural model

Initial runs with the model to simulate the current day environment, as experienced by common scoter in Liverpool Bay, predicted that the common scoter population would be widely scattered throughout the study area. Most of the areas predicted by the model to be used by common scoter do hold common scoter in reality. However, two areas of the bay that are rich in benthic bivalve resources and were accordingly heavily used by birds in the model are seldom used by birds in daylight in reality. These two areas were excluded from the majority of model runs, although the significance of birds' ability to utilise these areas in response to certain windfarm developments was explored.

The outputs of the model, when run to simulate the current environmental conditions in Liverpool Bay, were compared with independent empirical data concerning: the proportion of daylight hours spent feeding by birds, their daily rate of food consumption, daily rate of energy expenditure, seasonal variation in body mass, distribution (across 99 tidal grid cells) and over-winter mortality. In every case, the model output was in close agreement with independent data. In particular, the range (minimum to maximum) of over-winter mortality predicted by the model was between 5.4% and 8.8% of the common scoter in Liverpool Bay for the baseline conditions (Liverpool Bay with the existing North Hoyle windfarm). This estimate accorded well with the estimated real over-winter mortality (6.4%) of the common scoter population in Liverpool Bay, a value that was computed from published observations of common scoter mortality in the field and the known sex ratio of common scoter in Liverpool Bay (see section 7.2.16 and Appendix 20).

The model did not produce an absolutely perfect fit to the distribution of common scoter across the bay. In particular, several grid cells on Shell Flat that hold birds in reality were seldom or never used by model birds. This reflected the very low quality of the bivalve resources available in these areas and raises the question as to the usefulness of empirical over-flight distribution data in identifying common scoter feeding grounds.

Overall, there was, however, good quantitative agreement between model outputs and a variety of independent empirical data. This provides a basis on which to use the model to predict the likely consequences of novel environmental circumstances following the construction of windfarms in Liverpool Bay.

xi Predicting the consequences of offshore windfarm developments

The model was used to simulate a variety of combinations of existing (North Hoyle), consented (Rhyl Flats and Burbo Bank) and proposed (Gwynt-y-Mor and Shell Flat) windfarms. The model deals only with the predicted effects of the displacement of birds from an area of sea with either a 0km or a 2km radius around these windfarms. It does not deal with any other possible mechanism by which the construction, presence or servicing of offshore windfarms might affect common scoter.

The common scoter population was assumed to number 30,000 birds. Core simulations assumed access to a core of 99 tidal grid cells that encompass all those that are used by common scoter in reality plus twice as many again that are seldom or never used. They also assumed that common scoter only feed during daylight and used the best estimate of benthic resource abundance based on the results of the benthic survey. Additional simulations explored the sensitivity of the model's predictions to varying these baseline conditions/ assumptions.

The following is a summary of the predicted effects of existing/ consented and proposed windfarms.

North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor: The displacement of common scoter from areas of the sea around windfarms at Rhyl Flats, Burbo Bank and at Gwynt-y-Mor, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality. This conclusion holds regardless of the assumed radius of the buffer zone around the physical perimeter of the windfarms (up to a limit of 2km) and regardless of the sampling error inherent in the benthic resource database.

North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor + Shell Flat: The displacement of common scoter from areas of the sea around windfarms at Rhyl Flats, Burbo Bank, Gwynt-y-Mor and Shell Flat, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality if there is no buffer zone around the physical perimeter of the windfarms. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor + Shell Flat: The displacement of common scoter from areas of the sea around windfarms at Rhyl Flats, Burbo Bank, Gwynt-y-Mor and at Shell Flat, in addition to that at North Hoyle, is predicted to have a significant adverse effect on common scoter mortality if the buffer zone around the physical perimeter of the windfarms extends to a radius of 2km. In this scenario the median mortality of common scoter increased to 11.7% (range 11% to 12.2%) compared with the baseline condition (Liverpool Bay with North Hoyle) which resulted in a median mortality of 7.3% (range 5.5% to 8.8%). This conclusion holds regardless of the sampling error inherent in the benthic resource database.

It is the presence of a windfarm on Shell Flat which, in combination with the others, and on the assumption that the radius of the buffer zone around them all extends to 2km, leads to increased common scoter mortality. This reflects that the fact that only in the scenarios in which a 2km buffer zone around the Shell Flat windfarm was included did the model predict that common scoter would be excluded from a number of grid cells in which the model predicted they would otherwise feed heavily. The magnitude of this effect may be underestimated by the model, **but nonetheless, a significant effect is predicted.** However, this cumulative adverse effect may be negated if: i) the radius of the buffer zone is smaller than 2km, ii) common scoter redistribute to currently unused but apparently profitable feeding areas within Liverpool Bay such as Burbo Bank or iii) common scoter feed during the hours of darkness as well as during daylight.

xii Recommendations for future research requirements

The following recommendations for future research requirements are made:

- i) Re-examine the validity of over flight data as a means of identifying common scoter preferred feeding grounds
- ii) Conduct direct observations of common scoter foraging/resting activity throughout the tidal cycle,
- iii) Investigate night time movements and feeding activity. Quantify the extent to which common scoter feed during darkness and where they do so and whether this habit varies seasonally.
- iv) Identify the environmental factors that may exclude birds from feeding on areas that are apparently rich in profitable, benthic bivalve food supplies.
- v) Confirm that birds feed at sites off Lancashire.

vi) Investigate the spatial distribution of different age and sex classes within the common scoter population.
vii) Undertake observations of common scoter responses to small ship traffic (e.g. fishing vessels) and recreational boat user activities. Quantify the spatial and temporal variation in these activities across the bay.
viii) Implement more detailed study of disturbance effects of smaller vessels.
ix) Conduct detailed monitoring of the exclusion/ avoidance distances exhibited by sea ducks around all existing offshore windfarms. Establish whether birds habituate to such static structures over time.
x) Run Wave Amplitude Model for higher resolution calculations of physical forcing on the seabed.
xi) Run wave climate change model to predict changes in wave erosion in the future.
xii) Model the effects of windfarm arrays on dissipation of wave energy.
xiii) Fund desk based study to ascertain future risk of prey resource collapse with changes in sea temperature and possible extractive fishing activities.

xiii Project Achievements

Hitherto, one of the principal techniques employed in assessing the potential impact of offshore windfarms on bird populations due to avoidance displacement has been the use of 'proportional distribution maps' of aerial survey results. However, this technique leaves the key question of the ecological consequences of such displacement still outstanding. With this approach the corresponding population impact *(of a displacement)* can only be determined by **assigning** an associated mortality rate. In contrast, this project **provides** all of those concerned with predicting the ecological consequences of offshore windfarms in Liverpool Bay with **precisely such quantitative predictions of mortality**. This is the principal achievement of this project. However, the behavioural model is generic and hence, provided that empirical data are available for other areas, it is applicable to other situations.

This project has provided the **first quantitative predictions of the change in overwinter mortality rate of the common scoter population of Liverpool Bay** under various alternative windfarm scenarios. It is predicted that the displacement of common scoter from areas of sea around wind farms at Rhyl Flats, Burbo Bank and Gwynt-y-Mor, in addition to that at North Hoyle, will not cause any increase in over-winter mortality. These predictions hold irrespective of the assumed radius of the exclusion zone, the sampling error inherent in the benthic database and regardless of whether common scoter feed at night or not or whether they can or cannot relocate to currently unused areas of Liverpool Bay. Thus, the project has provided unequivocal quantitative predictions concerning the effect of four of the five existing/ consented/ proposed windfarm locations within Liverpool Bay.

Only in the case of the proposed wind farm at Shell Flat is the predicted change in common scoter mortality subject to uncertainty dependent upon the radius of the exclusion zone and whether common scoter will respond by feeding at night or by redistributing to apparently suitable but currently unused parts of Liverpool Bay. The uncertainty concerning these issues is not a failing of this study. Rather, the uncertainty reflects the current lack of knowledge in the wider scientific community concerning: i) the nocturnal behaviour of sea ducks in general and common scoter in particular, ii) the avoidance of offshore windfarms exhibited by sea ducks in general and common scoter in particular and iii) the total number and relative importance of environmental factors (other than food abundance/ availability/ quality) that influence the distribution of foraging birds. Even so, the ability to make quantitative predictions of mortality under alternative assumptions has allowed exploration of the significance of these areas of uncertainty and highlighting of the key issues that must be the focus of future research in order to increase certainty in the predicted effects of a wind farm on Shell Flat.

All approaches to predicting how populations of animals will respond to environmental change depend upon making assumptions. The individuals-based modelling approach upon which this project is founded is relatively complex and relies upon detailed information about the biology of the species concerned and its environment. The presentation in this report of all the information gathered during this project allows the reader to identify the uncertainties and assumptions. This transparency does not mean that the approach is any less credible than any other. The apparent simplicity of simple models often hides a very complex suite of un-stated assumptions. The open approach adopted has the advantage of making clear where further research should be focussed in order to continually improve the predictive power of such ecological models.

In conclusion, this study has resulted in the development of a new tool which enables the quantitative prediction of the population-level impacts of offshore windfarm development on over-wintering common scoter populations. This is a major advance on any previous approach applied in this field of research. It has indicated that the displacement of common scoter from the areas around four out of five existing/ consented/ proposed windfarms within Liverpool Bay will have no adverse effect on the over-winter mortality of the population. In contrast, it has indicated that the displacement of common scoter from an area around a wind-farm on Shell Flat, given the current best estimates of how these birds behave, will have an adverse effect on the over-winter mortality of the population. However, uncertainty concerning various aspects of the biology of this elusive species means that this prediction may not hold. This highlights the further research that is needed in order to improve the predictive power of future model applications.

1. Introduction

1.1 Context

In December 2003 the UK government increased its commitment to a new target of 15% of electricity to be generated from renewable sources by 2015, to which wind energy is likely to contribute a considerable proportion. Nevertheless, despite the advantages of renewable forms of energy, the construction and placement of windfarms has the potential to interact (positively and negatively) with other stakeholders and biological components of our environment. Environmental concerns have prompted country-based conservation agencies to initiate appropriate research studies to understand the broader ecological consequences of the construction and siting of windfarms in the marine environment. The main concerns relate to the impact upon bird migration patterns and disturbance at bird feeding areas. For example, the Countryside Council of Wales commissioned a study of the distribution of common scoter around Wales and into Liverpool Bay, in order to establish the impact of proposed developments off the north Wales and south Wales coast on this protected species. As a result of this work, Carmarthen Bay has become the first Special Protection Area designated for common scoter. The Crown Estate recognised the value of this research and contributed financially through its Marine Stewardship Fund along with other partners from the offshore wind industry who are hoping to develop projects in the Liverpool Bay area.

The environmental impact assessments (EIAs) of most offshore windfarm proposals raise the potential effects on birds as an important issue. The types of birds which may be displaced feed either on invertebrates (crustaceans, worms, shellfish) that live in or on seabed sediments or on fish. These birds include benthic feeding ducks such as common scoter and eider ducks or fish-eating birds such as terns, auks and divers. This present study addresses the disturbance / displacement of common scoter from the vicinity of the wind turbines and will provide a tool for predicting impacts that are currently uncertain. While the current study is focussed on common scoter in Liverpool Bay, the behavioural model the potential population level responses to windfarm developments is applicable to situations elsewhere.

This study focuses specifically on common scoter because:

1. Most of the proposed sites for offshore windfarm development on the west coast of the U.K. lie within, or close to, significant concentrations of common scoter that occur during the non-breeding season. The impacts on common scoter due to displacement are a key issue and an uncertainty in many emerging EIAs. There is concern that development of offshore windfarms could displace common scoter to less favourable feeding habitats due to both disturbance and/or barrier effects and physical changes in the habitat. A major uncertainty in predicting the impacts of the windfarms is therefore the sensitivity of common scoter populations to habitat loss and change caused by the offshore windfarms.

2. Adverse impacts of offshore windfarms (or other developments and activities) due to displacement / disturbance of birds are potentially more significant for benthic feeders such as common scoter as opposed to fish-eating birds. This is because their prey species (mostly bivalve molluscs) are not mobile, although the settlement of young prey (bivalve spat) will vary with time. This link between the distribution of common scoter and seabed fauna also means that it should be possible to build a model similar to those applied to studies of the interactions between wading birds and shellfish.

1.1.2 Objectives

The project had the following key objectives:

1. To develop a model to assist in predicting the effect of offshore windfarms (individually and cumulatively) on common scoter due to habitat loss and change.

2. To link the non-breeding distribution of common scoter with environmental variables at selected sites.

3. To identify the characteristics of preferred feeding areas for common scoter within these sites. This to include a description of density, species and size classes of prey.

1.1.3 Context – Liverpool Bay

Liverpool Bay is an important non-breeding site for common scoter. Birds are present in Liverpool Bay throughout the year with peak numbers occurring from October to March. The first full census of Liverpool Bay using aerial surveys during the winter of 2000/2001 recorded a peak count of c 16 000 birds (Oliver et al. 2001) with current estimates for 2003 approaching 30 000 birds (A. Webb pers. comm.). At these population levels, Liverpool Bay ranks as one of the most important wintering sites for common scoter. More than 1% of the European population occur in this locality during the overwintering period. Consequently, parts of Liverpool Bay are under consideration for Special Protection Area status (as defined under the provisions of the Birds Directive (Johnston *et al.* 2002)) because of the presence of qualifying numbers of non-breeding common scoter and red throated divers. Following data analysis by the Joint Nature Conservation Committee, English Nature and the Countryside Council for Wales a joint proposal has been submitted to the Department for Environment, Food and Rural Affairs and the Welsh Assembly Government seeking approval to carry out a formal consultation on proposals for selection of Liverpool Bay as a potential Special Protection Area (pSPA). The Welsh Assembly and the U.K. government response to this request is awaited.

1.1.4 Common scoter conservation importance

The common scoter areis a migratory species of sea duck that is protected in Europe through the provisions of the European Commission's Birds Directive (79/409/EEC) and Habitats Directive (92/43/EEC). Within the UK, this species is and is protected under the Wildlife and Countryside Act of 1981 as amended by the Countryside and Rights of Way Act 2000 which controls hunting and provide protection against disturbance to breeding birds. Elsewhere in Europe, common scoter are not protected from hunting. Thus, common scoter are wary of human activity and man-made structures, boats and vehicles (Garthe & Huppop 2004), the presence of which may exclude them from using potential feeding, roosting and breeding sites.

1.1.5 Common scoter

As common scoter are migratory, their survival and population size is affected by different factors at different sites. For example, common scoter have breeding grounds in northern Scandinavia, Iceland and Russia where their breeding success may be influenced by habitat quality factors and the prevalence of predators. Breeding success is also affected by adult body condition (amount of fat reserves) which will depend upon the quality of their feeding grounds. Common scoter migrate from their breeding grounds to moulting and overwintering grounds at more southerly latitudes and arrive in Liverpool Bay in large numbers from October onwards. Male birds arrive first (section 4) followed by females from December onwards. The females also depart for the breeding grounds before males (in February). Some birds remain in Liverpool Bay over the summer period but these tend to be immature or birds that are moulting. Liverpool Bay is an important overwintering site for common scoter due to its abundant bivalve shellfish stocks that occur in shallow waters at depths of less than 20 m. As bivalve shellfish live on the seabed, common scoter resting on the surface of the sea need to dive to the seabed to feed on their shellfish prey. As a result, water depth is an important factor as the deeper the birds are required to dive the more energy they will expend in searching for their food. Common scoter remain at sea for the entire time they are located in Liverpool Bay. As winter sea temperatures are usually warmer and more constant than terrestrial winter temperatures this may help the common scoter conserve energy. Common scoter also have few, if any, natural predators at sea, although they may suffer interference from larger predatory species such as gulls.

1.2 Habitat considerations and disturbance

Observations made from light aircraft indicate that common scoter in Liverpool Bay are located over discrete areas of the seabed. The reasons why common scoter are found in these areas is a key topic of this project. Areas of the sea utilised by common scoter are likely to be those that allow them to maintain a positive energy balance or at least minimise any negative energy balance. Such locations are likely to be those that i) provide a high intake of food, and ii) necessitate a low expenditure of energy. Energetic costs would include energy expended on relocating or maintaining position (by flying or paddling) which may occur due to: strong surface currents (drifting off position), strong winds (blowing birds off position), disturbance from vessels (commercial shipping, fishing vessels, aircraft, recreational boats, jet skiis) or the construction of manmade structures (windfarms, drilling platforms, breakwaters). Birds may also utilise particular areas of the sea for the purpose of moulting and roosting. However, the present study is primarily concerned with the importance of different areas of the seabed in terms of the quality and quantity of food resources that are available for common scoter.

In the context of the proposed and consented windfarm developments in Liverpool Bay (Fig. 1.1), it is necessary to ascertain whether the construction of one or more windfarms would result in a significant increase in the overwinter mortality rate of the common scoter population within Liverpool Bay. in comparison with the current level of mortality It is important to appreciate that the current distribution and mortality of the population occurs against a background of natural variability in prey populations (due to recruitment success and failure from one year to the next) and their other predators (e.g. fish and crabs), and a background of existing sources of disturbance (e.g. commercial shipping activities, fishing, hydrocarbon extractions etc).

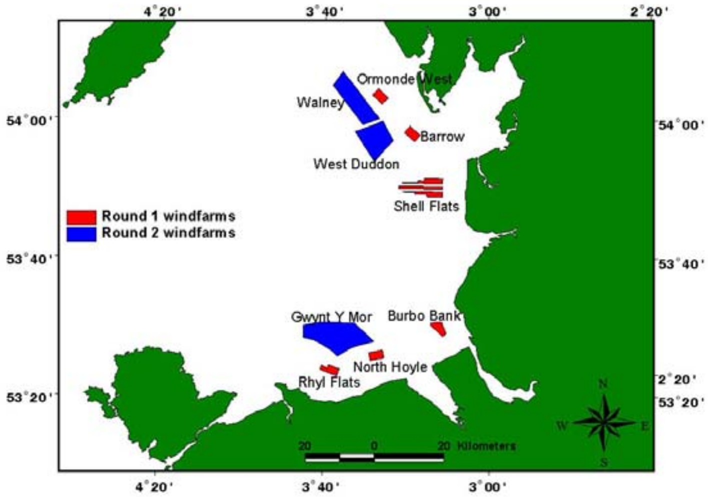


Figure 1.1 The location of round 1 and round 2 consented or proposed windfarms in Liverpool Bay, Irish Sea, UK.

1.2.2 How might windfarms affect common scoter?

It is important to understand the mechanism by which the construction of windfarms might have an effect on populations of common scoter. In contrast to some other types of birds e.g. raptors and vultures, it is unlikely that collision of seaducks with wind turbines is a serious source of mortality. There are no substantive reports in the literature that would, as yet, indicate that this is a problem for common scoter.

The maximum extent of the seabed area that serves as potential foraging habitat is defined by the 20 m mean depth bathymetric contour. This is related to the amount of time and energy that is required to dive to the seabed. Within this maximum area of exploitable seabed the largest amounts of suitable prey (in number and biomass) are found at depths that are shallower than 20 m (section 2), although the depth at which the greatest peak in prey occurs varies according to wave erosion and other physical characteristics at each different locality (section 3). Thus, the extent of the areas that are suitable for feeding in Liverpool Bay are finite. Within this finite area, some parts may be unsuitable because of existing disturbance (e.g. commercial shipping in and out of the River Mersey) while others may hold insufficient prey to make foraging by common scoter energetically efficient. It is assumed that the construction of a windfarm may exclude common scoter from the footprint of that windfarm (i.e. the area over which it extends) probably extending an unknown distance beyond the actual windfarm (i.e. creating a halo of disturbance). The construction and presence of offshore windfarms may, by exclusion of ducks from certain areas, effectively lead to habitat loss

If the windfarm is constructed over a particularly dense bed of suitable prey, these may be made unavailable to the birds. The birds will then need to relocate to other suitable feeding areas. If birds already exist in those areas this will increase the competition for the prey in those areas. This may occur either through interference competition between birds whereby once the density of competitors exceeds a certain value, their ability to forage efficiently is impaired or through depletion competition whereby more birds eat more prey thus leaving fewer for the next day. If, through either process, the rate of prey intake decreases below a certain threshold then birds may begin to lose condition (body fat) or even starve to death. While loss of condition may not lead to the death of birds directly, it may affect their reproductive success later in the year.

Given the constraints of current survey techniques, it appears that extensive prey resources exist that are apparently not utilised by the birds (e.g. Burbo Bank). While this may seem inexplicable, one has to remember that common scoter cannot see the distribution of their prey from the sea surface, they can only gain knowledge of the quantity and type of prey by diving to the seabed. As in many other group living organisms, individuals use social learning to recognise areas that are profitable for feeding. If there are no other common scoter in location X it is unlikely to be an area that holds food. A bird's perception of its available feeding habitat is strongly influenced by the distribution of other individuals. Thus, in the case of Burbo Bank, while it holds abundant prey resources, it may be unavailable to common scoter simply because they have no knowledge regarding the quality or quantity of food in that area. This is an important issue that is brought into clearer light by the bird behavioural model that will be dealt with later in this section.

Furthermore, our model predictions **do not** take into account any possible affects of offshore windfarms due to: **i) collisions ii) increased flight costs iii) changes to the benthos or iv) disturbance by maintenance traffic**. Our predictions are therefore conservative with respect to these additional variables that might impact populations of common scoter. The predictions of the behavioural model developed in the current study are purely based on displacements from feeding areas due to the presence of turbines.However the predictions of the behavioural model based on our current knowledge of the Liverpool Bay situation are probably over-cautious.

1.3 Project structure

The primary source of data regarding habitat use by common scoter in Liverpool Bay is derived from overflight surveys co-ordinated by The Wildfowl & Wetlands Trust. These surveys are conducted using observers in light aircraft that fly a predetermined route over Liverpool Bay. As such, these surveys can only provide a snap-shot of the distribution of the birds and cannot provide information about what the birds are doing at that time (roosting, feeding, relocating) or at night when such surveys cannot be undertaken. Nevertheless, this currently remains the only viable means of gaining an accurate population estimate for a bird that is distributed offshore and that avoids moving vessels. By using all available overflights for the period 2002 – 2004 (n = 12), it is possible to be confident that the distribution observed during daylight overflights is representative of the key areas of sea utilised by common scoter during daylight.

Given that data regarding the distribution of birds is only available for daylight hours, the modelled scenarios outlined in the report have a default assumption that common scoter do not feed at night in line with other diving species of duck. Given that night conditions last up to 16 hours in mid-winter, this assumption precludes common scoter from feeding during the majority of a 24 hour period. Given this fact, scenarios were also run that enabled the birds to feed at night. If this yielded a significantly lower mortality rate for some windfarm scenarios this would indicate that it is important to establish whether common scoter feed at night.

Using the above information as our baseline data, the project was broken down into the following major components:

Description of the physical habitat utilised by common scoter
Spatial and temporal variability in prey
Behaviour of birds at sea and their response to disturbance
Quantification of other forms of disturbance relevant to common scoter
A review of the diving seaduck literature
Development of a predictive behavioural model to predict responses to windfarms.

Description of the physical habitat utilised by common scoter

This was undertaken by using standard oceanographic models to delineate the water depth over which observed birds were recorded, to ascertain the bottom shear stress, surface current speed and mean water depth for each of 99 defined areas of the sea (3.7 x 3.35 km) that were specified within the behavioural ecology model. The output of the oceanographic modelling enables identification of the physical characteristics of areas of the sea over which common scoter occur most frequently.

Spatial and temporal variability in prey

An extensive baseline biological survey of seabed dwelling bivalves and other fauna quantified the prey available to common scoter at the start of the overwintering season. Repeated surveys of a selected number of sites enabled the survival rate (or decline) of prey species to be ascertained. Quantification of prey-type characteristics and energy content enabled the areas of the sea that contained the greatest amount of suitable prey to be identified.

Behaviour of birds at sea and their response to disturbance

Direct behavioural observations at sea and from land enabled quantification of the behaviour of common scoter in response to weather conditions and disturbance to be quantified. Flush distances from a vessel were quantified and used to define those areas of the seabed that are unlikely to be used by common scoter due to disturbance. Additional data enabled interpretation of model outputs for a species for which there is little observational information.

Quantification of other forms of disturbance relevant to common scoter

Other forms of disturbance from shipping and fishing activities were mapped according to available data held by National agencies or consultancies acting on their behalf. Nevertheless, many sources of potential disturbance from smaller vessels remain unquantified as these are not currently recorded.

A review of the diving seaduck literature

A review of the literature was undertaken to aide interpretation of model outputs and to gather information required to parameterise the behavioural ecology model (e.g. the energetic costs of diving). As common scoter are so infrequently studied, data were often gleaned from proxies (similar species or groups of species with similar body mass). The latter is the only option were data for common scoter did not exist in the literature.

Development of a predictive behavioural model to predict responses to windfarms

An existing individuals-based behavioural model (Stillman et al. 2000) was adapted for common scoter. This model was originally devised for oystercatchers and has been applied successfully to other species. The model is widely peer reviewed and well accepted among the ecology and ornithological community. The outputs of the model enable various scenarios of windfarm developments to be explored in terms of their likely effects on common scoter in Liverpool Bay. Once developed the model can be applied to similar situations elsewhere provided the appropriate input data are collected.

2. Common scoter distribution in relation to modelled physical parameters

2.1 Introduction

In Liverpool Bay, aggregations of common scoter are found primarily off Llanddulas (North Wales) and from an area off the mouth of the River Ribble up to Shell Flat, a shallow subtidal area off Blackpool, Lancashire, England (Figure 2.1). The development of offshore wind farms has the potential to influence common scoter duck distribution through two mechanisms. Firstly, the ducks may avoid areas of the sea populated by man-made structures and may thereby be prevented from accessing feeding areas, secondly, the foundation base of the each turbine and associated cable laying activities may alter near-bed hydrography such that the sediment environment changes its suitability for important prey species.

Common scoter are diving ducks that feed on prey that live upon or within the upper few cm of the sea bed. The diet of the common scoter is thought to comprise mainly bivalve molluscs, while other items (e.g. crabs, small fishes and gastropods) are incorporated less frequently. The exact mechanism of feeding is unknown although it is unlikely that they are visual feeders, particularly in Liverpool Bay where the water is particularly turbid due to riverine discharge from the Rivers Dee, Mersey, Ribble and Conwy.

Common scoter feed on benthic prey whose life-history strategies and production are intimately linked to the sedimentary and coastal environment (Snelgrove & Butman 1994). Sedimentary habitats are strongly influenced by near-bed hydrodynamic stress and hence this can be an important determinant of benthic assemblage distribution (Warwick and Uncles, 1980; Yates et al*.,* 1993). Shear bed stress will have both positive and negative effects on benthic communities. At low shear stress values, increasing shear increases the supply of food and hence production of the benthos until a threshold where further increases in shear stress inhibit feeding (Hiddink et al. in press). Increasing levels of wave erosion increase mortality of the benthos (Hiddink et al. in press). These two factors are likely to interact close to the coast and will have a strong influence on the production of the associated benthic communities. In addition, benthic communities are notoriously patchy in their distribution and the population sizes of benthic invertebrates fluctuate greatly from one year to the next (e.g. Rees et al. 1977). Thus food resources available for common scoter are unlikely to be uniformly distributed over the sea bed and certain areas will yield higher rates of energy intake than others. Presumably, common scoter distribute themselves over, or in close proximity to, areas that have a sufficient abundance of prey to maintain their energetic requirements and are able to assess the rate of encounter with suitable prey as they probe through the sediment with their bill. The profitability of prey will also be affected by the depth to which the birds need to dive for feeding, which is a continuously changing variable in tidal areas. The deeper the birds need to dive, the greater the energy expended acquiring prey (Lovvorn & Jones 1991).

A number of environmental and anthropogenic factors are likely to affect the distribution of the birds at the sea surface: the distribution and quality of the prey that may vary interannually and through the year, the depth of the water over the sea bed that fluctuates tidally, the surface current speed which, in Liverpool Bay, will move birds over the ground at speeds of up to 1–2 ms^{-1} at peak tidal flow, diurnal patterns in feeding behaviour and the proximity to human activity and structures. As in other species, the birds probably use visual cues to locate initial feeding sites before sampling other possible food patches. Surface currents may be important if birds are required to continually maintain their position over patches of prey by swimming against currents, or by relocating periodically by flying up-stream.

To answer some of the questions raised above, a tidal model of the Liverpool Bay region was developed as part of a multi-disciplinary study into the potential impact of offshore wind farms on the distribution of the common scoter. This paper presents the main results from the physical study.

2.2 Methods

2.2.1 The tidal model

A two-dimensional finite-difference hydrodynamic model of the Celtic and Irish Sea region was developed using standard techniques (Elliott & Clarke 1998; Tattersall et al. 2003). The depth-averaged shallow water equations of motion were solved on an Arakawa-C grid using centred time and space differences on a latitude/longitude grid. Centred differencing was used in both time and space, and time filtering (Asselin 1972) was used to suppress the computational mode caused by the leap-frog scheme. The grid covered a region from a southern limit in the Celtic Sea at a latitude of 50 18.1’ N to a northern limit in the North Channel at a latitude of 55 2.0’ N (Figure 2.2). The grid spacing was 1/30 of latitude by 1/20 of longitude which corresponds to approximately 3.70 km by 3.35 km and the grid contained 129 142 cells. Results from the Liverpool Bay region (Figure 2.1) were extracted from the main grid and mapped onto a 50×41 array for export to the common scoter related analysis.

The model was forced at the northern and southern open boundaries by specifying the surface elevations using the semi-diurnal tidal constituents M2 and S2 which represent the twice daily tidal signals due to the influence of the moon and sun. It is the beating between these two sinusoidal signals that creates the 14.8 day periodicity of the spring/neap cycle. The amplitudes and phases for the boundary conditions were obtained from the output of a North Atlantic tidal model developed at the Proudman Oceanographic Laboratory (R. Proctor pers. comm.). The east and north components of the tidal currents were interpolated to the centre of each grid cell and then tidally analysed, along with the surface elevation, to produce amplitude and phase constants which could be used in a tidal prediction programme to determine the water depth and current speed at any point within the computational grid.

The simulated values were compared against observational results (Jones 1983; Davies & Jones 1992; Young et al. 2000) using sea level records from both coastal and offshore sites and current data collected at offshore moorings. The modelled surface elevations were accurate to 0.10 m in amplitude and to 5° in phase (which corresponds to a time interval of about 10 minutes). For example, the amplitude and phase of the M2 surface elevation derived for Hilbre Island which is located near the mouth of the River Mersey at 53° 23’ N and 3° 13’ W were 3.27 m and 322°, while the observed values are 3.33 m and 317°. The agreement between the simulated and observed tidal currents displayed greater scatter, with errors of order 0.1 ms^{-1} and 10°. However, part of this discrepancy was due to the difficulty in comparing depth-mean currents derived from the model with the observations which were recorded at a range of depths within the water column.

As an example of the output from the tidal model Figure 2.2 shows a map of tidal vectors and the contoured sea surface elevation for 1500 UTC on August 19 2004. This was close to a time of spring tides and the high water at Liverpool occurred at about 1300 hrs when the sea level reached a height about 4.5 m above mean sea level. At 1500 hrs therefore the sea level was falling in Liverpool Bay as evidenced by the flow vectors which are directed out of the region and which show strong flow towards the south in the central portion of the grid. The right hand portion of Figure 2.2 shows that the tidal elevation was more than 2 m above the mean level in Liverpool Bay, while it was more than 3 m below mean sea level within the Bristol Channel. It is this pronounced slope of the sea surface that is driving the water through the Irish Sea from north to south. (There is also a less pronounced slope near the northern boundary which is driving the tidal flow westwards past the Isle of Man and out of the North Channel.)

Significant surface slopes can also exist within Liverpool Bay. At the time of high water during a period of spring tides, the sea level near Liverpool stands about 1.5 m higher than the water level near Anglesey.

2.2.2 The 1 km depth database

Although the sea surface elevation changes smoothly across a region and its variation can be adequately resolved by a hydrodynamic model with a grid resolution of the order of 3.5 km, water depths can vary on a significantly smaller spatial scale. To resolve such variability a dataset of water depths with a spatial resolution of approximately 1 km was obtained. The depth grid covered the study area with a latitude resolution of 1/120° (~925 m) and a longitude resolution of 1/60° (~1130 m). Figure 2.3 illustrates the spatial resolution of the grid by showing the land cells along with a contour plot of the offshore water depths. In order to estimate the water depth at the location of a duck observation, the tidal elevation with respect to mean sea level was derived from the tidal model and to this was added the water depth at the observed point taken from the 1 km dataset. In this manner an estimate of the instantaneous water depth was obtained.

2.2.3 The wave model

Engineering formulae, based on results from the JONSWAP experiment (Hasselmann et al. 1973) can be used to forecast wave conditions in coastal waters for practical applications. Events when the wind speed was relatively steady and directed offshore were isolated and used by Hasselmann et al. (1973) to determine the dependence of the wave conditions (i.e. wave height and period) as functions of the wind speed, wind duration, and the fetch. Carter (1982) subsequently re-analysed the JONSWAP data and developed empirical formulae that can be used to estimate wave height and period as a function of the wind conditions. For example, in a fetch limited growing sea when the wave conditions are independent of the duration of the storm the significant wave height, H_s, and peak wave period, T_p, can be calculated from:

$$H_s = 0.0163 X^{0.5} W$$

and

$$T_p = 0.566 X^{0.3} W^{0.4}$$

where W is the wind speed in ms^{-1} and X is the fetch in km.

The formulae derived by Carter (1982) parameterise wave conditions as a function of wind speed, wind duration and wave fetch and assume that the wind direction and speed are constant. For most applications, however, the results need to be generalised so that they can be used to simulate conditions when the wind speed and direction are not steady. This was achieved in the following manner:

Radial fetch lines, with an angular separation, , were defined from the target position and the fetch was estimated along each line. (Each grid point of the whole area Irish and Celtic Seas model was taken in turn as the target location. Radial lines were run along the principal compass directions from each point until they reached land or the edge of the grid to define the fetch for each point. A value for θ of 45° was used in the calculations.)

The wind was considered to be from a steady direction if it lay within ± θ /2 of a fetch line. Periods of steady wind direction were used to define each wind 'event'.

A new wind 'event' was defined each time that a new direction sector was entered and the duration of each event was measured from this time.

The JONSWAP formulae were used to estimate significant wave height using the appropriate value of fetch (determined by the wind direction), the duration (determined as the time elapsed since the start of the most recent wind event), and using the mean value of the wind speed during the event.

Wave energy was assumed to decay in an exponential manner at the end of a wind event, thus introducing an element of 'memory' into the wave height forecast. An e-folding time scale of 12 hours was found to give the best agreement with Meteorological Office wave model results as described below. If such a term is omitted the wave energy falls to zero at the start of each new wind event and the wave record shows an unrealistic level of high frequency variability.

Thus the wave model ignores the effects of wave refraction and assumes that the wind field is fixed spatially while varying with time. There are therefore similarities between this approach and the Hydraulics Research HINDWAVE model (Hawkes 1987). The model had previously been validated by comparing its results against both field data and the output from the UK Meteorological Office wave model for sites near the Shetland Islands and near Skomer Island off the coast of West Wales to the north of Milford Haven (Elliott 2001). The model produces realistic wave heights and periods during storm conditions but tends to underestimate the wave energy during light wind conditions. It is therefore suitable for the present application where it was used with wind data from Liverpool Bay covering the period from 1997-2001 (Elliott 2004).

2.3 Results

Figure 2.1 shows the water depth contours with respect to the mean sea level (solid curves) plus the position of the 20 m isobath at the time of high and low water during a period of spring tides (dashed curves). The 20 m isobath moves shoreward at the time of high water and moves offshore at the time of low water. For the Lancashire coastline between Liverpool and Blackpool this displacement is of the order of 10 km. In consequence the area of the sea bed that lies in water depths of less than 20 m (i.e. within the diving depth range of common scoter) increases at the time of a spring tide low water. The statistics of the sea bed area for the region where the water depth is less than 20 m are presented in Table 1. The change in area between the times of high and low water during spring tides equals 1.45×10^9 m^2 which amounts to about 9.3% of the total area of the sea bed in the Liverpool Bay region and to 42.3% of the area shallower than 20 m with respect to the mean sea level. At high water during spring tides 17.4% of the sea bed within the Liverpool bay region would have a depth of less than 20 m, and this percentage would increase to 26.7% at the time of low water. Thus if the common scoter are able to dive to a maximum depth of 20 m to forage for food then the area of the sea bed with this property varies significantly during a tidal cycle at a time of spring tides. (While 20 m has been used as a representative maximum dive depth, the program that computed Table 1 was able to accept any such selected depth as its input parameter). The dashed contours immediately to the north of the Shell Flat near Blackpool mark the position of the Lune Deep where the water depth reaches 50 m (Figure 2.1). In general, the eastern half of Liverpool Bay contains water depths of less than 40 m while depths of up to 80 m occur in the western portion.

An object that drifts on the surface of the sea in the presence of an oscillatory tidal current will be carried a distance of $UT/$ during each half of the tidal cycle (Elliott et al. 2001). In this expression for the tidal excursion, U is the amplitude of the tidal current (ms^{-1}) and T is the length of the tidal period (s). Figure 2.4 shows the tidal excursions within Liverpool Bay at a time of mean tides (midway between springs and neaps). The depth-mean current obtained from the tidal model was scaled to a surface value using the depth profile derived by Prandle (1982) in which the surface current has a speed of 1.17u and the near-bed flow a speed of 0.70u where u is the speed of the depth-mean current. Along both the North Wales and the Lancashire coastlines the surface displacements are of the order of 10 km at the time of mean tides, and would increase to 13.7 km during spring tides. Knowledge of this factor should therefore be taken into account when analysing bird locations or estimating their energy expenditure if they relocate above a feeding ground by swimming or flying. Thus for a bird to remain in the same location for one complete tidal cycle it would have to swim the equivalent of 13.7 km during a spring tide, unless it chose to reposition by flying.

An estimate of the bottom stress associated with the tidal currents was obtained by computing U_B^2 where U_B is the speed at the bed. This parameter is presented in Figure 2.4d which shows contours of U_B^2. In general, values of 0.5 m^2s^{-2} were obtained along the Lancashire and North Wales coasts with the maximum values occurring around the western and northern shores of Anglesey. This result will be discussed further in the next section.

The wave model was applied to the Liverpool Bay region using 6 hourly wind data from 1997-2001 and a 5 year time series of significant wave height and peak period was computed for each grid point. Parameters such as the mean wave height, the rms wave height and the maximum wave height were then extracted for each grid cell. (In this context, wave height refers to the significant wave height.) In a similar manner, the mean, rms and maximum wave periods were also computed. Figure 2.5a presents a contour plot of the maximum wave heights. The highest waves (up to 7 m) were encountered along the southwest coast of Anglesey due to the increased fetch associated with waves approaching from the southwest. In contrast, the coastline of North Wales where the maximum waves were around 4 m was sheltered by the presence of Anglesey. In the northern portion of the region and near the Blackpool coast the maximum waves reached 6 m. The wave periods displayed a similar pattern, with values of about 9 s along the Lancashire coast and values of 7 s off North Wales (Figure 2.5b).

The near-bed current due to the orbital motion of the waves, u_o, was computed using linear theory (Bowden 1983) after solving the dispersion relationship to determine the wavelength of the wave as a function of water depth. The value of u_o^2 is shown contoured in Figure 2.5c. Maximum values of 5-10 m^2s^{-2} were derived along the Lancashire coastline; this reflects the combination of large waves with relatively shallow water that occurs there. (The orbital velocity of the waves decreases in an exponential manner with increasing water depth). In contrast, values of less than 1 m^2s^{-2} were computed for the central waters of Liverpool Bay and for the sea around Anglesey due to the depth of water in those regions.

Figure 2.4d shows a measure of the bottom stress due to the extreme spring tides that occur in the region. This parameter was obtained from the M2 tidal current results by scaling using a factor of 1.67. This factor was derived by computing the ratio between the offset for chart datum with respect to mean sea level with the amplitude of the M2 surface elevation for all available ports within the Irish Sea. (The chart datum offset, z_o, represents the lowest tidal level likely to be experienced at a location. It can be compared with the M2 amplitude at a port using values that are tabulated in the Admiralty Tide Tables (2005)). Thus the M2 tidal currents were scaled using a factor of 1.67 to derive estimates of the currents that would occur at a time of extreme spring tides.

A comparison of Figures 2.5c and 2.5d suggests that wave action dominates the sea bed stress in the near-shore waters along the Lancashire and North Wales coasts where there is an order of magnitude more energy in the wave associated motions. Tidal stirring is only likely to dominate the sea bed characteristics to the western and northern tips of Anglesey and at the southern tip of the Isle of Man.

Figure 2.6 shows the positions at which common scoter ducks were observed during aerial surveys that were conducted between August 2002 and November 2004. There was a total of 4226 individual data points after error checking had removed positions that were on land. For each of the data points there was information on the time/date and the latitude/longitude of a duck observation. These data were then used with the tidal model to predict the water depth, the depth-mean current (speed and direction) at each duck position. A similar analysis was performed using 1023 land-based observations that were collected from two sites at Anglesey and Llanddulas (Figure 2.1) during December 2003 to March 2004. While fewer in number, this latter data set contained information on the duration of the dive times for the observed ducks that were ascertained by direct observation from land-based sites at Llanddulas and Red Wharf Bay (see section 4).

Figure 2.7a-c presents histograms derived from the aerial survey data. The uncorrected water depth (i.e. the chart value which represents the depth with respect to mean sea level) is displayed in Figure 2.7a and suggests a Gaussian distribution with the greatest number of ducks located in water depths of 10-12 m and with a span from 2 m to 22 m. After correction for the tidal effect, which could add up to ±5 m to the uncorrected value, the distribution became more ramp-like with a steady increase of numbers until the water depth reached a value of 15-17 m followed by a rapid decrease in numbers where the depth was greater than 20 m. A similar trend was shown by the histogram of bird numbers against current speed (Figure 2.7c). This latter characteristic is probably a consequence of the manner in which the current speed generally increases with distance from the shore due to the effect of friction in the shallow water, thus the two physical parameters of depth and current speed are strongly correlated and it is difficult to ascertain which is the more critical determinant of habitat use (see section 3).

Most of the biological parameters showed poor correlation with the physical variables. For example, Figure 2.7d presents a scatter diagram of dive duration against the water depth. While the dive durations varied between 15-55 s there is a weak association between dive duration and depth although this varied with observation site (see section 3).

2.4 Summary

The Liverpool Bay portion of the eastern Irish Sea is a high energy region in terms of its hydrodynamic regime. At the time of spring tides the tidal range between high and low water is around 10 m and the near-shore tidal currents can reach speeds of 1.5 ms^{-1}. The significant change in water depth during the tidal cycle causes the 20 m isobath to migrate on/offshore by approximately 10 km during each tidal cycle at the time of spring tides. This migration causes the area of the sea bed where the water depth is less than 20 m to change from 4.18×10^9 m^2 at the time of low water to a value of 2.73×10^9 m^2 at the time of high water. This variation amounts to a fraction of 45% of the area that is shallower than 20 m with respect to the mean sea level.

In Round One of the programme for the development of offshore wind power, an area of order 7×10^7 m^2 was allocated for turbine sites, with a further 23×10^7 m^2 allocated during the Second Round. In consequence a total of 0.3×10^9 m^2 of the sea bed could eventually be covered by wind farms which are being sited in water depths of typically 15 m with respect to the mean sea level. This amounts to approximately 10% of the area of the sea bed within Liverpool Bay where the depth is less than 20 m. The impact of such farms will therefore depend critically on their location with respect to the regions within which the common scoter forage for food.

Waves from the North Atlantic cannot penetrate into Liverpool Bay due to the sheltering effect of Anglesey on waves from the southwest and the restricted entrance through the North Channel at the northern limit of the region. The wave energy is therefore generated locally by the action of the local wind. A simulation of the wave field using archive winds from the 5 year period 1997-2001 produced maximum wave heights of 6 m with periods of about 9 s along the Lancashire coast. In combination with the relatively shallow water in that region this resulted in a sea bed stress that was an order of magnitude greater than that due to the maximum tidal currents. The wave exposure was less along the North Wales coast, with the simulated waves reaching maximum heights of 4 m with periods of around 7 s. However, in this region the wave associated bed stress was still a factor of 2 stronger than the tidal stress. The differences observed in wave stress at the bed may explain the differing depth distribution of peak bivalve biomass off the Lancashire and North Wales coastline (see section 3).

The tidal model allowed the water depth at the common scoter positions to be corrected for the variation of the sea surface height within the tidal cycle (and during the spring/neap cycle). It also allowed an estimate to be made of the current speed at the site of each duck observation. The corrected water depths suggested that the common scoter were limited to locations where the water depth was less than about 18 m. However, no correlation could be established between the water depth and the dive duration of the ducks.

It is generally accepted that the feeding areas used by common scoter are restricted to water of less than 20 m depth due to the constraints imposed by the energetic costs of diving to the sea bed to consume benthic prey species. Currents and the associated sea bed shear stress can influence food availability for benthic communities (Jenness & Duineveld 1985) and benthic secondary production (Warwick & Uncles 1980; Wildish & Peer 1983). High shear stress results in scouring and high current velocities inhibit feeding activity, while water movement at the sea bed is necessary for the supply of food to the benthos. Below a certain current velocity threshold, food particles transported from other areas may begin to sink to the seabed, where they become available as food to the benthos (Creutzberg 1984). In additional to the natural mortality rates, which relate to body-size, sediment movement due to wave action caused by wind and tides, can be a major cause of mortality among benthic animals and has been shown to affect secondary production (Emerson 1989). Both shear and erosion are likely to interact with depth such that at some distance from the shore it is likely that a critical depth occurs where food supply from shear and mortality from erosion coincide to generate optimal conditions for growth.

The impact of the wind farm developments on the common scoter duck population will depend on the location of the turbine structures in relation to the feeding areas of the ducks. While there may be adequate bivalve biomass on the bed in the deeper offshore waters it may be impossible for the common scoter to feed in such regions due to the limitation on the depth to which they can dive. A budget evaluation of the energy expended by common scoter during diving against the energy gained from their food is the subject of a behavioural modelling component of this multi-disciplinary study and will be reported separately.

	MSL	**HWS**	**LWS**	**HWN**	**LWN**
No. of grid cells < 20m	277	220	337	244	308
Area < 20m (10^9 m^2)	3.43	2.73	4.18	3.02	3.82
% of total area < 20m	21.9	17.4	26.7	19.3	24.4

Table 1 Sea bed area statistics for the portion of the region where the water depth is less than 20 m. The total area of the sea bed in the Liverpool Bay region (Figure 2.1) is 15.67×10^9 m^2. (MSL = mean sea level, HWS = high water springs, LWS = low water springs, HWN = high water neaps, LWN = low water neaps)

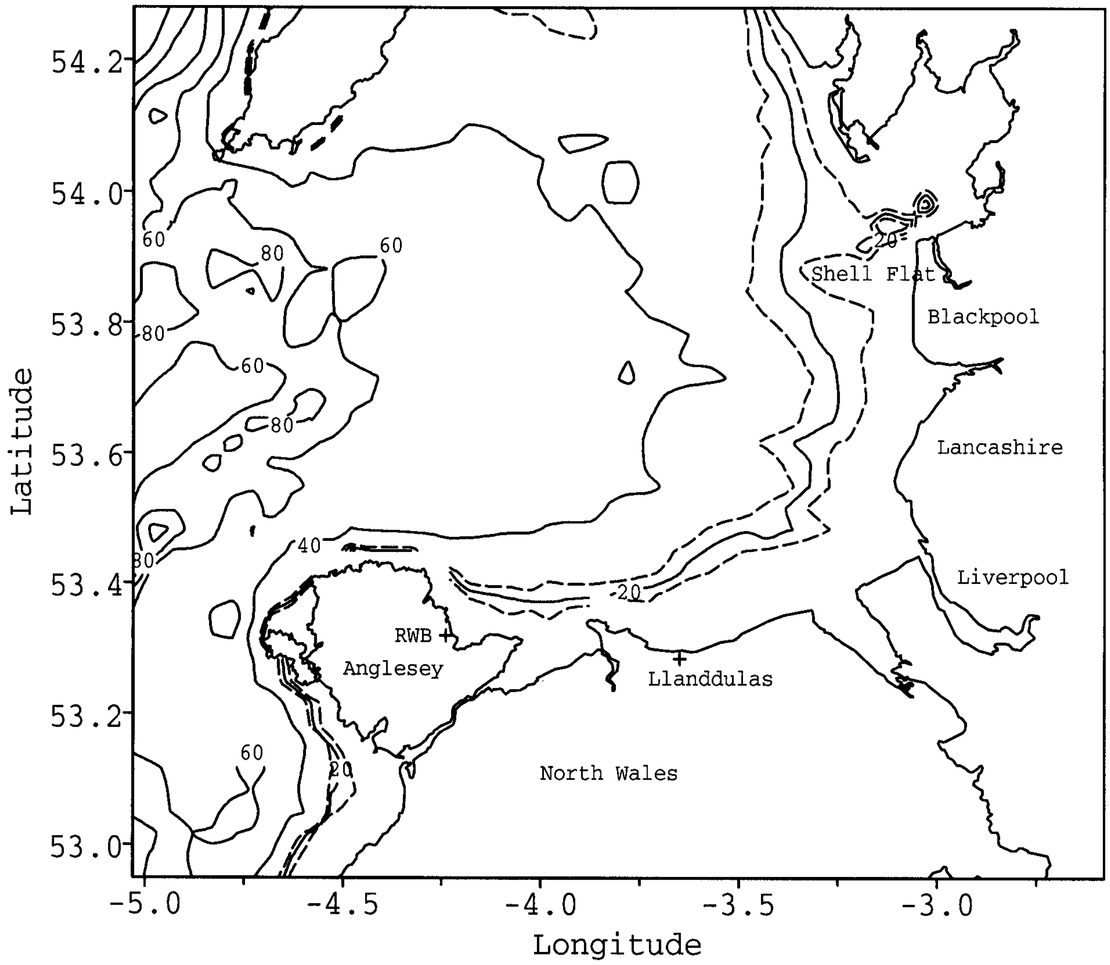


Figure 2.1 Liverpool Bay showing water depth contours (m) with respect to mean sea level (solid curves) and the 20 m isobath (dashed curve) at the time of high and low water during spring tides. The location of the two land-based common scoter surveys are marked by (+) symbols on Anglesey at Red Wharf Bay (RWB) and at Llanddulas on the North Wales coast.

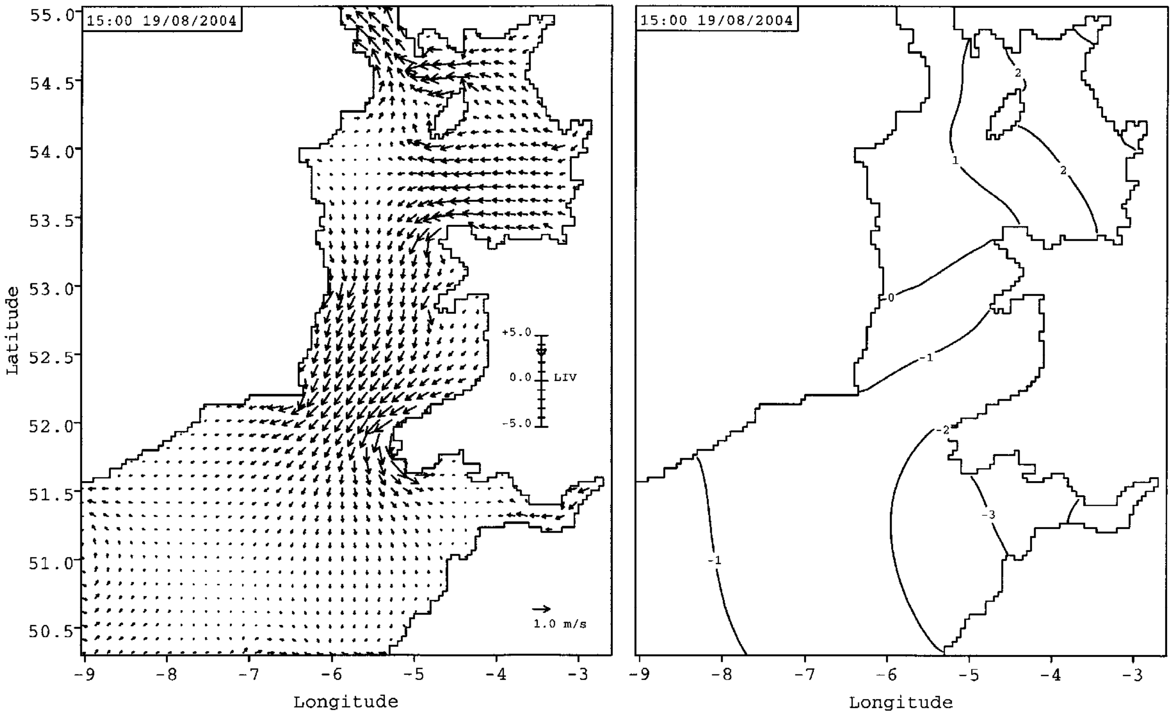


Figure 2.2 An example of the tidal vectors and sea level elevations produced by the tidal model. The tidal staff on the left hand portion of the figure represents the tidal elevation at Liverpool. (For clarity only every 3rd vector in each direction is plotted.)

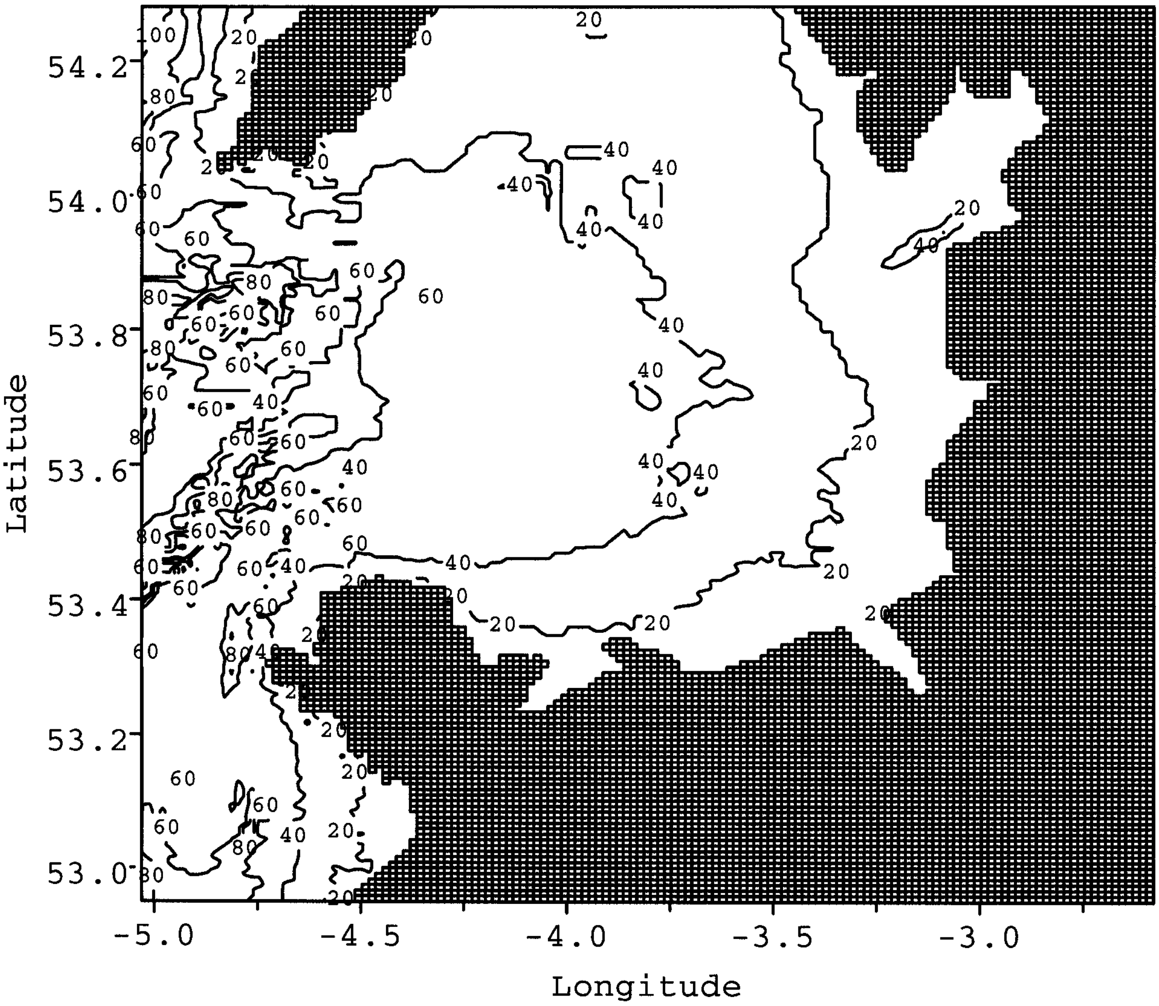


Figure 2.3 Water depths in Liverpool Bay derived from the 1 km database. The spatial resolution of the database is revealed by the cells drawn on the land.

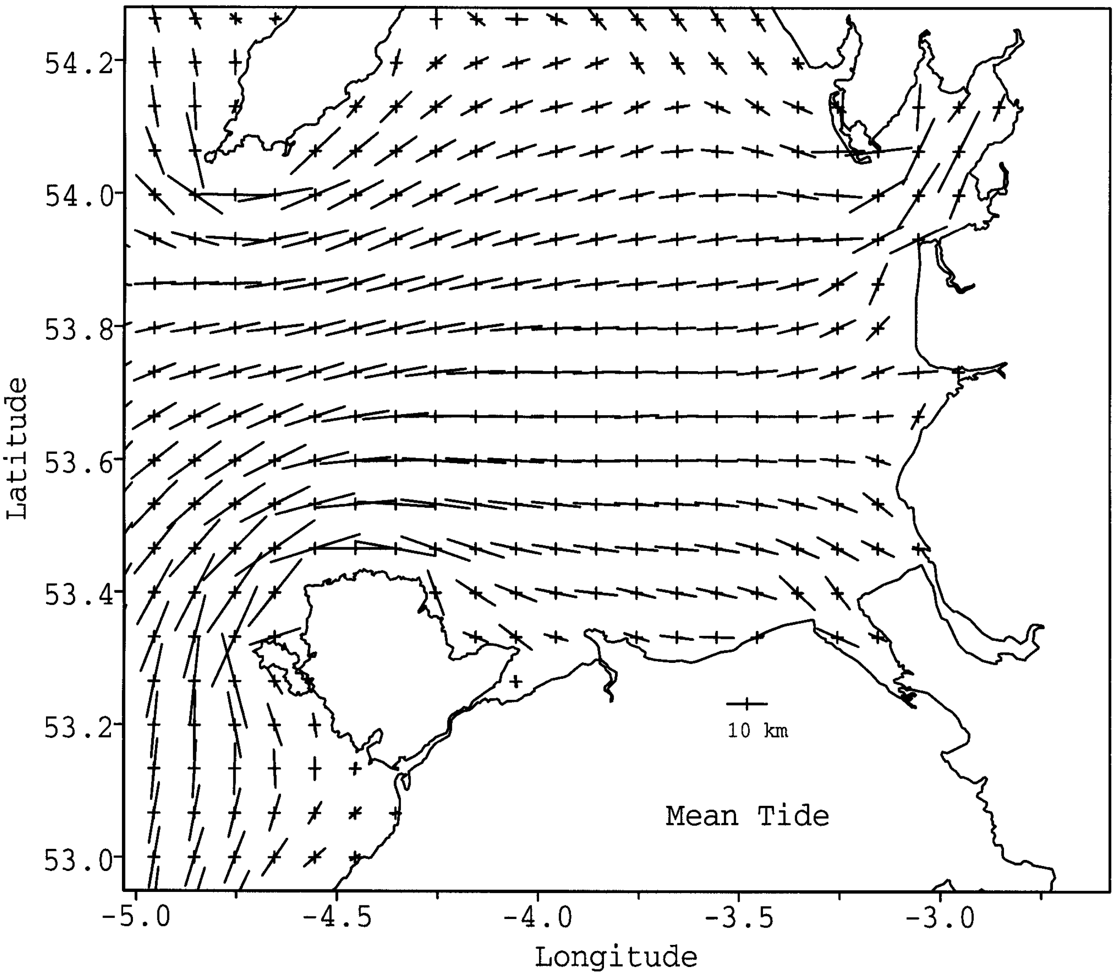


Figure 2.4 Surface tidal excursions during a period of mean tides (mid-way between springs and neaps). (For clarity only every 2^{nd} point has been plotted in each direction.)

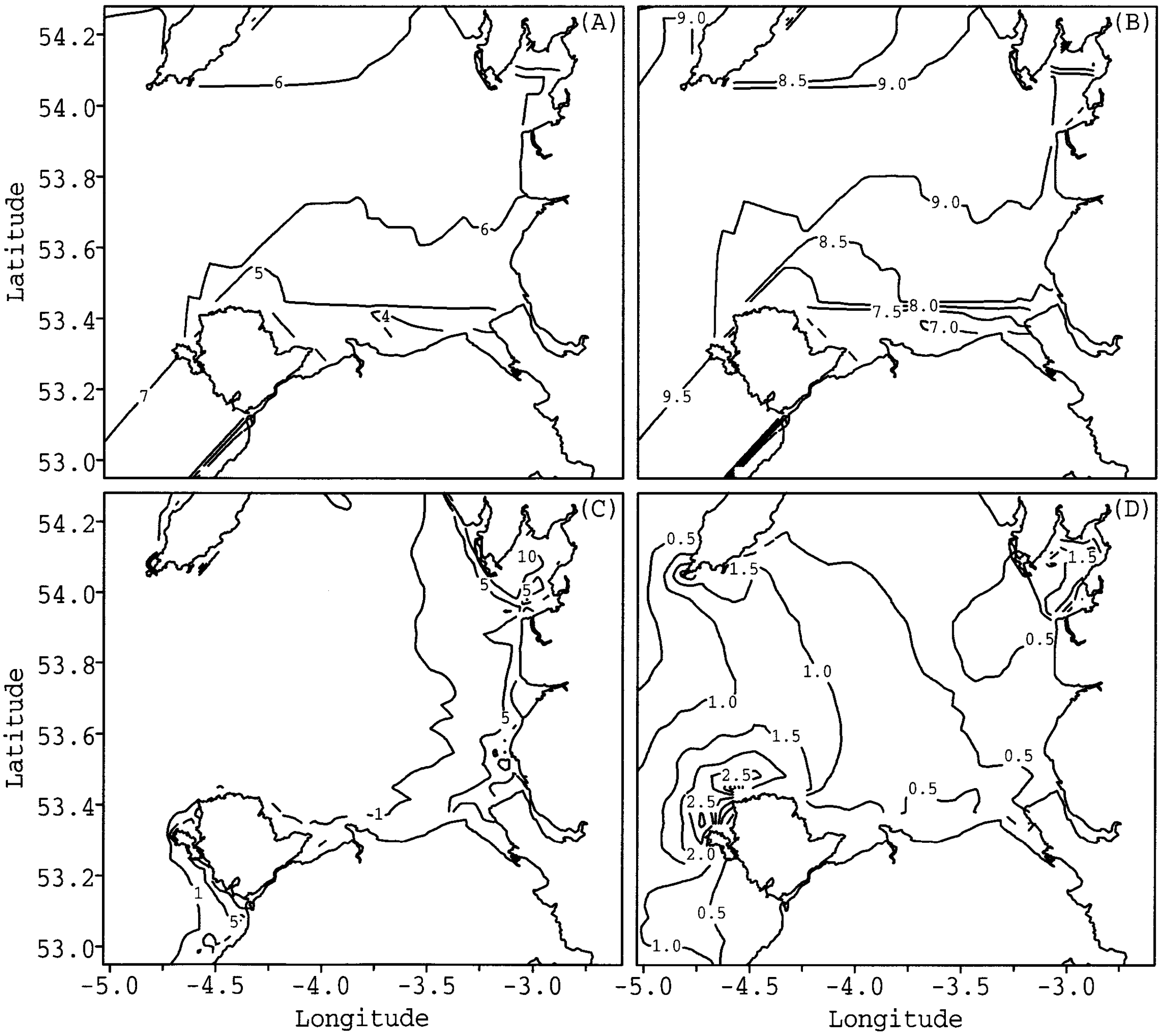


Figure 2.5 (a) Contours of computed maximum significant wave height (m) during 1997-2001. (b) Computed maximum wave period (s) during 1997-2001. (c) Measure of sea bed stress due to the waves (m^2s^{-2}). (d) Measure of sea bed stress due to the tidal currents (m^2s^{-2}).

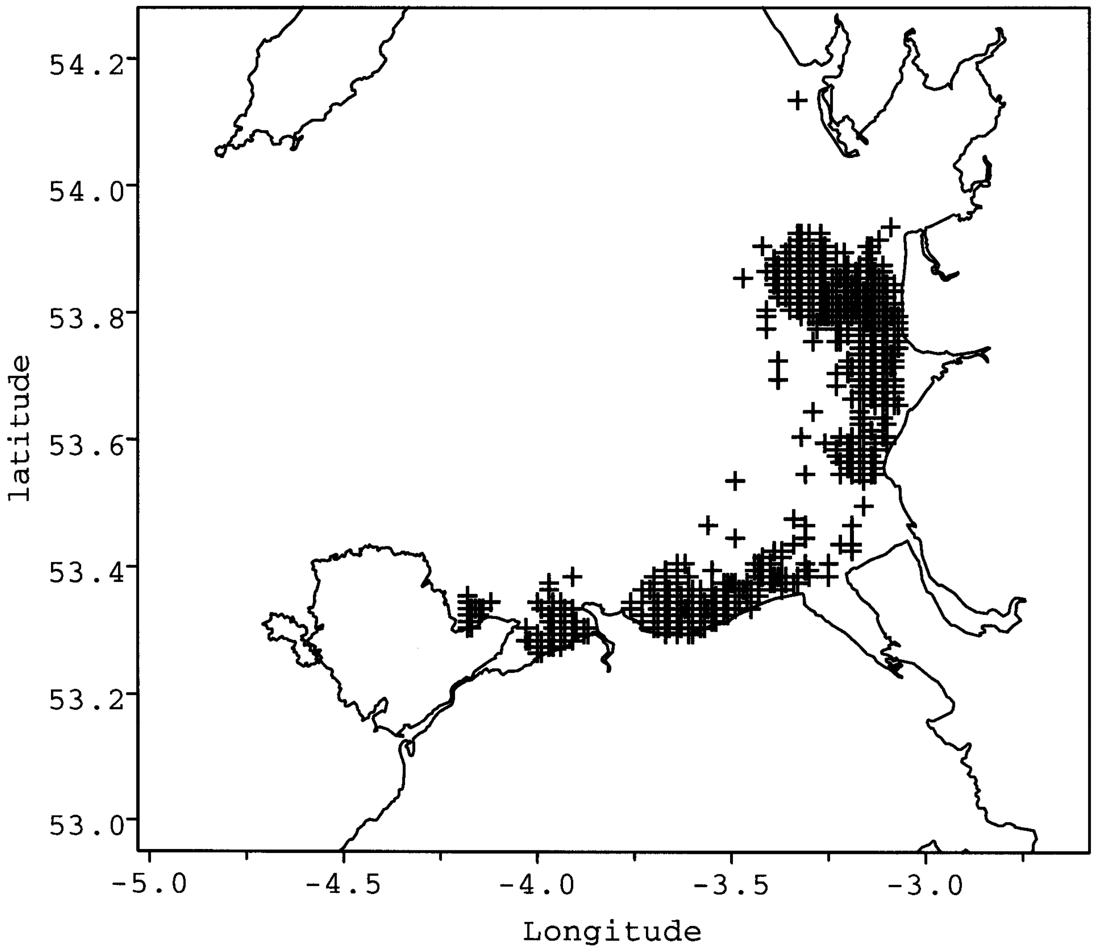


Figure 2.6 Locations at which common scoter were observed during aerial surveys.

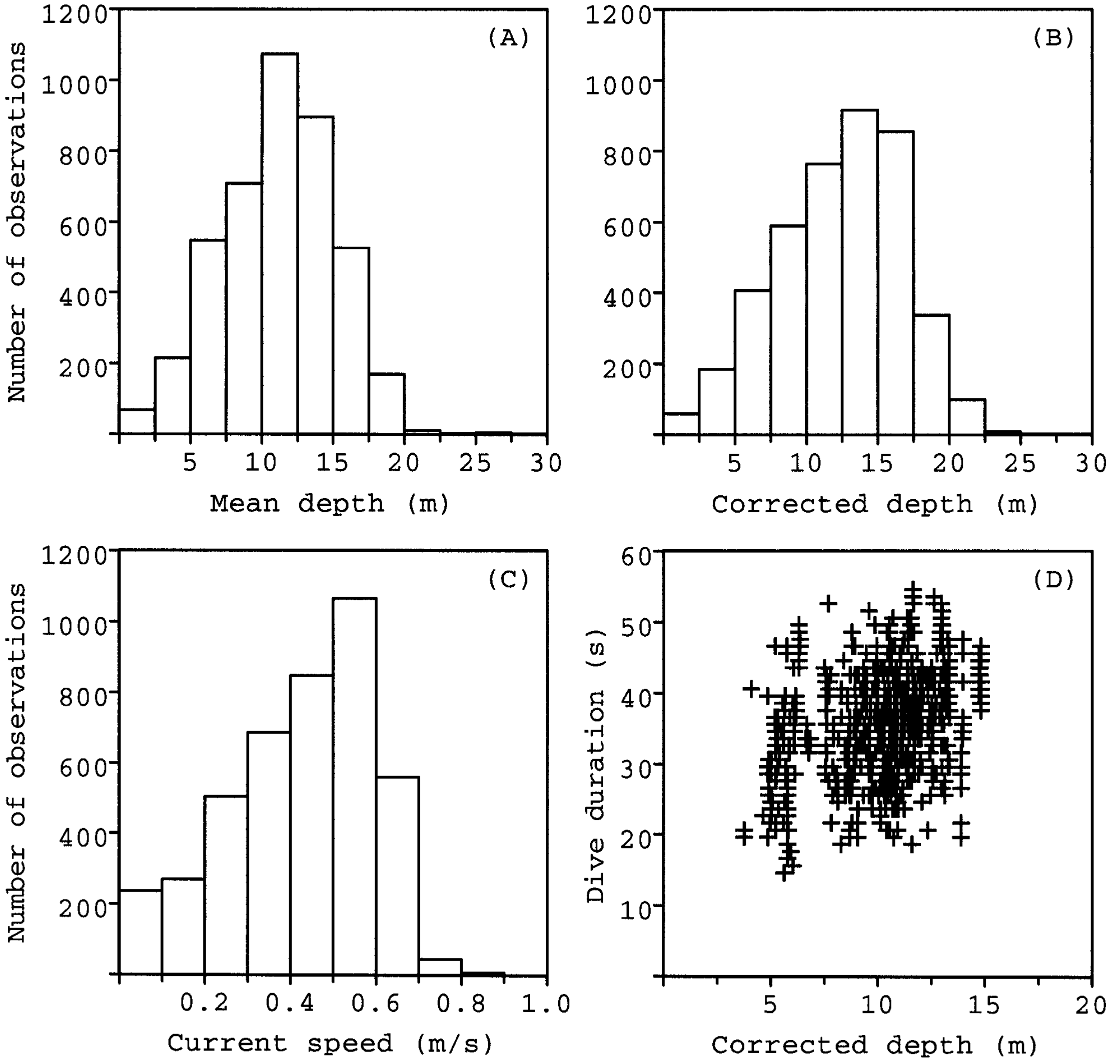


Figure 2.7 (a) Histogram of common scoter numbers versus the water depth with respect to mean sea level. (b) Histogram of common scoter numbers versus the tidally corrected water depth. (c) Histogram of common scoter numbers versus the speed of the tidal current. (d) Scatter plot of dive duration versus the tidally corrected depth.

3. Common scoter distribution in relation to prey-types

3.1 Introduction

Common scoter are diving ducks that feed on prey taxa that live upon or within the upper few cm of the substratum. The diet of common scoter is thought to comprise mainly bivalve molluscs, while other taxa are incorporated less frequently (e.g. crabs, small fishes and gastropods). Echinoderms seem to be included in the diet at such a low frequency that they are presumed to be ingested incidentally (Stott & Olson, 1973; Bourne, 1984; Ferns, 1984; Stempniewicz, 1986; Aulert & Sylvand, 1997; Vaitkus & Bubinas, 2001; present study). Common scoter tend to be highly aggregated and, like other diving ducks, have been reported to severely deplete their food resources over one season (Stempniewicz 1986, Guillemette et al. 1996, Guillemette 1998, Nehls & Ketzenberg 2002 although see Nilsson (1972) for evidence to the contrary). They may, therefore, exert considerable mortality to populations of certain prey-types. The exact mechanism of feeding is unknown although it is unlikely that they are visual feeders, particularly in Liverpool Bay where the water is particularly turbid due to riverine discharge from the Rivers Dee, Mersey, Ribble and Conwy.

Common scoter feed on benthic prey whose life-history strategies and production are intimately linked to the sedimentary and coastal environment that is strongly influenced by near-bed hydrodynamic stress and hence this can be an important determinant of benthic assemblage distribution (Warwick & Uncles 1980; Yates et al. 1993). Shear bed stress will have both positive and negative effects on benthic communities. At low shear stress values, increasing shear increases the supply of food and hence production of the benthos until a threshold where further increases in shear stress inhibit feeding (Hiddink et al. in press). Increasing levels of wave erosion increase mortality of the benthos (Hiddink et al. in press). These two factors are likely to interact close to the coastline and will have a strong influence on the production of the associated benthic communities. In addition, benthic communities are notoriously patchy in their distribution and the population sizes of benthic invertebrates fluctuate greatly from one year to the next (e.g. Rees et al. 1977; Somerfield et al. 2002). Thus food resources available for common scoter are unlikely to be uniformly distributed over the seabed and certain areas will yield higher rates of energy intake than others. Presumably, common scoter, like other diving ducks, distribute themselves over, or in close proximity to, areas that have a sufficient abundance of prey to maintain their energetic requirements and are able to assess the rate of encounter with suitable prey as they probe through the sediment with their bill (Stott & Olson 1973, Phillips 1991). The consistency of the sediment is likely to affect foraging efficiency if selection of prey is by passive sifting through the bill. Sediments that contain a proportion of 'prey-sized' inedible particles may interfere with efficient ingestion such that foraging efficiency is compromised. The profitability of prey will also be affected by the depth to which the birds need to dive for feeding, which is a continuously changing variable in tidal areas. The deeper that benthic feeding birds need to dive, the longer they must take to travel to and from the seabed (Dewar 1924) and the greater the energy that they must expend acquiring prey (Lovvorn & Jones 1991). However, because buoyancy is the predominant force against which ducks have to work during dives (Stephenson et al. 1989), and the uplift generated by air in the lungs decreases as a function of depth and hence increasing pressure, the increasing relationship between depth and energy expenditure may be non-linear (Wilson et al. 1992).

A number of environmental and anthropogenic factors are likely to affect the distribution of the birds at the sea surface: the distribution and quality of the prey that may vary interannually and through the year, the depth of the water over the seabed that fluctuates tidally, the surface current speed which, in Liverpool Bay, will move birds over the ground at speeds of up to 1 – 2 ms^{-1} at peak tidal flow, the distribution and density of conspecifics, diurnal patterns in feeding behaviour and the proximity to human activity and structures. As in other species, the birds probably use visual cues such as the density of conspecifics to locate initial feeding sites before sampling other possible food patches (Nilsson 1972). Because swimming against a current is costly (Woakes & Butler 1983, Hawkins et al 2000), surface currents may be important if birds are required to continually maintain their position over patches of prey by swimming against currents, or by relocating periodically by flying up-stream (see section 2).

Previous studies of the relationship between common scoter and their prey have inferred diet by surveying general areas of seabed in the vicinity of known aggregations of birds (e.g. Degraer et al. 1999). However, in the present study, we were able use aerial surveys of common scoter to generate a more accurate picture of the distribution of a regional population of birds in direct relation to quantitative samples of the benthic assemblage and environmental characteristics of the surveyed area. The specific aims of the present study were to: 1) ascertain whether the distribution of common scoter in Liverpool Bay was related to the distribution of key prey-types, 2) determine environmental factors that may predict either the distribution of common scoter or key prey-types and 3) to ascertain to what extent existing anthropogenic activities influence or constrain the distribution of common scoter. These data provide the basis for predictive modelling of the population effects of likely windfarm construction in Liverpool Bay on the common scoter population (section 8 onwards).

3.2 Methods

3.2.1 Spatial and temporal variation in prey-types

In order to quantify the distribution and quality of food types available in Liverpool Bay it was necessary to undertake an extensive stratified survey that sampled areas of the sea where common scoter had been observed and also areas where common scoter were not observed. For the purposes of the present study, we divided Liverpool Bay into two main areas; the Lancashire coast that extended from just north of Shell Flat to the centre of the entrance to the River Mersey, and the North Wales coast that extended from Red Wharf Bay across to the centre of the entrance of the River Mersey. These two areas held distinct high density aggregations of common scoter. The outer limits of our survey area were set by the reported maximum dive depth for common scoter which is commonly believed to be 20 m (Degraer et al. 1999). As depth directly affects energy expended on travelling to and from the seabed and while foraging on it, we calculated depth bathymetries at 5 m intervals for both spring and neap tides. When possible, a selection of our sample sites coincided with the intersection between these depth bathymetries and the aerial survey flight paths that would enable a direct analysis of the relationship between common scoter abundance and prey abundance at these sites. Additional survey sites were selected to ensure that the full gradient of depth zones was sampled across Liverpool Bay. Three surveys were undertaken from the RV Prince Madog in August and December 2003 and April 2004 to span a full overwintering season of common scoter in Liverpool Bay.

During the initial survey in August 2003, 81 and 88 sites were sampled off the Lancashire and North Wales coast respectively (Fig. 3.1). At each site, three 0.1 m^2 Day grab samples were taken and the contents of the first two were sieved over a 1 mm mesh aboard ship. Bivalves were picked off the mesh by hand and frozen for later biomass analysis. All other residues and biota were preserved in 4% buffered formalin. A sediment sample was collected from the third Day grab and the rest of the sample was discarded. Of these sites, a total of 24 sites (12 in each area) were selected for monitoring purposes (total of 4 Day grabs). These sites were termed monitoring sites and were resampled with the same sampling effort in December 2003 and April 2004 to enable the rate of decline of prey types to be calculated (mortality rate). Seventeen of the 24 monitoring sites occurred in areas over which common scoter were not observed or occurred in low numbers throughout the overflight surveys. These 17 sites provide important information on the natural seasonal changes in potential prey abundance in the absence of common scoter. In addition to these sites, we sampled two transects of 6 sites spaced at an interval of 200 m to gain an estimate of small-scale variability in terms of prey-types and their abundance. Four Day grab samples were collected at each of these sites.

Given the necessity to collect a large number of samples across as wide an area as possible, our ability to analyse all components of the benthos within samples was constrained by time and manpower. As a result, we undertook an extensive search of the literature to ascertain the main recorded prey types of common scoter. Twenty one separate publications that dealt with the diet of common scoter or velvet scoter *Melanitta fusca* were polled. Of 199 records of prey types consumed, c. 75% were bivalves (Table 3.1). As a consequence we have focused our analysis in the present study on the distribution of mollusc prey in Liverpool Bay, although we also quantified seasonal changes in total benthic biomass.

3.2.2. Long-term variation vs spatial variation

Prey resources for common scoter may fluctuate on an annual basis as a result of variation in juvenile recruitment and rates of predation on adult stocks. We investigated the degree of interannual variation from a dataset of bivalve abundance sampled in Liverpool Bay from 2001 to 2004. These samples were collected from Conwy Bay in November 2001 and 2004, from the area off Llanddulas and Shell Flat in March 2002 and August 2003. In all cases sampling was undertaken using the same 0.1 m² Day grab and all bivalves retained on a 1 mm mesh sieve were counted and identified. The mean abundance and standard deviation for each species collected on each sampling occasion was calculated and the coefficient of variation (S.D./mean) ascertained. The mean ± S.D. and C.V. for mean of each species across years (2001 – 2004) was also calculated to enable a comparison of spatial variation (within one year) with the interannual variation.

3.2.3 Bivalve biomass

The literature search yielded a list of in excess of 30 different species of bivalve that have been recorded in the diet of common scoter. We considered that it is unlikely that common scoter are species specific in their choice of prey, but that selection in more likely to be determined by prey morphology, digestibility and energy content. As a result we considered mollusc prey to fall into three main prey morphologies; elongate prey (e.g. *Ensis, Pharus, Phaxas*), ovate brittle shelled (e.g. *Abra, Fabulina, Lutraria*) and ovate hard shelled (e.g. *Nucula, Donax, Chamelea*) (Table 3.2). All of these species are either surface dwelling or are in direct contact with the sediment/water interface and hence all are considered available as potential prey for common scoter. For each sample site, mollusc prey-types were defrosted and their shell dimensions measured to the nearest 0.1mm using Vernier callipers. Maximum length was measured along the anterior-posterior margin axis. Maximum width was measured by placing the callipers on the umbo and sliding them along the ventral margin until the maximum width was reached. For each species, 50-70 individuals were randomly selected from all the samples for each area and season in order to establish Length-Ash Free Dry Weight relationships. Mollusc flesh was removed from the shell and was dried to a constant weight at 90°C for 24 hours in pre-weighed crucibles. Dry flesh was then placed in a muffle furnace set at 550°C for 2 h to determine the ash free dry weight content (AFDW) to the nearest mg. Shells were dried and ashed separately following the same methodology. Elongate bivalves (particularly *Pharus*) were quite commonly broken during sampling and only the anterior part was collected in the samples. For theses species, we established Length-Width relationships with regression analysis (for each area and sampling occasion) in order to calculate their length. Pooling together the data on species for the three prey types, length – AFDW (flesh and shell) equations were calculated for each prey type, area and sampling occasion with regression analysis and these relationships were used to estimate the AFDW of the remaining bivalves.

The relationship of AFDW on depth was modelled as a Gaussian curve according to:

$$G = G_{\min} + \left(G_{\max} - G_{\min}\right) e^{\frac{(S-S_m)^2}{-V}}$$

where G is the depth dependent bivalve biomass modifier, G_{min} is the minimal biomass, G_{max} is the maximum biomass, S is depth (m), S_m is the depth at which the maximum biomass is attained and V is the variance of the Gaussian curve.

3.2.4 Survival rates

Daily survival rates of the bivalve prey throughout the overwintering period were calculated from monitoring station abundances. Of the 24 monitoring stations, only the 17 that fell outside dense common scoter aggregations were included in the analysis in order to remove the effect of common scoter predation. Since common scoter have different functional responses for different prey sizes, it was decided that the prey type abundances would be divided into 4 size classes for the oval brittle and oval solid bivalves (0-12, 12-24, 24-36 and >36mm) and 6 size classes for the elongate bivalves (0-12, 12-24, 24-36, 36-48, 48-72 and >72mm) and survival rates were calculated accordingly by prey type and size class. Bivalve data were pooled by area and the daily survival rates for the periods of August to December and December to April were calculated from the formula:

$$(\mathit{final\,abundance} / \mathit{initial\,abundance})^{-\mathit{number\,of\,days}}$$

3.2.5 Infaunal residue

The remaining biota in the formalin preserved benthic samples were stained with rose Bengal, washed over a 0.5mm sieve, sorted into major taxonomic groups (Actiniaria, Bryozoa, Decapoda, Echinodermata, Fish, Gastropoda, Tunicata, small bivalves, small crustaceans and worm-like animals) and preserved in 70% ethanol. Small bivalves include mostly juvenile representatives (<2mm) of the recorded bivalve species, small crustaceans consist of mysids, cumaceans, amphipods and juvenile decapods and worm-like animals include polychaetes, oligochaetes, sipunculids, nemerteans and the anemone Edwardsia by exception to the rest of the Actiniaria because of its resemblance to other representatives of this group. Organisms were blotted dry and the groups were weighed to the nearest mg. (Due to time restrictions, only one out of the two replicate grabs in each station was processed). Dry mass was converted into AFDW using established conversion factors reported by Thomas Brey (electronic reference).

3.2.6 GIS generated data for behavioural model

3.2.6.1 Interpolations

Bivalve data (abundance/0.2m^2) from the sampled stations were used to predict the distribution of the respective bivalve prey type-size class groups, as described above, in areas potentially available to the birds as feeding grounds through spatial interpolation methods. All interpolations were carried out with ArcView GIS and Spatial Analyst and were based on the Inverse Distance Weighted method with a fixed radius of 2.5km. The next step was to bring the bivalve data to the same spatial reference level with the environmental data provided by the tidal model and the common scoter behavioural model which will combine all the available data and will function on the basis of the tidal model grid. Hence, the tidal model grid cells were overlaid on the interpolated abundance grid maps and the average (max and min) bivalve abundance was calculated for each of the relevant grid cells.

3.2.6.2 Proposed windfarms and shipping activity

One of the data requirements of the behavioural model was the estimation of the potential feeding area of the common scoter that would be unavailable to them due to anthropogenic activities such as windfarm developments, shipping traffic and aerial traffic. All spatial data were processed and analysed with ArcView GIS. The positions of the proposed windfarms were entered into ArcView as a map layer together with the tidal grid cells. Shipping intensity data was made available to us by Anatec UK Ltd as number of ships passing from each tidal grid cell per year. The potential effects of disturbance by helicopter flights to and from oil and gas installations were also considered. These potential sources of disturbance are dealt with in more detail in section 5.

3.2.6.3 Environmental parameters

Data on mean water depth, surface current speed (m/sec) and bottom sheer stress (N/m^2) were derived from the tidal model for the central points of the 3.70 x 3.35 km grid cells (section 2). The data were then used to produce interpolated continuous raster grids, from which relevant information could be extracted for any point of the tidal grid surface. Sediment parameters were investigated from samples collected during the benthic surveys.

Sediment samples were defrosted, dried at 90°C to dry weight and 25 g were removed for analysis. Samples were soaked overnight in 250 ml of water with 10ml sodium hexametaphosphate (6.2g/l) to desegregate the sediment particles (Buchanan, 1984). After wet-sieving over a 63 µm mesh sieve to remove the fine particles, the sediment was re-dried and then separated into its component size fractions by dry-sieving with a reciprocating shaker. The different fractions were then weighed. The total organic carbon contents (TOC) of the sediment was determined from sub-samples of the dried sediment, weighed before and after combustion in a muffle furnace for 2 h at 550°C, and hence provided an estimate of the ash-free dry weight of the samples (Buchanan 1984).

3.2.7 Statistical analyses

In order to determine which of the measured suite of variables best explained the observed distribution of common scoter we used a general linear modelling procedure after log10 transformation of observed common scoter numbers. We related each individual recorded geo-referenced sighting of common scoter for the period August 2003 to May 2004 (total of eight overflights) to the associated environmental and biological variables at that location (determined from the GIS layers described in 3.2.5.2). Therefore this analysis relates only to those locations where common scoter were observed. Prior to undertaking the GLM, a correlation matrix for all variables was constructed and strongly auto-correlated variables removed. The variables included were: shear stress, mean surface current velocity, mean depth, sediment type (either sediment with a mud content of < 5% or > 25% derived from British Geological Survey data), bivalve biomass, and number of ships per annum. The correlation matrix gave a coefficient of -0.97 for the relationship between shear stress and surface current velocity, so the former was removed from further analysis. This makes sense as shear stress is the product of the relationship between surface current velocity and depth (see section 2).

As bivalves are key prey for common scoter we investigated which suite of environmental parameters best explained variation in total bivalve biomass at each sample location. For this analysis we were able to utilise sediment characteristics for each site as opposed to interpolated values determined from British Geological Survey data as in the GLM analysis above. General Additive Modelling (GAM) was used as this approach can cope with non-linear relationships among predictor and response (bivalve biomass) variables. The following variables were examined: surface current velocity, shear stress, distance from shore, depth, gravel content (%), sand content (%), mud content (%), organic matter content (%), and median phi.

Generalized additive models extend linear models and generalized linear models by flexibly modelling additive non-linear relationships between the predictors (e.g. environmental variables) and the response (bivalve AFDW). Whereas linear models assume that the response is linear in each predictor, additive models assume only that the response is affected by each predictor in a smooth way. The response is modelled as a sum of smooth functions in the predictors, where the smooth functions are estimated automatically using smoothers.

Smoothing is a non-parametric technique which relies on the data to specify the form of the model and fit a curve to the data locally. With this technique, the curve at any point depends only on the observations at that point and some specified neighbouring points. In locally weighted regression smoothing, the smooth function is built as follows:

1. Take a point. Find its nearest neighbours, which constitute a neighbourhood. The number of neighbours is specified as a percentage of the total number of points. This percentage is called the span.
2. Calculate the largest distance between and another point in the neighbourhood.
3. Assign weights to each point.
4. Calculate the weighted least squares fit of on the neighbourhood. Take the fitted value.
5. Repeat for each predictor value.

As a result of using such a technique, the degrees of freedom (df) generated are may be somewhat unfamiliar to those used to dealing with linear models. Given a linear smoother operator S , we define the degrees of freedom df to be simply df=tr(S). Thus df is the sum of the eigenvalues of S , and gives an indication of the amount of fitting that S does. The number of df is a function of the span and the predictor values in the data set, and is not a function of the response Y. A span of 100% appears to imply a linear regression and thus two df; the use of only 50% of the data, corresponds to about four degrees of freedom (Hastie & Tibshirani, 1990).

3.3 Results

3.3.1 Spatial and temporal variation in prey-types

Benthic samples from Shell Flat were numerically dominated by the small nut shell *Nucula nitidosa* followed by *Pharus legumen* and *Abra alba.* In contrast, samples from Llanddulas were numerically dominated by *Donax vittatus* followed by *Abra alba* and *Pharus legumen* (Table 3.3). *Nucula* contributed most to the similarity among sites sampled off the Lancashire coast, but did not contribute greatly (if at all) to the similarity of sites sampled off the North Wales coastline. *Abra* and *Pharus* contributed most to the similarity among stations off the North Wales coast (Table 3.4).

The median biomasses (AFDW) of bivalves per unit area sampled from the Lancashire and North Wales sites were not significantly different (Fig. 3.2, M-W, U = 7057, d.f. = 167, P = 0.18) although there was some evidence to suggest that there was less variability in bivalve biomass at the sites off Lancashire. Mean AFDW of bivalves was higher than that of other components of the benthos across Liverpool Bay. At the monitoring sites, AFDW of bivalves and other benthic fauna was lower in April 2004 than in August 2003 but this was not a significant decrease for the bivalves (Table 3.5). However, the coefficient of variation of bivalve AFDW increased significantly from August 2003 to April 2004 which indicated that biomass was more patchily distributed across the seabed by the end of winter (Table 3.5). At both locations, the biomass of bivalves was significantly related to depth according to a Gaussian relationship. The Gaussian relationship for each site indicated that a peak in bivalve biomass occurred at a depth of 7.88 m and 13.96 m off the North Wales and the Lancashire coasts respectively (Fig. 3.3, Table 3.6). The use of tidal models to hindcast the depth of water beneath common scoter observed during overflights indicated that most birds occurred more frequently over water between 7 – 15 m deep off North Wales (mean±S.D. 11.12±2.82 m) and between 13 – 18 m (13.95±2.81 m) deep off Lancashire (Fig. 3.4). Thus, birds were observed most frequently over water that was significantly deeper off Lancashire than off the North Wales coastline (Wilcoxon Z = -1.94, P = 0.025) (see also section 2). Further examination of the distribution of common scoter across the different depth zones (based on mean depth) indicated that birds were skewed in their distribution across shallow (8 m) water out to the 20 m depth zone but rarely beyond (Fig. 3.4b, $x^2 = 64.4$, d.f. = 1,11, $P < 0.0001$).

The spatial distribution of different prey types was highly aggregated (Fig. 3.5). Small oval hard shelled prey (e.g. *Nucula*) were ubiquitous off Lancashire and to a lesser extent off the North Wales coastline but were particularly abundant on the northern shoulder of Shell Flat off Blackpool (Fig. 3.5a). Very high densities of *Donax* were sampled off the mouth of the River Dee on Chester Flats (Fig. 3.5a). Oval brittle prey types were relatively ubiquitous but were particularly abundant on Burbo Flats off the mouth of the River Mersey and off the North Wales coast and locally at Shell Flat (Fig. 3.5b). Elongate prey such as *Pharus* were locally abundant off the River Ribble and off the North Wales coastline and occurred in very high abundance in Red Wharf Bay (Fig. 3.5c). The interpolated map of total bivalve biomass (all species amalgamated) indicates that the highest concentrations of bivalve biomass occurred on Shell Flat, off the River Mersey and in Red Wharf Bay (Fig. 3.6). Survival rate data for each prey-type were calculated to enable parameterisation of the behavioural ecology model. The data for these calculations can be found in Appendix 3.#. Spatial variation in the abundance of selected species of bivalves and all bivalves pooled together was greater than inter-annual variation in 28 out of 35 occurrences (Fig. 3.7).

3.3.2 Explanatory variables

After the removal of shear stress prior to the GLM analysis, all of the variables contributed significantly to the model that explained best the relationship with the abundance of common scoter. Of these variables bivalve AFDW explained the greatest proportion of the variance, followed in rank order by: depth, sediment type, surface current velocity and finally ship disturbance (Table 3.8). The GAM for bivalve biomass indicated that Log depth (P = 0.01) and Log phi (P = 0.04) were the only variables that explained significantly the variation in bivalve biomass (Table 3.8, Fig. 3.8). Depth is frequently an important explanatory variable of benthic community distribution and composition. In this study depth affects the extent to which wave action influences erosion at the seabed which is a key environmental forcing agent in Liverpool Bay (see section 2). The GAM results suggest declining bivalve AFDW with depth and increasing bivalve AFDW with increasing values of median phi (Fig. 3.8).

3.4 Summary and discussion

Overflight observations of birds at sea have the advantage that they enable large-scale surveys of population density to be undertaken within a short time period (Cranswick et al. 2003). Nevertheless, this approach is problematic for a number of reasons, but particularly for diving ducks found in areas of high tidal amplitude. As water depth is a critical parameter for common scoter that feed on the seabed, the relative position of an aggregation may shift according to tidal state (low to high water) which can vary considerably between the start and end of the survey. Thus we felt using the sum total of two years of overflight observations would eliminate some of the spatial variation of common scoter attributed to tidal fluctuations. In addition, we were able to utilise tidal models to hindcast the depth of water beneath each separately logged record of common scoter. Common scoter located off Lancashire were primarily observed over deeper water than birds observed off the coast of North Wales (Fig. 3.4). Other shore-based studies have indicated that common scoter are found over water depths of between 3 – 20 m which is similar to our shore based observations for Llanddulas and Red Wharf Bay (Dewar 1924; Madsen 1954; Stott & Olson 1973; Cramp & Simmons 1977; Goudie & Ankney 1986; Meissner & Brager 1990; Durinck et al. 1993; Brager et al. 1995). However, seaducks can be found in areas where the water is too deep to dive for food (Degraer et al. 1999). It is clear from the aerial survey that common scoter utilise areas of the sea beyond the range of normal telescopic observations and occur over water up to a maximum depth of 25 m although the majority of birds are found in water shallower than 20 m.

Most authors agree that feeding areas used by common scoter are restricted to water of less than 20 m depth due to the constraints imposed by the energetic costs of diving to the seabed to consume benthic prey species. The present study is to our knowledge the first that has quantified the biomass density of prey across the full range of water depth reported by other authors. The depth distribution of common scoter off Lancashire and North Wales appears to closely coincide with the depth at which the peak in bivalve biomass occurs in both locations. This depth zone of the biomass peak differed for the two localities and was significantly deeper off Lancashire. Currents and the associated seabed shear stress, can influence food availability for benthic communities (Jenness and Duineveld 1985) and benthic secondary production (Warwick and Uncles 1980; Wildish and Peer 1983). High shear stress results in scouring and high current velocities inhibit feeding activity, while water movement at the sea bed is necessary for the supply of food to the benthos. Below a certain current velocity threshold, food particles transported from other areas may begin to sink to the seabed, where they become available as food to the benthos (Creutzberg 1984). In additional to the natural mortality rates, which relate to body-size, sediment movement due to wave action caused by wind and tides, can be a major cause of mortality among benthic animals and has been shown to affect secondary production (Emerson 1989). Both shear and erosion are likely to interact with depth such that at some distance from the shore it is likely that a critical depth occurs where food supply from shear and mortality from erosion coincide to generate optimal conditions for growth. Although the Gaussian model that described the relationship between bivalve biomass and depth was significant for both survey areas there were some sites that had an exceptionally high biomass of bivalve prey, particularly off Lancashire. These exceptional biomass sites occurred in the depth range over which most birds were observed.

Previous studies have attempted to relate the constituents of a benthic community to known large-scale aggregations of common scoter. For example, Degraer et al. (1999) inferred that the benthos found on offshore subtidal sand banks was indicative of common scoter diet given that large aggregations of ducks were observed over these seabed features. Nevertheless, while Degraer et al.'s (1999) findings concur with the assertions of other studies (e.g. Durinck et al. 1993; Leopold et al. 1995; Stempniewicz 1986), their study was not designed to resolve the relationship between the spatial distribution of ducks and the spatial variation in the abundance or biomass of potential prey. Lovvorn & Gillingham (1996) stated that "detailed mapping of benthic foods on a scale relevant to the foraging energetics of highly mobile birds is currently not feasible, despite the importance of food dispersion to their foraging profitability and sustainable population levels". The present study is the first in which it has been possible to discern the relatively fine-scale distribution of common scoter over their feeding grounds in relation to potential prey species. All of the prey species reported in the present study have been reported as prey of common scoter in previous studies. It is clear that individual prey species are highly patchy in terms of their distribution, but when the sum biomass of all species was interpolated it was clear that some of the areas with the highest biomass density of potential prey species did not coincide with observations of common scoter (e.g. off the River Mersey). It is noteworthy that although there was a very high biomass of bivalves in Red Wharf Bay, common scoter were only observed here towards the end of the 2003/2004 winter season. Direct observations of dive times of birds in Red Wharf Bay indicated that dive time was significantly longer than at shallower water sites off Llanddulas North Wales (Fig. 3.9). As common scoter appeared in Red Wharf Bay only towards the end of the season it may be that they preferentially choose shallow sites whenever possible to minimise energy expended on diving.

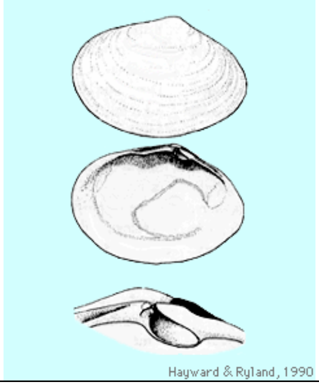
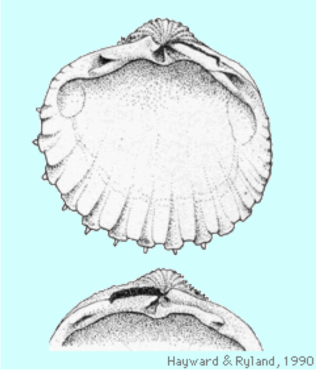
The prey-size categories reported in areas utilised by common scoter concur with previous studies that have reported that common scoter consumed prey of 5 – 40 mm shell length in size (Kube 1996; Meissner & Bräger 1990; Durinck et al. 1993). If length describes the maximum dimension of a prey item this may not be the most relevant parameter with respect to ingestion capability, for example a razor shell (*Ensis* sp.) may be over 50 mm long but only 10 mm wide (MJK personal observations), and the elongate bivalve *Phaus legumen* appeared to be important across Liverpool Bay. Other species such as *Nucula* spp. may be highly abundant but have a small maximum size. They were particularly abundant on the northern shoulder of Shell Flat. Although abundant, consumption of this prey-type may be relatively unprofitable due to the additional energetic costs and dietary constraints associated with processing a high proportion of shell material (Bustnes & Erikstad 1990; Bustnes 1998; Hamilton et al. 1999; Lovvorn et al 2003). The spatial patchiness of the individual species of bivalve prey indicated that it is highly unlikely that common scoter are species-specific in terms of prey choice, hence the decision to amalgamate our consideration of prey distributions in terms of 'prey-types' seems most appropriate.

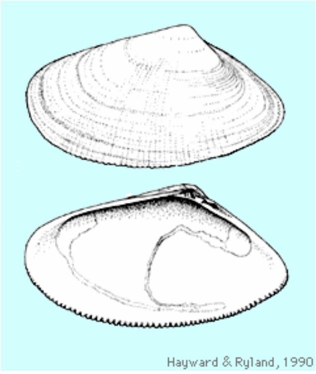
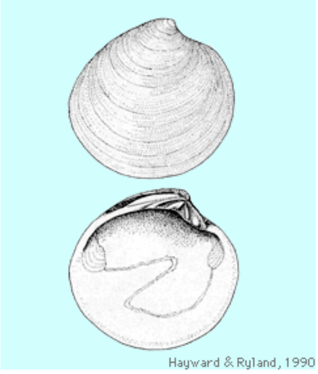
While overflight observations provide useful information on the large-scale distribution of birds at sea, it is infeasible to make detailed observations of birds in situ using such techniques. Birds aligned themselves into the wind when wind speed was force 4 or higher (see section 4). At lower wind speeds the orientation of birds on the water was influenced by sea surface currents. Woakes & Butler (1983) found that the energetic cost incurred by Tufted ducks swimming against a current increased rapidly above current speeds of 0.5 ms^{-1}. No common scoter were observed in areas of the sea with a surface current speed of > 0.6 ms^{-1} (from overflight data). Surface current speed is related to seabed shear and while birds may have to reposition more frequently in areas with high surface current speed, these areas may also have lower bivalve biomass. Common scoter were observed infrequently in Conwy Bay, yet this sheltered site might provide shelter during periods of severe weather. However observations in the present study indicated that common scoter remain at the sites of the main common scoter aggregations and did not utilise sheltered areas even in conditions of force 7/8 onshore winds (see section 4 for further details).

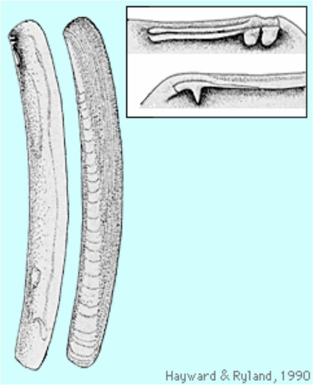
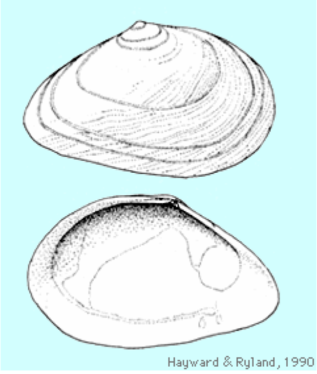
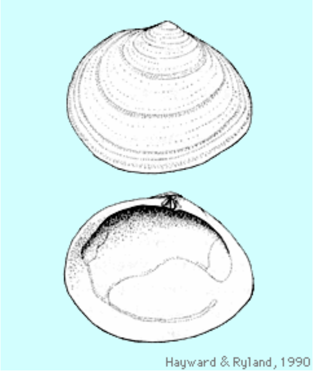
Table 3.1 Number of separate instances of different prey types recorded in the diet of common scoter (n = 199) or velvet scoter (n = 6) from 21 separate publications and shown as a percentage of all recorded instances. The category 'Other' includes chironomids, fish eggs, dragon fly larvae, insects and plants.

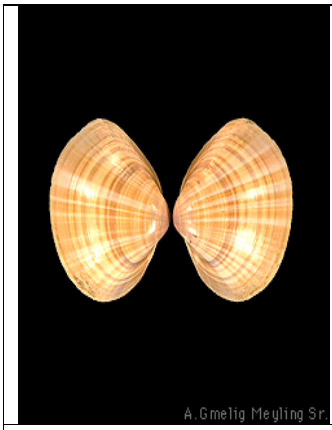
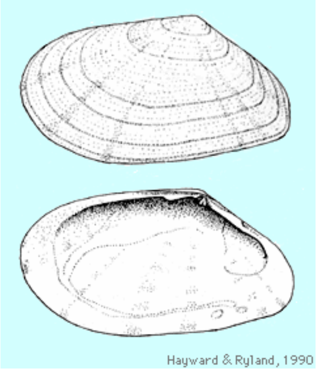
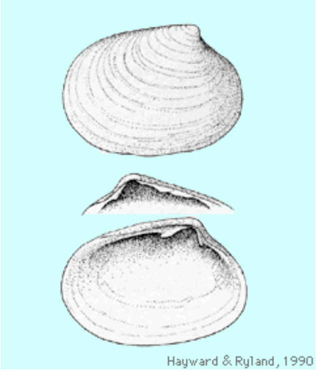
	Number	%	%
Bivalves	128	62.4	
Molluscs indet.	11	5.4	
Gastropods	14	6.8	
All molluscs			74.6
Crustaceans	21	10.2	
Other	13	6.3	
Fish	7	3.4	
Annelids	6	2.9	
Echinoderms	5	2.4	
All other prey			25.4

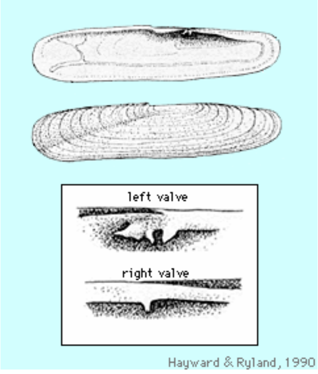
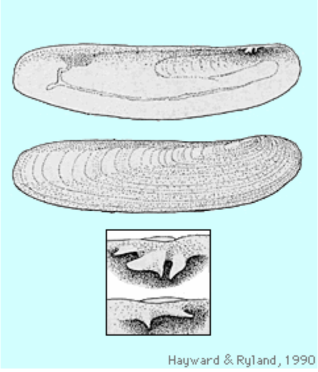
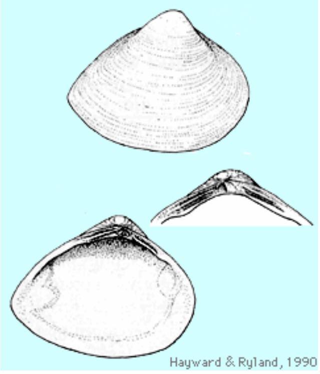
Table 3.2 Bivalve species found in the survey and some key features of their morphology and habitat.

Species	Description	Colour	Size	Habitat
Abra alba  Hayward & Ryland, 1990	Shell thin and brittle, broadly oval	White and glossy; periostracum thin	Up to 25 mm long	Burrows in groups in soft substrata; occasionally on the lower shore but most abundant in shallow, offshore waters (to about 60 m) where it may be a dominant member of the benthic infauna.
Acanthocardia tuberculata  Hayward & Ryland, 1990	Shell thick and strong, approximately rhombic in shape. Sculpture of 18-20 bold ribs and fine concentric grooves and ridges. Each rib has a central keel, bearing short pointed spines	Off-white, yellow, or light brown, often in concentric bands of different shades. Periostracum thin, yellowish	Up to 90 mm long	On muddy sand and gravel, from the lower shore into the shallow sublittoral

Chamelea gallina  A.Gmelig Meyling Sr.	Shell is solid, thick, equivalve and broadly triangular in outline. Sculpture of numerous concentric ridges	Dirty white, cream or pale yellow, occasionally polished, usually with three red-brown rays of varying width, radiating from the umbones	Up to 4.5 cm long	Inhabits bottoms of clean sand and muddy sand, from above low water-mark to 55 metres
Corbula gibba  Hayward & Ryland, 1990	Shell thick, broadly oval to subtriangular, umbones close to midline; right valve convex, enclosing and overlapping left. Sculpture of coarse concentric grooves and ridges	Dull white to cream; periostracum coarse, grey-brown, usually worn at the umbones	Up to 15 mm long	I In muddy sand and gravel, occasionally on the lower shore, most abundant offshore
Donax vittatus  Hayward & Ryland, 1990	Shell roughly wedge-shaped, umbones posterior to midline, ventral margin distinctly crenulate. Sculpture of fine concentric grooves and numerous fine radiating striations	White, yellowish, light brown, or purple, frequently lighter about the umbones. Periostracum light brown to olive-brown, glossy.	Up to 35 mm long	In sand, from the lower shore into the shallow sublittoral
Dosinia sp.  Hayward & Ryland, 1990	Shell almost circular, inequilateral. Anterior hinge line shallowly concave below lunule. Sculpture of numerous fine concentric ridges, shell surface smooth to touch	Off-white, fawn, or light brown, umbones often tinted yellow or pink. Periostracum thin	Up to 40 mm long	In sandy mud, sand, and shell-gravel, from the lower shore to at least 120 m

Ensis ensis  Hayward & Ryland, 1990	Shell thin and brittle, dorsal and ventral margins distinctly and symmetrically curved about midline of shell; anterior margin rounded	Dull white or cream, with pale reddish or purplish brown streaks and spots; periostracum glossy, light to dark olive or green	Up to 130 mm long	Burrows in fine sand on the lower shore and in the shallow sublittoral
Fabulina fabula  Hayward & Ryland, 1990	Shell is brittle, somewhat flattened, slightly inequivalve. Sculpture of concentric lines with, in the right valve only, diagonal lines superimposed upon them.	White in colour with tinges of yellow or orange	Up to 19 mm long	Clean silty sand, sand, or muddy sand, from the middle or lower regions of the intertidal zone to a depth of about 55 m.
Lutraria sp.  Hayward & Ryland, 1990	Shell elongate, somewhat quadrate, anterior hinge line sloping more steeply than posterior. Umbones anterior to midline. Sculpture of numerous fine grooves.	Dull white or yellowish, periostracum pale yellowish brown	Up to 100 mm long	In mixed soft substrata, offshore to about 50 m
Macoma balthica  Hayward & Ryland, 1990	Shell broadly oval, umbones more or less on midline. Sculpture of numerous, fine, concentric lines	Colour very variable: white, yellow, pink, or purple, in various shades, unicolorous or banded.	Up to 25 mm long.	Burrows in soft substrata, particularly in estuaries and on tidal flats, where it may be abundant.
Mactra stultorum	Shell thin and brittle, oval, umbones just	White, tinted purple about		

 A.Gmelig Meyling Sr.	anterior to midline. Sculpture of very fine concentric lines, growth stages clear. Shell margin prominent at hinge line	the umbones, with light brown rays of varying width radiating from umbones; periostracum light brown, thin	Up to 50 mm long	Burrowing in clean sand, from the lower shore into the shallow sublittoral
Moerella donacina  Hayward & Ryland, 1990	Shell is brittle, slightly inequivalve, right valve a little more convex than the left. Inequilateral, beaks in the posterior half. Oval in outline anteriorly	Background colour of dirty white or pale yellow ornamented with pink rays radiating from the beaks. Periostracum is faint, red-brown	Up to 25.4 mm long	Around the British Isles inhabits coarse sand and shell-gravel, offshore to about 45 metres but may occasionally be collected between tide-marks
Mysella bidentata  Hayward & Ryland, 1990	Shell thin and fragile, oval, the umbones are posterior to midline. Sculpture of fine, closely spaced, concentric lines; growth stages are clear	White or translucent, periostracum light brown or olive	Up to 3 mm long	From ELWS to about 100 m, in muddy sand or fine gravel, in crevices of dead oyster valves, in the burrows of the sipunculid Golfingia , or associated with the ophiuroid Acrocnida
Nucula nitidosa  Hayward & Ryland, 1990	Shell solid, equivalve; inequilateral, beaks behind the midline; triangular in outline. Fine radiating striations and fainter concentric lines	Shell white or grey with bluish growth lines; periostracum very glossy, olive or yellow-olive, often with concentric bands of light yellow	Up to 13 mm long	On silt and fine sand. Down to 100 m

Pharus legumen  Hayward & Ryland, 1990	Shell thin and brittle, elongate, about four times as long as deep; anterior and posterior margins rounded, gaping at both ends. Anterior end distinctly tapered.	White or light brown, with a glossy, light olive or yellow periostracum.	Up to 12.7 cm long	Burrowing in sand, from the lower shore into the shallow sublittoral.
Phaxas pellucidus  Hayward & Ryland, 1990	Shell thin and brittle, elongate; dorsal margin practically straight, ventral margin curved. Anterior end rounded and upturned, posterior slightly truncate	White or cream, sometimes with dark markings; periostracum glossy, light yellow-brown or olive	Up to 40 mm long	In mixed fine substrata, offshore to about 100 m.
Spisula elliptica  Hayward & Ryland, 1990	Shell thin, elongate oval, umbones close to midline. Sculpture of fine concentric lines and grooves, growth stages clear	Dull white with greenish or greyish brown periostracum	Up to 30 mm long	In mixed soft substrata, offshore to about 100 m
Spisula subtruncata  Hayward & Ryland, 1990	Shell thick and strong, subtriangular but distinctly asymmetrical; umbones close to midline, posterior end appearing slightly drawn out	Dull white to cream, periostracum greyish brown	Up to 30 mm long	Burrowing in muddy or silty sand, from the lower shore into the shallow sublittoral.

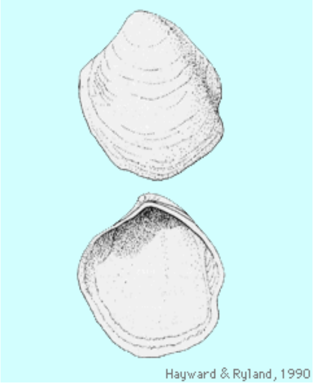
Tellymia feruginosa  Hayward & Ryland, 1990	Shell is fragile, equivalve and inequilateral, beaks in the posterior half. Outline is regularly oval	White. Periostracum is thin, often covered by a thick rust-coloured deposit	Up to 7.9 mm long	Particularly in fine muddy sand. A common commensal of Echinocardium cordatum , one of the sand-burrowing echinoderms
Thracia phaseolina  Hayward & Ryland, 1990	Shell is brittle and inequivalve. Approximately oval in outline with the dorsal posterior line straight, and the posterior margin truncate. Sculpture of smooth concentric lines and ridges	White	Up to 38 mm long	In sand, muddy sand and sandy gravel from very low in the intertidal zone to about 55 m
Thyasira flexuosa  Hayward & Ryland, 1990	Shell thin and fragile, broadly oval, tending to be irregular. Umbones on midline. Each valve marked on either side by distinct groove; lower groove causes deep indentation.	Dull white, with pale yellowish brown periostracum	Up to 18 mm long	Offshore, to the edge of the continental shelf, in muddy sand

Table 3.3 The most common species sampled off Lancashire and in the south of Liverpool Bay in August 2003. Sample size n = 81 stations Lancashire, n = 88 North Wales (two samples at each station, mean abundance of two samples shown).

Lancashire		**North Wales**	
Nucula nitidosa	1204	*Donax vittatus*	699
Pharus legumen	475	*Abra alba*	426
Abra alba	413	*Pharus legumen*	378
Spisula subtruncata	151	*Lutraria*	244
Mactra stultorum	102	*Mactra stultorum*	116
Phaxas pellucidus	87	*Fabulina fabula*	99
Ensis	55	*Echinocardium cordatum*	89
Chamelea gallina	43	*Nucula nitidosa*	86
Echinocardium cordatum	36	*Spisula subtruncata*	79
Mysella bidentata	32	*Phaxas pellucidus*	50
Corbula gibba	23	*Ensis*	47
Polinices pulchellus	20	*Mysella bidentata*	36
Lutraria	19	*Polinices pulchellus*	31
Acanthocardia echinata	18	*Chamelea gallina*	18
Thracia phaseolina	10	*Lutraria siphon*	17
Donax vittatus	10	*Dosinia*	11
Lutraria siphon	8	*Thracia phaseolina*	11
Fabulina fabula	5	*Spisula solida*	10
Philine aperta	4	*Spisula elliptica*	7
Retusa	2	*Tellimya ferruginosa*	5
Dosinia	1	*Acanthocardia echinata*	3
Mya siphon	1	*Acteon tornatilis*	3
Mya truncata	1	*Moerella donacina*	3
Thyasira flexuosa	1	*Thyasira flexuosa*	3
Acteon tornatilis	0	*Pharus legumen siphon*	2

Table 3.4 SIMPER analysis on root-transformed benthic community data for North Wales and Shell Flat. Species are ranked according to their percentage contribution to the overall similarity among samples for either area (North Wales or Lancashire).

North Wales
Average similarity: 21.81

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Abra alba	4.88	4.09	0.57	18.76	18.76
Pharus legumen	8.23	3.91	0.55	17.91	36.67
Ensis ensis	0.95	3.04	0.35	13.96	50.63
Mactra stultorum	1.35	2.79	0.44	12.80	63.43
Fabulina fabula	1.50	1.89	0.37	8.66	72.09
Donax vittatus	13.06	1.54	0.25	7.04	79.14
Phaxas pellucidus	0.64	1.23	0.28	5.64	84.77
Spisula subtruncata	0.93	1.05	0.28	4.84	89.61
Lutraria sp.	1.41	0.53	0.18	2.44	92.05

Lancashire
Average similarity: 43.37

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Nucula nitidosa	27.47	18.58	1.30	42.84	42.84
Abra alba	6.58	6.24	0.78	14.39	57.23
Pharus legumen	10.31	5.68	0.76	13.10	70.33
Phaxas pellucidus	1.89	3.23	0.60	7.45	77.78
Mactra stultorum	1.95	2.98	0.56	6.88	84.66
Spisula subtruncata	3.30	2.85	0.54	6.58	91.23

Table 3.5 Change in mean (± S.D.) AFDW g 0.1m-^{2} of bivalves and all other benthic biota for 24 monitoring stations with either low or zero observations of common scoter (within 250 m radius of station). The coefficient of variation (C.V.) for bivalves is also given.

	Aug-03	Apr-04	t	df	P
Bivalves	4.31±6.37	2.85±4.83	0.89	46	0.19
Bivalves C.V.	0.62±0.53	0.93±0.44	-2.16	46	0.017
Other benthos	2.17±2.06	0.69±0.54	3.39	46	0.0007

Table 3.6 Estimates for the Gaussian relationship for biomass with depth giving the mean ± 95% C.I. for each parameter G is the depth dependent bivalve biomass modifier, Gmin is the minimal biomass, Gmax is the maximum biomass, S is depth (m), Sm is the depth at which the maximum biomass is attained and V is the variance of the Gaussian curve.

Parameter	Estimate	Upper C.I.	Lower C.I.	F	d.f.	P
North Wales						
Gmin (Log 10)	-1.2	-1.63	-0.78	15.53	4,84	0.05
G (Log 10)	0.32	0.02	0.63			
S max.	7.88	6.24	9.52			
V	17.7	-5.21	40.6			
Lancashire						
Gmin	0.668	-2.65	3.99	6.59	4,77	0.05
G	3.05	1.41	4.7			
S max.	13.96	12.26	15.66			
V	8.03	-19.93	35.99			

Table 3.7 General Linear Model of environmental factors that best explained variation in the abundance of common scoter.

Variable	df	SS	MS	F	P
bivalve biomass	1	10.09	10.09	38.54	<0.0000000007
depth	1	6.84	6.83	26.08	0.0000003
sediment	2	5.75	2.87	10.97	0.00002
current	1	3.41	3.41	13.03	0.0003
ship disturbance	1	3.17	3.16	12.08	0.0005
error	4245	1112.37	0.26		

Table 3.8 The Generalized Additive Model for the best explanatory factors for the variation in bivalve biomass. The model was estimated with the dispersion factor for a Gaussian type distribution of data set at 35.196. The table gives the predictor variables (Log 10), the d.f. for terms and F-values for non-parametric effects.

	d.f.	non-para d.f.	non-para F	P
Mean surface current velocty	1	3.7	1.08	0.36
Shear stress	1	3.6	0.67	0.59
Distance from shore	1	3.1	2.08	0.11
Depth	1	2.8	4.07	0.01
Gravel content (%)	1	5.2	1.66	0.15
Sand content (%)	1	3.1	0.77	0.51
Mud content (%)	0	3.1	0.91	0.44
Organic content (%)	1	3.9	1.21	0.31
Median phi	1	3.6	2.64	0.04

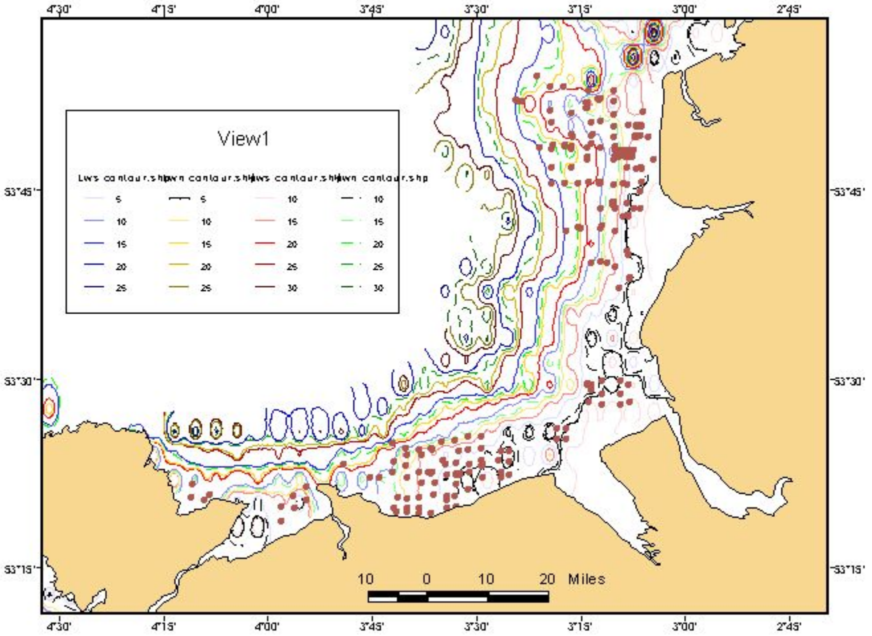


Fig. 3.1 Map indicating the position of Liverpool Bay within the Irish Sea UK, with the modelled bathymetries for spring and neap tides at high and low water at 5 m depth band intervals. Sites sampled for benthic prey species are shown as filled circles.

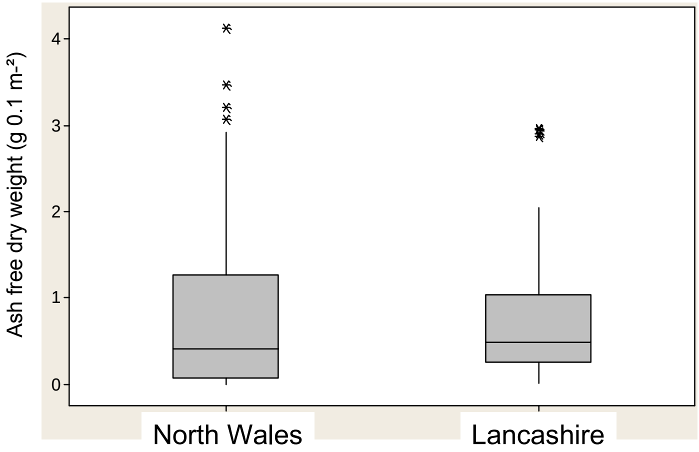


Fig. 3.2 Box and whisker plots of the mean AFDW (g 0.1 m-²) for bivalves sampled off the North Wales and Lancashire coast in August 2003 prior to the arrival of over-wintering common scoter.

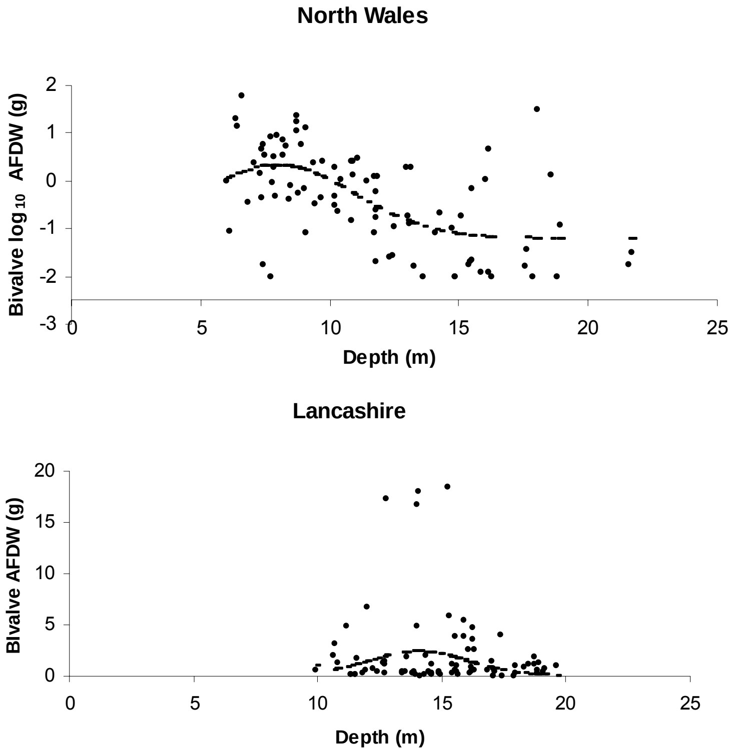


Fig. 3.3 The relationship of bivalve AFDW with depth off North Wales and Lancashire in August 2003. Trend lines are the fit of a Gaussian model (see Table).

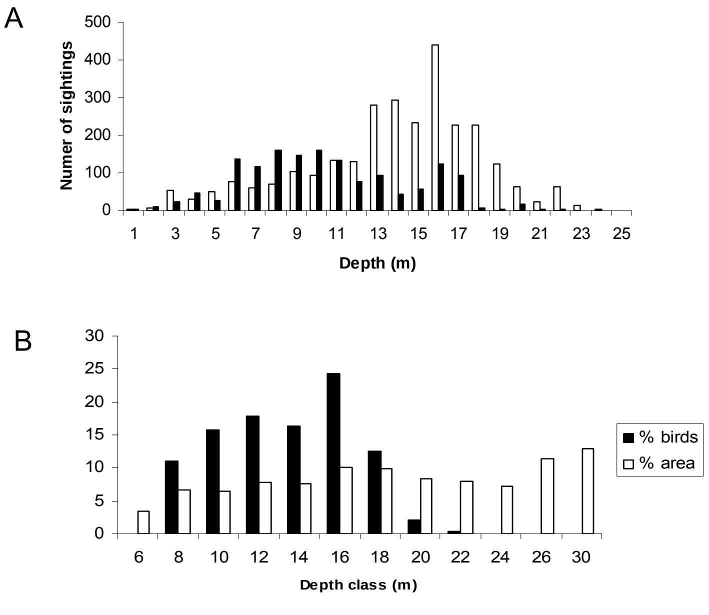


Fig. 3.4 A) The number of sightings of common scoter off North Wales (black bars) and off Lancashire (open bars) in relation to the depth of water over which they were observed. Observations derived from overflights from two over-wintering periods: 2002/2003 and 2003/2004. B) The percentage of the study area (open bars) within each mean depth category and the percentage of all common scoters observed that occurred within each of these mean depth zones.

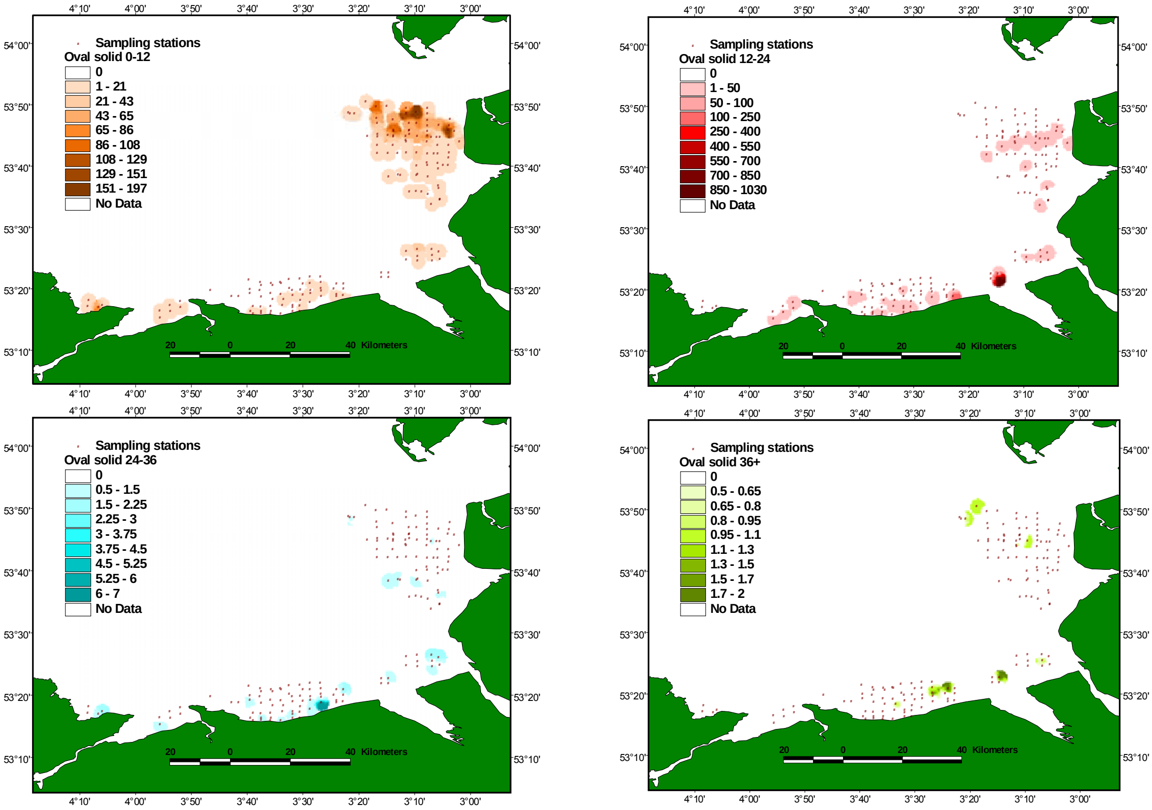


Fig. 3.5a Interpolated grids of oval solid bivalve prey divided into four length classes and expressed as numbers per 0.2 m². For each prey type the distribution of four size (shell length mm) categories are given. Data are interpolated from a total of 169 sample sites across the study area. The interpolation is constrained to within a 2 km radius of each sample site.

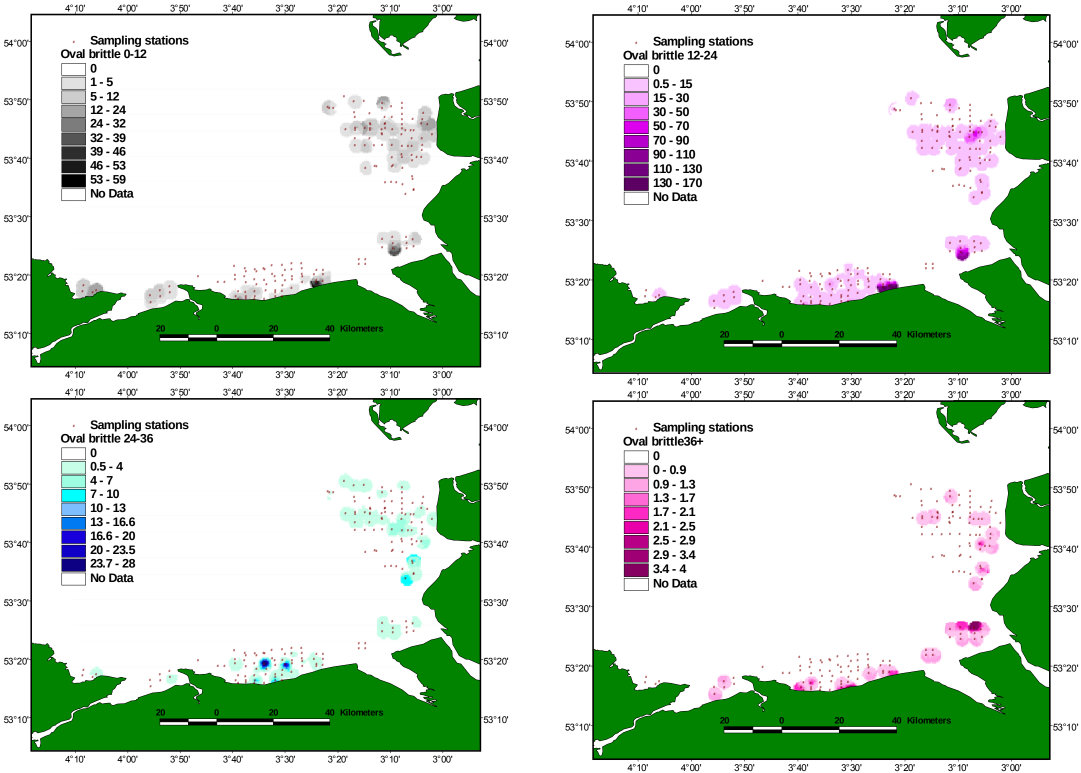


Fig. 3.5b Interpolated grids of oval brittle bivalve prey divided into four length classes and expressed as numbers per 0.2 m². For each prey type the distribution of four size (shell length mm) categories are given. Data are interpolated from a total of 169 sample sites across the study area.

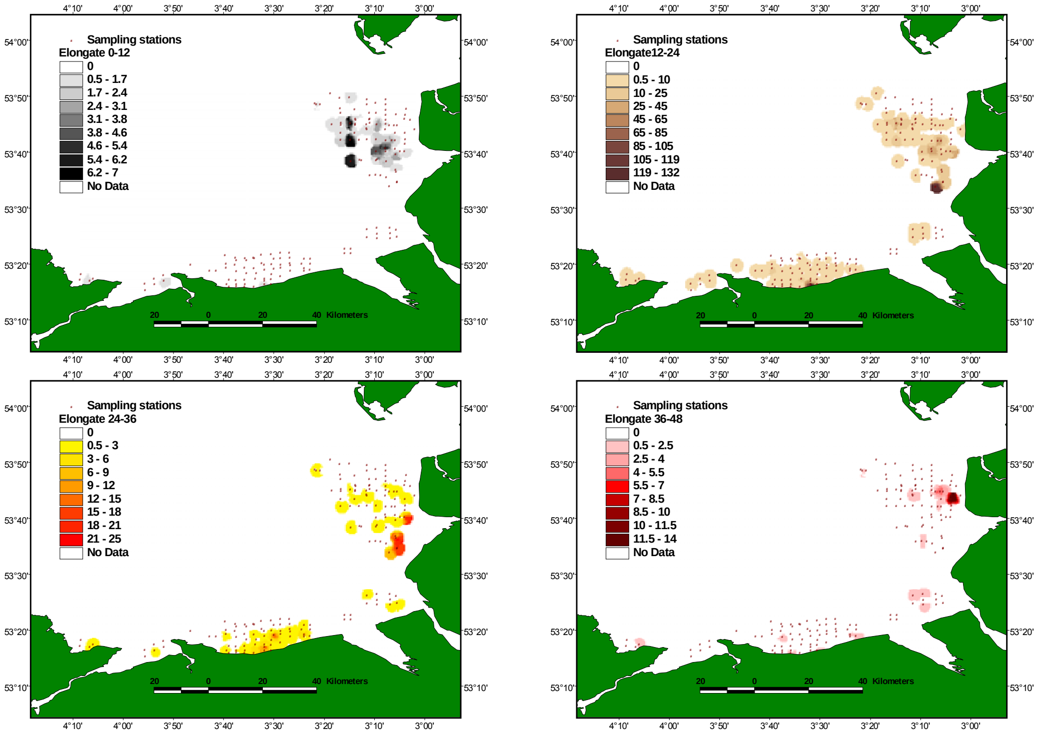


Fig. 3.5c Interpolated grids of elongate bivalve prey divided into four length classes and expressed as numbers per 0.2 m². For each prey type the distribution of four size (shell length mm) categories are given. Data are interpolated from a total of 169 sample sites across the study area.

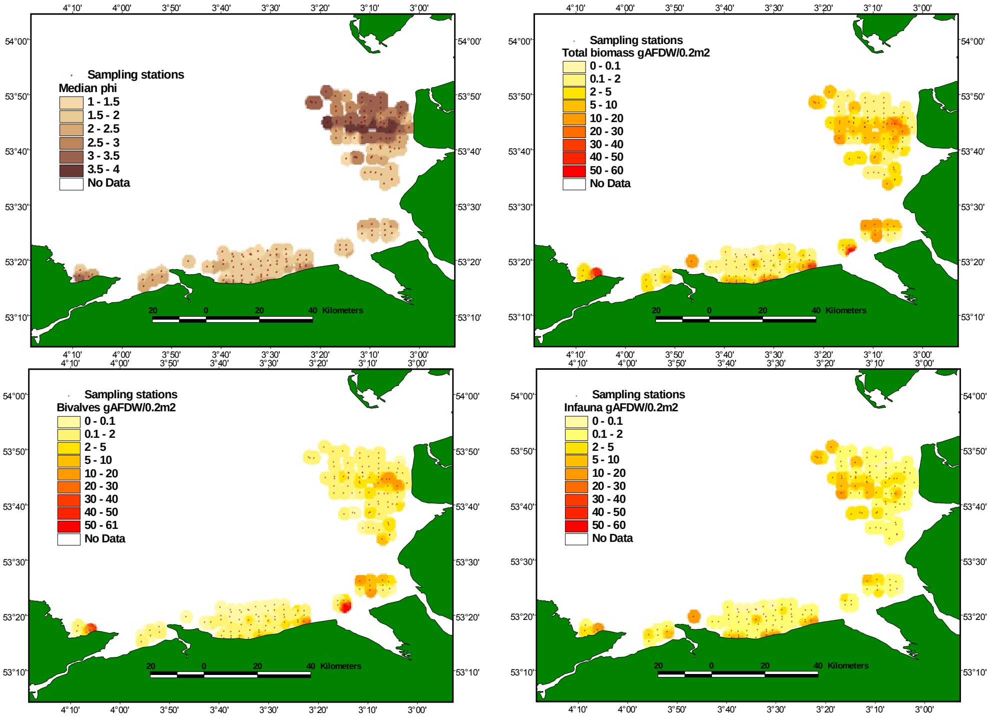


Fig. 3.6 Median phi of the sediments sampled at each sampling station (higher phi = finer sediment), the total biomass of all benthic invertebrates, the total biomass of bivalves only and the total biomass of all invertebrates excluding bivalves (AFDW g/ 0.2 m²)

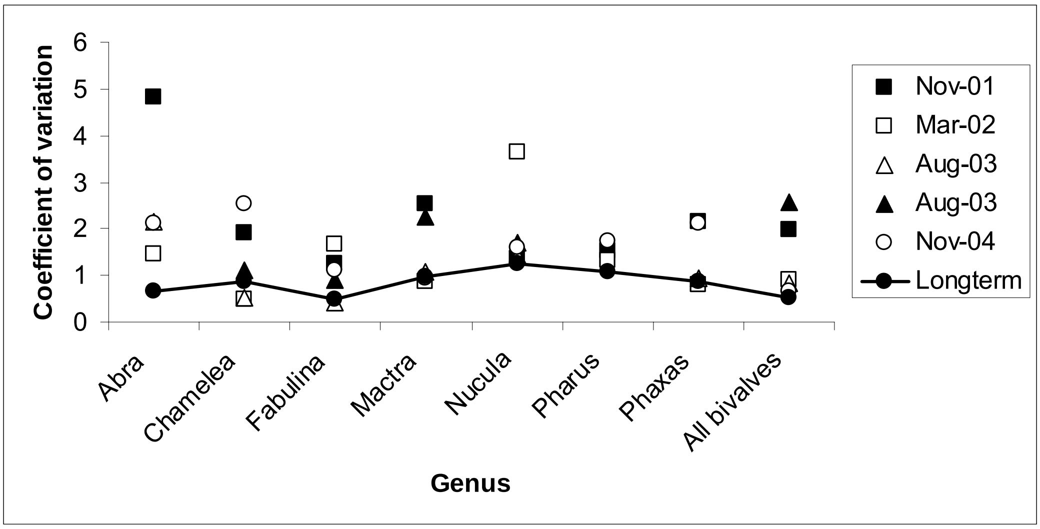


Fig. 3.7 Spatial and interannual variation in bivalve abundance for selected bivalve species and all bivalve species pooled together in Liverpool Bay 2001 -2004. In 28 out of 35 records, spatial variation was greater (i.e. C.V. was higher) than the interannual variability for the same prey species.

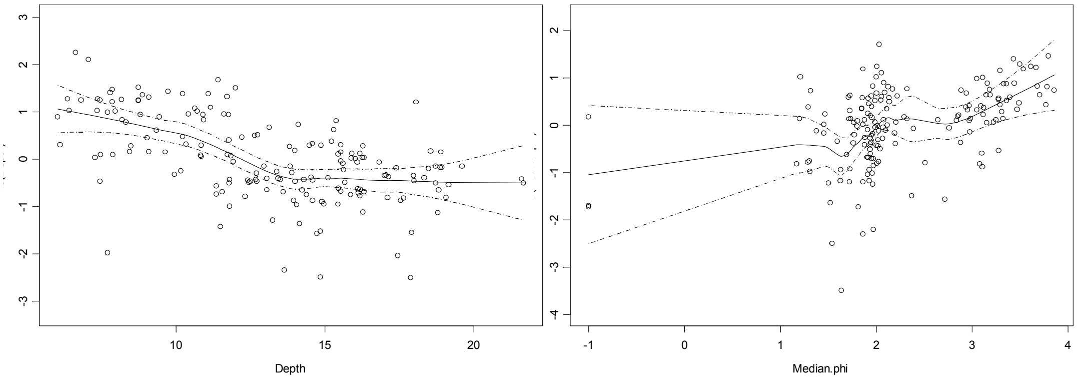


Fig. 3.8 Partial residuals for the Generalized Additive Model for bivalve biomass, showing only the residuals for the two predictors that had significant effects (A) depth (m) and (B) median phi.

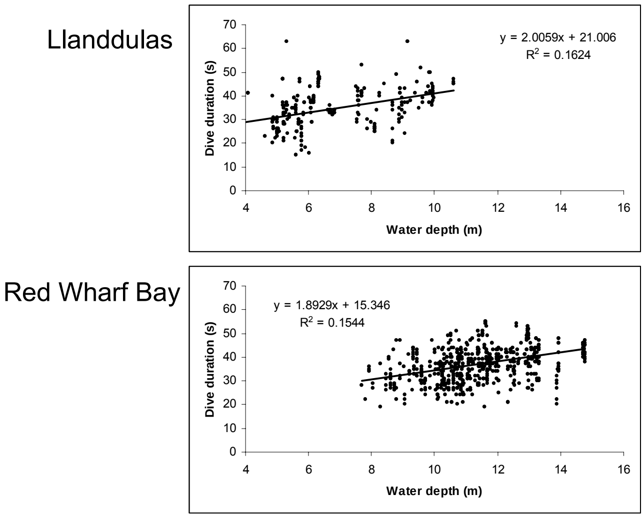


Fig. 3.9 Dive duration (s) of common scoter observed primarily from the shore off (A) Llanddulas and (B) Red Wharf Bay, both North Wales. These observations have been tidally corrected from hindcast modelling. Common scoter were only observed in Red Wharf Bay towards the end of the over-wintering season. The observations of dive time are reported in section 4.

4. Behavioural observations

This section describes the direct behavioural observations that were made to parameterise the behavioural ecology model described later and to elucidate those environmental and human factors that may influence the behaviour of common scoter. Observations were made through the winter period of 2003/2004 to quantify the sex ratio of birds and how this changed through time, to describe flush distances in response to an approaching vessel to ascertain the level of disturbance created by such activities, to quantify whether surface water currents or wind speed affected the orientation of common scoter when sitting on the water, to quantify patterns in flight movements at different times of the day or state of tide, to quantify dive duration in relation to water depth and finally to quantify any change in habitat use during periods of rough sea state.

4.1 Preliminary common scoter surveys

Preliminary land-based surveys were undertaken from 14 to 17 October 2003 and a sea-borne survey on board the RV (research vessel) Prince Madog on 18 October 2003. Suitable land-based observation points were identified and field methodologies tested. During this period observation conditions were good with light winds and calm to moderate seas. A summary of common scoter observations and localities visited during preliminary surveys is presented in Appendix 1.

4.2 Study sites

Study sites were selected initially on the basis of preliminary common scoter surveys undertaken in October. Blackpool was rejected as it was not possible to see birds in sufficient detail for the purposes of data collection. The localities visited (from west to east) comprised; Red Wharf Bay (Anglesey); Conwy Bay observing from Llanfairfechan, Penmaenmawr and Llanddudno West Shore and Great Orme; Colwyn Bay observing from Llanddudno Little Orme, Penmaen Rhôs, Llanddulas and Abergele. Of these localities only in Colwyn Bay between Penmaen Rhôs (SH881788) east to Abergele (SH943788) were large numbers of common scoter visible and close enough inshore to afford data collection opportunities. An especially good locality situated between these two points, Llanddulas (SH906786), was selected as the main survey locality. From Llanddulas it was possible to observe consistently between several hundred and up to 2000 common scoter. Observations were made from the area of the beach car park situated north of the A55 coast road.

Occasional observations during the subsequent two-week survey periods in each of December 2003, February 2004 and March 2004, were made at localities visited in October. This was done to assess for presence/absence of common scoter and to identify any additional survey sites. Of the latter, only at Red Wharf Bay were significant numbers of common scoter located close enough inshore (< 1.5 km) for observations to be undertaken, with an estimated 900-1000 birds present in February. Red Wharf Bay therefore provided an additional study site during the last two survey periods in February and March 2004.

4.3 Common scoter sex/age ratio

Aims: To assess the ratio of male to female/immature common scoter and to identify any changes in sex ratio through the wintering period.

4.3.1 Methods

Sex and age data was collected during the course of direct observations. This was undertaken during each the four survey periods (October and December 2003, February and March 2004) adding to current information regarding arrival dates and proportions of male to female/immature common scoter wintering in Liverpool Bay. Observations were made using binoculars and a telescope mounted on a tripod both from the shore and at sea. During the first two survey periods (October/December) at each locality where common scoter were encountered, at least 100 birds were assigned to one of two age/sex categories:

i) Female/1st autumn
Due to the similarity in plumage of female and juvenile (1st autumn) common scoter in the autumn and early winter (basically brown with pale cheeks) coupled with the observation distance (i.e. common

scoter often >800 m from the observer), it was not possible to distinguish between them. All such birds were thus placed in one category i.e. female/1st autumn.

ii) Adult and sub-adult (2nd winter) male
Adult males are easily identified having all black plumage except for pale undersides to flight feathers. Sub-adult males (approaching their second winter) are black with a pale belly (only visible in flight, when wing-flapping on water's surface with body raised or when roll-preening). Adult and sub-adult males were thus placed together in the second category.

As winter progresses young males (1st autumn entering their 1st winter) gradually attain an adult-like plumage with black feathers that appear from December onwards. During the February/March surveys these could not be distinguished from adult/sub-adult males, except at relatively close range (< c.600 m) in good light when the dark brown wings and brownish black rather than pure black upper parts were apparent. As observation conditions were rarely conducive for such determination, 1st winter males were placed in the 'adult and sub-adult male' category in the post December 2003 surveys.

4.3.2 Results

October
Although only a relatively small number (N=102) of common scoter were sexed/aged in October it was very apparent from *ad hoc* observations of c. 3,500 - 5,000 common scoter (spread over several kilometres from 2 km west of Llanddulas east to Rhyl) that most were adult males. The ratio of 8.3 adult/sub-adult males : 1 female/1st autumn derived from the sample is therefore considered a good estimate.

December
In December a total of 1,744 birds were sexed/aged at four different sites. Sample sizes in excess of 100 birds (the minimum desired sample size) were achieved for all sites except Penmaenmawr (Conwy Bay). Here the sample size (N = 18) was low as these were the only common scoter at the time of observation close enough to be sexed/aged. However, this small sample still reflects the overall situation recorded in December with a sex/age ratio of about one male to one female/1st autumn (1.1:1.0).

February
In February a total of 519 birds were sexed and a sex ratio of 3.3 males:1 female estimated at Llanddulas. Sexing was limited to those birds closer inshore (< c.800 m) due to prevailing poor observation conditions during much of the survey period. This may not have reflected the true sex ratio, the overall impression being that there were probably c.5 males : 1 female present. At Red Wharf Bay an estimated 900-1000 birds where present in February. The vast majority were more than 3 km offshore but several small flocks totalling 80-90 birds came within 1 km of the shore. Those that were sexed/aged (N = 81) resulted in a ratio of 4.1 males to 1 female. Llanfairfechan and Penmaenmawr were each visited once but common scoter were too far offshore to be sexed.

March
In March a total of 163 birds were sexed and a ratio of 5.0 males:1 female estimated at Llanddulas. At Red Wharf Bay 135 birds were sexed and a ratio of 3.2 males:1 female estimated. Llanfairfechan and Penmaenmawr were also visited twice and once respectively but the few common scoter visible were too far offshore to be sexed.

May
From 5-7 May inclusive, seabird surveys onboard the RV Aora were undertaken in the vicinity of the North Hoyle windfarm (situated off the coast north of Rhyl/Abergele) west to almost the Great Orme. Although not within the core common scoter wintering areas, transects passed within c.5 km of where several thousand birds were congregated during the winter months off Llanddulas. Despite good weather and intensive observations, no scoter of any species were observed.

Table 4.1 Sex/age ratio of common scoter observed off the north coast of Wales, winter 2003-2004

Site	Date	Adult & sub-adult males	Adult females + 1st autumn males & females	Ratio
October				
[1]><Llanddulas and Rhyl	18/10/03	91	11	8.27 : 1
December				
Llanddulas	11/12/03	269	374	1 : 1.39
[1]Shell Flat	12/12/03	32	38	1 : 1.18
[1]Rhyl	13/12/03	147	60	2.45 : 1
Penmaenmawr (Conwy Bay)	14/12/03	8	10	1 : 1.25
Llanddulas	14/12/03	88	117	1 : 1.33
[1]Shell Flat	15/12/03	371	230	1.61 : 1
All December observations		915	829	**1.10 : 1**
		All males	**Adult + 1st winter females**	
February				
Llanddulas	20/2/04	178	45	3.96:1
Llanddulas	21/2/04	79	26	3.04:1
Llanddulas	28/2/04	142	49	2.90:1
Red Wharf Bay	25/2/04	65	16	4.06:1
All February observations		464	120	**3.87:1**
March				
Llanddulas	17/3/04	136	27	5.04:1
Red Wharf Bay	8-9/3/04	103	32	3.22:1
All March Observations		239	59	**4.05:1**

[1]observations taken offshore aboard the RV Prince Madog

4.3.3 Discussion

In marked contrast to the adult/sub-adult male : female/1st autumn ratio determined from observations undertaken on 18 October estimated to be 8.3 : 1, the mid-December data reveals a much more balanced ratio, overall approaching 1:1.

This concurs with the expected pattern of arrivals of common scoter in the western seaboard (Cramp & Simmons 1977) where males arrive on the wintering grounds earlier in the autumn with the proportion of females/juveniles rising steadily until passage ends in December. In Britain peak wintering numbers are usually present from December to February (Lack 1986).

In October and December common scoter were placed in one of two categories i.e. females plus 1st autumn males and females; adult and sub-adult males (see Methods above). From December onwards first winter males become mottled with black but do not assume adult plumage until their second autumn (Cramp & Simmons 1977). However, no 1st winter males could be distinguished during the mid-December survey and presumably most of these young males still retained plumage resembling that of females. In contrast, by mid-February first winter males were apparent with blackish-brown upperparts, brown flight feathers and dull yellowish culmen, contrasting with the jet black plumage and bright yellow culmen of adult males.

Unfortunately however, these 1st winter males were difficult to distinguish due to their similarity to adults when viewed at distance, confounded by often overcast conditions. During the February and March surveys, 1st winter males were thus placed with adult and sub-adult males. This therefore prohibits direct comparisons with the earlier surveys but non-the-less it appeared that the proportion of male birds rose later in the winter. It may be that the shift to a higher proportion of males can be simply attributed to the placement of 1st winter males in the 'male' category in the latter two months as opposed prior to this being placed with adult female and 1st autumn females. However, this would imply a disproportionately high number of immature males in the population in an order of magnitude 3-4 times greater than the combined number of adult and immature females. It may be that some movement of birds occurred in the interim period (between the December and February surveys). A higher proportion of female and immature common scoter are present in more southerly wintering areas (Cramp & Simmons 1977) and some females and/or 1st autumn birds present in December may have continued on to more southerly wintering areas after a stop-over in Liverpool Bay. All surveys in February and March were land-based and it is also possible that the majority of certain cohorts e.g. adult females and/or immatures winter further out to sea and could not be observed from land. However, comparing the data collected in December from land (1 male:1.4 female/1st autumn) and sea (1.6 male:1 female/1st autumn) this does not appear to be the case but given the small data set collected at sea over only three days, it is not possible to draw any firm conclusions.

Return common scoter movements occur in late February through to April in the Atlantic and North Sea (Cramp & Simmons 1977). It was hoped that further sex ratio data gathered in April might identify any disparity in return movements between sexes but unfortunately due to inclement weather no data was collected (P. Robinson pers. comm.). Offshore observations in early May yielded no common scoter sightings. By this time most would have migrated to northerly breeding grounds and although surveys in May were not within core wintering areas it was still surprising given the intensive survey effort, that non were seen. This is even more so given that some non-breeding common scoter are reported to summer in Liverpool Bay (E.I.S. Rees pers. comm..).

Environmental impact assessments should take into account the staggered dates of arrivals of M.nigra on their wintering grounds and the higher proportion of females and immatures present in southerly wintering areas. In considerations of the locality of offshore windfarms, regard should be given to the male-biased sex ratio within common scoter populations, numbers of females being lower than males. On the breeding grounds this has been shown to be in the order of 1.2-2.0 males: 1 female (Bengtson 1972). Adult female annual survival is therefore an especially important population parameter in this species (Fox et al. 2003). Disturbance or loss of habitat in southern wintering localities could potentially have a disproportionately high adverse knock-on effect upon the population as a whole. Population declines would be expected if females experienced increased mortality and/or suffered a loss of fitness and hence fecundity due to a loss or decline in the quality of their wintering habitat.

4.4 Flush Distance

Aim: To record the flush distances of common scoter at the approach of the research vessel.

During the construction phase of an offshore wind farm there will inevitably be considerable disturbance from boat traffic travelling to and from the site and in the vicinity of the construction area itself. After the construction phase, as well as the presence of the wind turbines themselves, boats carrying crews to undertake routine maintenance will be an ongoing source of disturbance to common scoter. Potentially other species of seabirds such as other wintering ducks (Anseridae), wintering divers (Gaviidae), auks (Alcidae) and terns (*Sterna* spp.) may also be adversely affected.

There is little empirical data regarding the effects of disturbance from boats on common scoter but it is known that they are intolerant of approaching vessels and are easily flushed from their feeding/loafing areas. Therefore an attempt was made to generate some such data whilst on board the Prince Madog research vessel in December 2003. Some researchers (e.g. P. Cranswick pers. comm. 2003 and during provisional fieldwork during this survey) have highlighted the great problem of estimating distances from an observer to birds out at sea several hundreds metres away and as distances increase. Therefore the ship's (RV Prince Madog) radar was used in combination with field observations to assess flush distances of common scoter flocks at the approach of the research vessel.

4.4.1 Methods

Two observers (using binoculars) positioned on the ship's bridge located and counted the number of common scoter in a flock as they rose from the sea surface at the approach of the research vessel. They alerted a third observer manning the ship's radar to the presence of flushed birds. From the radar, knowing the position of the ship and the point at which the birds rose, a 'flush distance' and bearing was determined. The ship travelled on a steady course at a speed of about 10 knots whilst observations were made. Vessels undertaking maintenance within a windfarm array are likely to traverse at lower speeds for safety, but these vessels are unlikely to cause disturbance to birds that avoid the footprint of a windfarm due to its presence. Vessels en-route from port to a windfarm array are likely to travel at cruising speeds to conserve fuel, which for a vessel of the size of Prince Madog is likely to be in the region of 10 knots.

4.4.2 Results

Simple linear regression analysis was performed on the observations of common scoter flock size and flush distance (N=59). There was no significant relationship between flock size and flush distance ($P = 0.508$ $r^2 = 0.008$ $df = 57$). However, examination of the raw data revealed the presence of a critical flushing distance of c.1000 m, at which flock size increased quite dramatically.

Thus the data set was divided into two samples:

i) those flocks for which flush distances were < 1000 m (N=23)
ii) those flocks for which flush distances were >< 1000 m to 1999 m (N=26)

The remaining flush distances (N = 10) > 2000 m were disregarded for the purpose of this analysis as at this distance it became difficult to be sure if birds were being put up by the approaching research vessel or responding perhaps to another stimulus, although the former appeared to be the case.

A Mann-Whitney Test performed on these samples revealed a highly significant difference between the flock sizes at flush distances of less than 1000 m, as opposed to flock sizes at flush distance between 1000 m to 1999 m. At around a flush distance of c.1000 m, flock size increased quite dramatically. $U= 38.5$ $P = <0.001$

4.4.3 Discussion

A number of potential biases should be highlighted in the methodology. In some cases small flocks flushed by the boat in areas of higher concentrations of birds went unrecorded as the observers could not record every flock in such a short space of time. Some smaller flocks (< c.10 birds) were also not apparent on the radar screen as the radar was not sensitive enough to pick them up. At times background interference from wave crests appearing on the radar screen made it impossible to locate flocks - flush distances can only be recorded using this technique in calm weather. The closer birds were to the boat (< c. 500 m) the more difficult it was to get a fix on the rising birds in part because of the wave interference but also as there were usually fewer individuals. Therefore, in combination with the radar, some flushing distance estimates of closer birds were made to the nearest 100 m.

Whilst there was no significant relationship between the flush distance and flock size of the data set as a whole, it was very apparent that the vast majority of larger common scoter flocks took flight at the approach of the research vessel at a distance of greater than c.1 km. Smaller flocks (< c.15 individuals) were less inclined to take flight allowing a closer approach but birds showed signs of alarm with neck up-stretched in an alert posture, before flying away. It was also apparent that there was a 'wave effect' - as birds were flushed and flew, in response ones a little further away would rise, then those behind these would rise and so on. Thus some birds over 2 km from the boat rose from the water's surface in response to those flushed much closer to the research vessel. Other than broadly stating that common scoter wintering in Liverpool Bay are extremely wary of shipping, as noted elsewhere within their European wintering range, it is difficult to make other inferences from this data.

Presumably flush distances vary dependent upon factors such as the prevailing weather conditions, the speed of approach of a vessel, the angle of approach, the size (and even colour) of the vessel, human activity visible on the deck, and the fitness of the birds themselves. It may also be that along regularly used shipping lanes birds might become habituated to the presence of boats. This was beyond the scope of the current project.

The effect of human disturbance is often measured in terms of behavioural changes in response to human presence but from a conservation perspective such disturbance is important only if it affects survival or fecundity and hence a population decline (Gill *et al.* 2001). To demonstrate any such effect on common scoter populations through disturbance on their wintering grounds would be virtually impossible, catching and tagging individuals would be a huge task in itself. However, common scoter as demonstrated, are extremely wary and it has been suggested that species showing the greatest avoidance require the greatest amount of protection (Klein *et al*. 1995). This though may not be true for species where the costs of moving to an alternative site are likely to be small (Gill *et al.* 2001). Wigeon *Anas penelope*, for example show a strong human avoidance (Tuite *et al.* 1984) but for this mainly herbivorous species often grazing on short sward with many nearby alternative feeding sites, costs are probably low. One could argue that this is the case for common scoter as upon disturbance if there are sufficient areas of undisturbed sea to which they could fly and settle presuming that the birds have knowledge that suitable alternative areas exist. On the other hand fitness costs may be high if there are few or no other nearby suitable feeding areas to which they can go.

4.5 Dive duration

Aims: To identify any relationship between dive duration and water depth

4.5.1 Methods

Common scoter dive duration time (in seconds), time of day and location of all field observation points were recorded. Common scoter dive individually, or more often as a group when in a small flock. When in a flock they have a strong tendency to dive almost simultaneously, resurfacing together or staggered over a period of a few seconds (pers. obs..). When staggered, an estimated time ± two seconds was assigned to each individual.

Observations, were made using a telescope mounted on a tripod. The distance of birds offshore was estimated to the nearest 50 m, using known reference points i.e. surface marker buoys, to assist in estimate accuracy. Water depth when on board the RV Prince Madog was recorded using the ship's sonar.

For each land-based observation a water depth estimate will be generated using the tidal model being developed at the Centre for Applied Marine Science, Bangor. The data will subsequently be used in to identify if there is any relationship between dive duration and water depth.

4.5.2 Results

Dive durations and water depths recorded in October and December whilst on board the RV Prince Madog. Other December data from land-based observations (currently lacking water depths) are presented on an Excel spreadsheet. A preliminary analysis of the relationship between dive duration and tidal elevation indicates that common scoter dive time increases with tidal height (i.e. water depth). See also analyses in sections 2 and 3.

4.5.3 Discussion

In total 1103 individual dive times were recorded in the four survey periods as follows: October - 48; December - 111; February - 142; March – 802. Data collected to date provide a broad indication of the dive durations (time spent submerged diving to seabed, foraging for food and resurfacing) of common scoter. It had therefore been proposed to correlate dive durations with water depth but this has proved difficult for a number of reasons. Primarily few common scoter have actually been observed feeding. It may be that feeding activity is mostly nocturnal but this would not appear to be the case from observations of common scoter in other parts of their European wintering ranges [M Leopold pers. comm.]. It may be that the majority of feeding common scoter cannot be seen from land. However, few birds were observed further out to sea from the research vessel feeding perhaps owing to their timid nature, they ceased foraging at the approach of the boat and then did not resume until they were beyond observation range. It was hoped that ship borne observations (using the onboard sonar to calculate the water depth in the vicinity of feeding birds) would enable the gathering of large quantities of such data. However, due to the lack of feeding birds, whether through the wariness of the birds (see Flush Distances, above) or not, and severe constraints of time onboard the research vessel confounded by inclement weather, little data could be gathered. Land-based observations from Llanddulas beach car park yielded little data despite 7 man-days spent undertaking observations, although other data in addition to dive durations, were also being collected. Later surveys could be geared to concentrating on collecting more dive duration data if deemed pertinent.

Apart from in exceptionally calm weather it was difficult to observe common scoter on the water's surface due to their distance offshore (most 800 m distant, stretching well out to sea) and intermittently being obscured by waves. Thus even when diving birds were located, some dive observations had to be abandoned as birds could not be seen at the time of resurfacing. Biases might also be a problem e.g. inevitably it was only the closest birds that could be seen properly to record dive times. In some cases short dives might represent an aborted dive or a quick find of a good prey item/s. Attempts to correlate dive duration with water depth might be confounded by the fact that in shallow water, birds might spend more time feeding on the sea bed as it takes less time to reach it, thus dive times might not necessarily reflect water depth. More data is needed to elucidate this.

An attempt to look at feeding intensity in relation to tide was going to be made but has proved impossible to pursue due to a combination of factors including: birds being very distant and often obscured by waves; the common scoter flock being observed (off Llanddulas) is dispersed over a distance of several kilometres; and most importantly, very few birds could be seen diving.

Table 4.2 Mean (± 95% confidence intervals) dive duration for each observation locality by sample month (December 2003, February and March 2004). Below is an analysis of variance table showing the significant interaction between location and season. This variation may be attributed to tidal height on each observation date.

Location	Month	Mean	Lower 95% CI	Upper 95% CI
Llanddulas	December	36.1	33.75	38.4
	February	33.2	31.7	34.7
	March	35.2	33.7	36.6
Red Wharf Bay	February	45.7	44.5	46.9
	March	36.34	35.8	36.8

Factor	df	ss	F	P
Season	1	37.0	0.68	0.40
Location	1	1926.9	35.77	0.0001
Season * Location	1	3032.5	56.30	0.0001
Residuals	1018	54830.2	53.86	

4.6 Orientation on water

Aims: To identify relationships of orientation of common scoter on the water's surface with wind, tide and current.

Common scoter feed by day drifting along with tide, wind or current, flying back to regain their original station (Cramp & Simmons 1977). Reattainment or maintenance of position can be achieved by swimming against the prevailing breeze and/or current when wind speed and current velocity are low. Orientation and flight direction observations were thus undertaken to examine relationships with wind, tide and current.

The more-or-less east-west running coastline at Llanddulas provided a good locality to undertake observations. Here, on a rising tide water floods from the west and the current flows eastwards, whilst during a receding tide the current direction reverses and flows westwards.

4.6.1 Methods

During land-based observations from Llanddulas, each hour or half hour, a sample of 100 common scoter sitting on the water were assigned one of four orientations (north, south, east or west) dependent upon which direction they were facing. If the required number of birds was not visible in the initial field of view of the telescope (looking out perpendicular to the coastline), the sea was scanned east or west (dependent upon position of the sun and location of birds) until the required number was tallied. Wind direction (N,NE,E,SE etc.) and windspeed (Beaufort Scale) were recorded at the end of each survey.

4.6.2 Results

A total of 45 orientation counts were made. The field data and results of Rayleigh's test for circular uniformity analyses (Zar 1996).. Observations undertaken on a given day in similar weather conditions during either a rising (east-flowing current) or ebbing (west-flowing current) are pooled in the analysis, also all are tested separately. Almost all orientations were not uniformly distributed i.e. there was a significant direction in which the majority of birds were facing ($P < 0.001$ in all non-uniform cases) explained by most birds facing into or at 45^o to the prevailing wind.

At wind speeds greater than force 1 (>5 km/h), orientation of common scoter was clearly linked to wind direction, most birds facing into the prevailing wind irrespective of the state of the tide e.g. 10-11/12/03 data. During the first 10 of the 15 survey periods (windspeeds force 3-5) between 67% to 100% of birds were facing either west or north (mean = 81.9, SE = 3.32, SD = 10.51) during prevailing north-westerly winds. During the five remaining periods, with a shift to northerly winds and on a receding tide (i.e. current flow east to west) most birds (48,63,75,89 and 92%) were recorded facing east (mean = 73.4, SE = 8.20, SD = 18.34) with 32,14,26,8 and 10% (mean = 18.0, SE = 4.69, SD = 10.49) facing north. In the latter five periods the current may have also influenced orientation (but also see biases in Discussion, below).

As wind speeds increased there was a tendency towards a higher proportion of birds to face into the wind i.e. greater non-uniform distribution, hence a higher Z-value. The mean Z-value plotted against wind speed displays this trend, although non-significant $P = 0.175$ $r^2 = 0.510$ df = 3 (force 1 mean Z = 25.266; force 2 mean Z = 56.498; force 3 mean Z = 40.906; force 4 = 41.885; force 5 mean Z = 74.561). Care should be taken when interpreting this data as it does not take into account the confounding effects of current direction/speed.

At low wind speeds (force 0-1, 0-5 km/h) there was still a predominant direction in which birds faced, however, orientation patterns were not linked to wind direction and appears explained by the current direction. On a rising tide when the current flow is from west to east, birds face westwards i.e. into the current. On a receding tide when the current flow is reversed, birds face eastwards.

For only one group of three pooled observations on 21 February was there no significant difference in orientation ($Z = 0.328$, $P = >0.5$). This coincided with a period of more-or-less slack water either side of high tide with a light (force 2) easterly breeze. At this time common scoter were milling around on the water's surface generally loafing but with many displaying.

Likewise, for observations tested separately almost all were not uniformly distributed ($P = <0.001$). The five exceptions and explanations for possible non-significance are:

i) one on 17 December ($Z = 2.740$, $P = >0.05$); this simply did not conform to the general pattern. During a light (force 1) southerly, with a westerly current the majority of birds were recorded facing east (50%) with fewer (35%) facing west. The pattern at periods of such low wind speeds was for the majority to face into the current.

ii) three on 18 December; the first ($Z =1.588$ $P = >0.20$) coincided with low tide (slack water), with the subsequent observations, although non significant ($Z=2.900$ $P = >0.05$, $Z=2.260$ $P = >0.10$) still conforming to the general pattern during periods of low wind speed with the majority facing into the current. Interestingly, as presumably the current speed increased later in the tidal cycle the proportion of birds facing into the current also increased.

iii) one on 21 February – see explanation above for pooled analysis on this date.

4.6.3 Discussion

It is apparent from the data and general field observations that common scoter, unsurprisingly, like many bird species, orientate themselves into the direction of the prevailing wind. There was also a tendency for a greater proportion of birds to face into the wind as wind speeds increased. In periods of low wind speeds (< 5 km/h) common scoter were often observed engaged in display (male-male aggressive chases, water spraying etc.), some males pursuing females, with many birds loafing and a few birds diving. However, at these times there still appeared a distinct preference to facing in a particular direction, either east or west. Looking at data gathered in such calm periods orientation can be explained by current direction. On a receding tide when the current flows from east to west the birds face east i.e. into the current. On a rising tide when the current flow is reversed the common scoter accordingly re-orientate, rotating 180^o. At wind speeds of force 2 (6 to 12 km/h) there were indications that this trend was followed but more data would be required to draw any firm conclusions.

Likewise, more data from periods of higher wind speeds would have been desirable. However, during the last two field periods priority was given to gathering dive duration data. It should be borne in mind that observations become increasingly difficult in progressively rougher weather as wave crests frequently hide birds, thus an elevated observation point, as at the west end of Llanddulas Beach car park, is essential. Also, whilst common scoter could be seen to be facing left (west) or right (east), it was difficult to say if they were facing 'in' (south) as opposed to 'out' (north) as birds were usually very distant. This was a potential source of bias and although care was taken not to ignore such birds it was difficult at times to be sure of their true orientation. Wind was recorded as one of eight directions i.e. north, north east, east, south east etc., but because of observation difficulties it was only possible to afford one of four directions i.e. north, south, east or west, to common scoter orientation, thus making data interpretation more problematic.

Overall the observations suggest that higher wind speeds outweigh the effect of the current (regardless of its direction) and this is the force which governs common scoter orientation. In periods of calm weather however, common scoter orientate themselves towards and presumably swim against the current in order to maintain their position over foraging areas.

4.7 Flight direction

Aims: To examine the influence of wind and current upon common scoter flight direction.

Flight direction observations were undertaken from Llanddulas to look at how flight behaviour was influenced by wind strength and direction, and tidal state hence the direction of the current flow (see also 5.0 Orientation on water).

4.7.1 Methods

From a fixed observation point with telescope mounted on a tripod at a fixed angle looking out perpendicular to the shoreline, for 10 minutes each hour or half hour, the direction of flight of all common scoter flying through the field of view was recorded. A dictaphone was used so that observation was continuous throughout the duration of each survey, thus at no time was it necessary to stop viewing (and potentially miss birds) in order to write down observations.

All flying individuals were counted regardless of the flight distance i.e. a short rise and ditch consisting of tens of metres, or a flight passing from one side of the field of view to the other. The flight direction was recorded as north, south, east or west. Circling birds landing in approximately the same position from which they rose were recorded as 'circling'. Wind direction (N,NE,E,SE etc.) and windspeed (Beaufort Scale) were recorded at the end of each count.

4.7.2 Results

The proportion of common scoter flying into or within 45° of the prevailing wind increased with increasing windspeed ($P = 0.012$ $r^2 = 0.828$ $df = 4$ (force 1 mean = 27%, force 2 = 65%, force 3 =

71%, force 4 = 63%, force 5 = 91%, force 6 = 100%)). On days with a fairly constant moderate wind there appeared to be a discernable change in flight activity with the change in current direction. e.g. 11 December. On this date a day-long synchronised flight count was undertaken from two points; the west end of Llanddulas beach car park and 3 km to the east. Wind was a fairly constant westerly force 4 (veering NW at 14:00), with a lull at 11:30 to force 2. Due to boat disturbance (cross-sea ferry) during the 13:30 count when many common scoter were flushed, and the midday count during a period of slack water (high tide 12:08 at Llandudno, source: UK Hydrographic Office), these data are excluded from the analysis. With wind and current acting together, a greater proportion of birds flew in the opposing direction; west Llanddulas: 74.2% (SE = 7.41 SD = 16.57); east Llanddulas: 75.2% (SE = 8.22 SD = 18.39) in comparison with when wind and current countered each other when the proportion of birds flying into the wind reduced; west Llanddulas: 55.4% (SE = 5.45 SD = 12.18) east Llanddulas: 47% (SE = 5.51 SD = 12.32).

4.7.3 Discussion

Wind direction and strength would appear to be the driving force behind flight patterns in the dispersed common scoter flock off Llanddulas. As they are blown downwind they re-position themselves by periodically flying back. A significantly higher proportion of common scoter flew into or within 45° of the prevailing wind as windspeeds increased, presumably in order to maintain their position close to or over foraging areas.

Day-long observations also suggested that in periods of moderate windspeed, when the current flow was against the prevailing wind the proportion of birds flying against the wind was reduced in comparison to those periods when wind and current were in the same direction. Logically, a current direction opposing the prevailing wind negates to some extent the effect of the prevailing wind thus accounting for these observations.

In combination with the observations of the orientation of birds on the water, during days of exceptionally calm weather when wind speeds remained below 5 km/h, common scoter could probably mostly maintain there position by swimming rather than needing to fly, the latter presumably being more energy demanding. Unfortunately however, no direct comparison of actual numbers of birds flying at different windspeeds could be made as this would require a constant number of birds to be present during each survey. One would expect reduced activity on calmer days as it would take fewer flights to maintain position.

No regular dawn/dusk movements for common scoter are described and it is assumed that they roost in or close to daytime feeding areas (Cramp & Simmons 1977). No large scale movements of common scoter at dawn or dusk were noted during any land-based observation, however, it is possible that nocturnal movements occur. Night-time radar observations in December in the vicinity of Shell Flat from the RV Prince Madog hinted at a northerly movement after dark but it may simply have been birds being flushed and repositioning themselves behind the vessel as it made its way southward. Early morning observations before dawn when anchored off Llanddulas suggested a movement of birds southwards. Only with more intensive night-time radar surveys will any nocturnal movements be identified.

4.8 Surveys during inclement weather

Aims To determine if distribution of common scoter wintering along the north Wales coast is influenced by inclement weather

Most ecological data concerning winter ecology of common scoter, including aerial surveys conducted to determine their numbers and distribution at sea, not surprisingly stems from observations undertaken during periods of good weather. Therefore, on an *ad hoc* basis during periods of inclement weather (and incidentally when collection of higher priority data was not feasible) some additional land-based common scoter observations were undertaken. These were conducted to give an insight into whether common scoter distribution appeared influenced by adverse conditions e.g. using sheltered bays not usually used as foraging areas to seek refuge from high seas during storms.

4.8.1 Methods

During periods of inclement weather i.e. c. force 6 or above (wind speeds > 40 km/hr) localities along the north Wales coast from Red Wharf Bay east to Abergele were assessed for presence/absence of common scoter by scanning with telescope and binoculars from land-based observation points. Basic behavioural activities i.e. feeding, loafing and displaying, were noted when possible.

4.8.2 Results

Observations, undertaken on two dates, are summarised below.

14 December 2003
Weather: NW, variable force 6-7 (occasionally gusting 8); sea state very rough in areas exposed to the prevailing wind with no protective land-mass.

a) Areas where no significant numbers of common scoter observed previously in autumn/winter 2003/04 but affording some shelter from prevailing wind/high seas:
i) Red Wharf Bay - no common scoter observed.
ii) west Colwyn Bay (sheltered by the Great Orme) from Llandudno - no common scoter observed.

b) Areas usually supporting significant numbers of common scoter but affording no shelter from the prevailing wind/high seas:
i) central Conwy Bay viewed from Llanfairfechan/Penmaenmawr - c.200 common scoter 1-2 km offshore on water, occasional more distant birds observed in flight. The majority of closer common scoter were loafing with some small groups displaying. No common scoter were observed feeding. Note: due to the rough seas severely limiting visibility, Conwy Bay was also viewed from Llandudno (east side of the Bay) to increase coverage but no common scoter were observed.

ii) Llanddulas – c.2,000-3,000 common scoter, distribution appeared more-or-less the same as observed in calmer weather. As at Llanfairfechan the majority were loafing although many were engaged in intermittent display and very occasionally diving.

24 February 2004
Weather: N 6; sea state rough; intermittent heavy rain.
All sites were visited with the exception of Llandudno. Red Wharf Bay in comparison with the December survey when the north end of Red Wharf Bay was partially protected from the prevailing north westerly wind, received the full force of the northerlies.

a) Areas where no significant numbers of common scoter observed previously in autumn/winter 2003/04 but affording some shelter from prevailing wind/high seas:
i) East Conwy Bay (sheltered by the Great Orme) viewed from north Conwy – no common scoter observed.

b) Areas usually supporting significant numbers of common scoter but affording no shelter from the prevailing wind/high seas:
i) central Conwy Bay viewed from Llanfairfechan/Penmaenmawr - c.150 common scoter c.3-4 km offshore visible only in flight due to rough seas and observation distance. This was the approximate location where this flock appeared to remain throughout most of the winter.

ii) Llanddulas – c.1,000 + common scoter but difficult to estimate because of poor visibility due to rough seas and rain. Their distribution appeared the same as in periods of calmer weather.

c) Areas where no significant numbers of common scoter observed previously in winter 2003/04 and affording no shelter from prevailing wind/high seas:
i) Red Wharf Bay – c. 80 common scoter 800 m and 900 common scoter over 1.5 km, offshore.

4.8.3 Discussion

From these limited land-based observations the distribution of common scoter appeared little or unaffected during periods of inclement weather. In the consistently occupied wintering localities i.e. off Llanfairfechan/Penmaenmawr and Llanddulas/Abergele, common scoter distribution remained more-or-less unchanged. Usually unoccupied areas but which afforded some protection from inclement weather in the vicinity of these localities remained unoccupied.

In December the numbers and distribution of common scoter appeared more-or-less the same as that in periods of calmer weather experienced in mid-October and other survey periods. About half of the Llanfairfechan flock (c. 200 individuals) were closer inshore (c.1-2 km) in comparison with the previous fairly calm day when 350 were counted 3.6 km offshore from the RV Prince Madog. These 200 common scoter were presumably part of this flock and additional birds could be seen in flight c. 3-4 km offshore in the vicinity of the previous day's observations. Llanfairfechan is a locality which most years harbours large numbers of common scoter (c.1000+) but numbers in the winter of 2003-2004 appeared down with the maximum count (350) made from the research vessel. Counts were not possible from shore owing to the great distance of the birds offshore, the results of aerial surveys may yield more precise information. The main flocks visible from land off the north Wales coast in winter 2003-2004 were to the east in Colwyn Bay spread from Penmaen Rhôs (just west of Llanddulas) to Abergele. Here the distribution appeared the same as in calmer conditions but with the majority of the closest birds perhaps 200 to 500 m further offshore.

In February the distribution of common scoter off Llanfairfechan (c.150 observed c.3-4 km offshore) and Llanddulas/Abergele was the same as usually encountered in calmer conditions. Very few common scoter were seen in Red Wharf Bay during the early winter (October/December survey periods). The only observations were of 28 during one visit in October 2003. The single December visit was made during very rough seas and it is possible that distant common scoter were overlooked. In February an estimated 900-1000 common scoter were present. There is apparently movement of common scoter between Red Wharf Bay and Conwy and Colwyn Bays and in the past Red Wharf Bay has harboured large numbers e.g. a flock of 1,800 present in December 1976 and 992 in December 1990 (Lovegrove *et al.* 1994). Common scoter often appear in this Bay from December onwards (D. Brown pers. comm.) and it appears that there may be some regular seasonal movement, presumably common scoter frequenting the area dependent upon food availability. Studies have shown that prey depletion influences Common eider *Somateria mollisima* distribution over the winter, patch use being correlated with food availability (Guillemette & Himmelman 1996), and that they locally track annual variation in food abundance, primarily related to the presence of mussels *Mytilus edulis* (Larsen & Guillemette 2000). It is reasonable to assume that common scoter exhibit similar behaviour and also adjust their feeding areas through the wintering period according to prey abundance and availability.

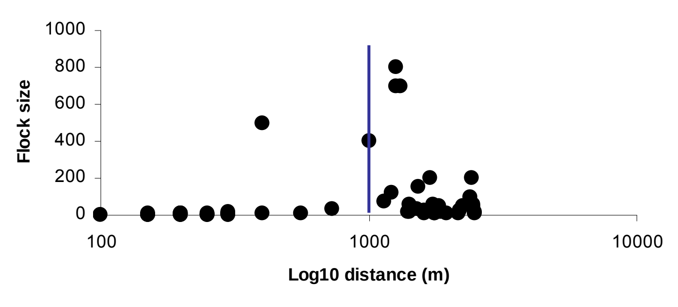
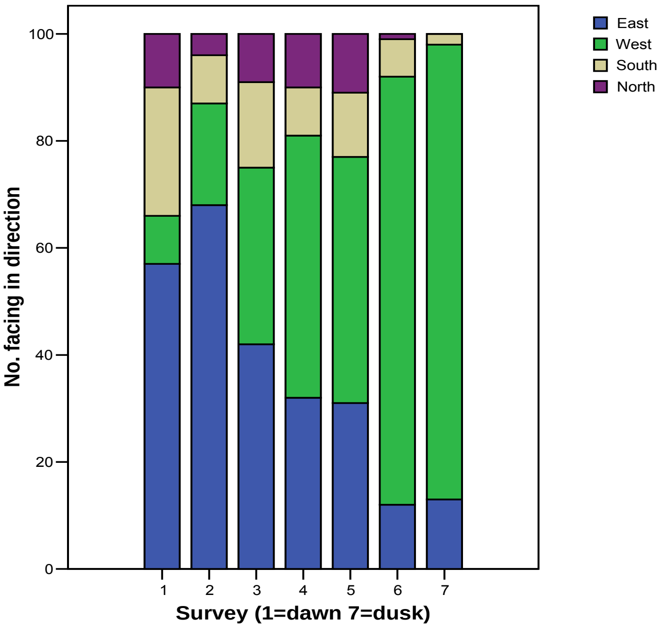


Fig. 4.1 Flush distances of common scoter from the RV Prince Madog showing the relationship between flock size and flush distance. Flush distance is plotted on a log scale.



surveys 1-2: current flow east to west (receding tide)
survey 3: slack water, no current (c. low tide)
surveys 4-7: current flow west to east (rising tide)

Fig. 4.2 Orientation of Common Scoter on a day (18/12/03) with wind speeds < 5 km/hr showing change in orientation with change in current direction.

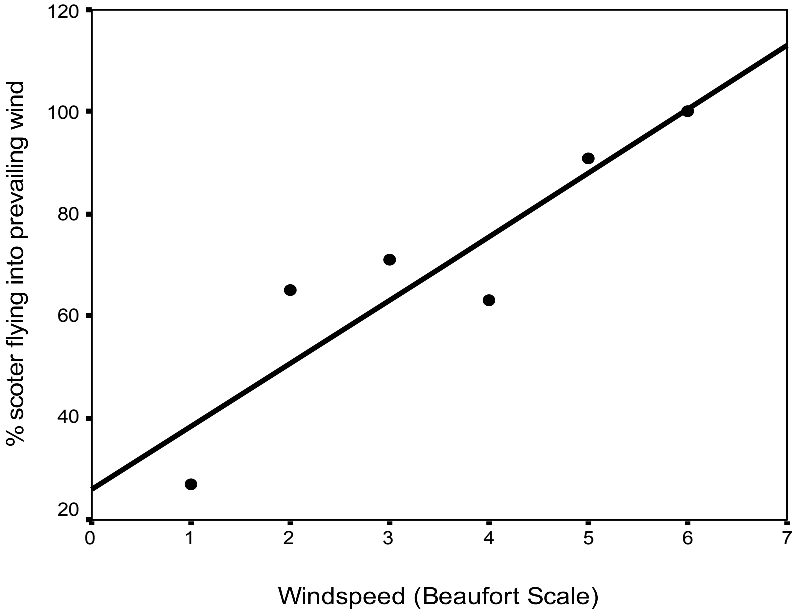


Fig. 4.3 Proportion of common scoter flying into/within 45°of prevailing wind with increasing windspeed.

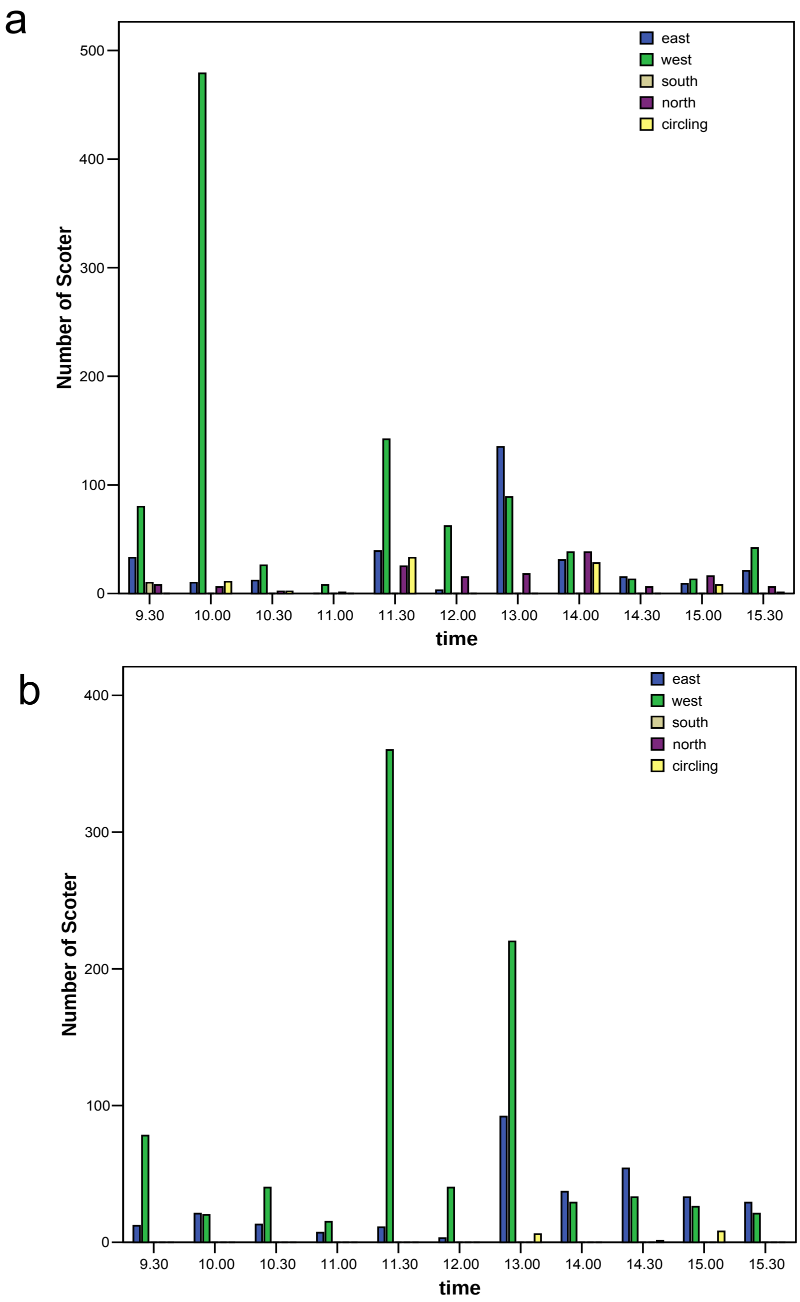


Fig. 4.4 (a) Flight direction of common scoter off west Llanddulas, 11/12/03. (b) Flight direction of common scoter off east Llanddulas, 11/12/03.

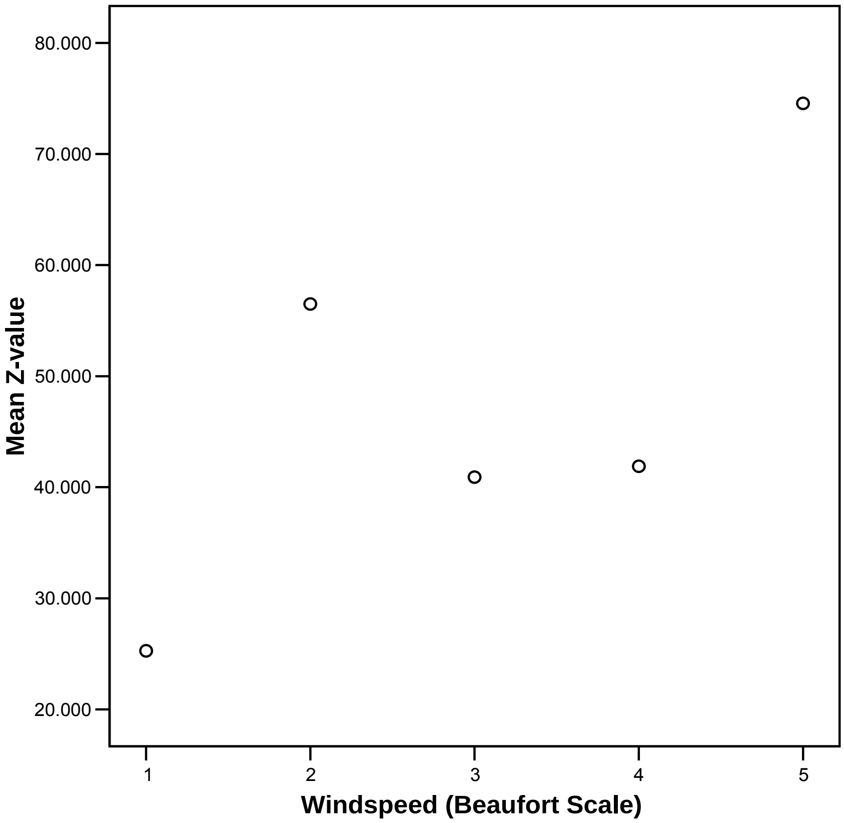


Fig. 4.5 Common Scoter orientation - mean Z-values plotted against windspeed (irrespective of current direction) indicating a trend (non-significant) towards a greater proportion of scoter facing into the prevailing wind with increasing wind speed.

5. Existing forms of disturbance

5.1 Introduction

One of the data requirements of the behavioural model was the estimation of the potential feeding area of the common scoter that would be unavailable to them due to existing anthropogenic activities such as shipping and aerial traffic. Garthe & Huppop (2004) classified common and velvet common scoter as the most sensitive of 26 species of seaducks and seabirds to disturbance by ship and helicopter traffic. In addition to studying the distribution of common scoter in relation to environmental parameters and the distribution of their prey, we were able to obtain information regarding the distribution of human disturbance from shipping and fishing disturbance. Repeated disturbance by ships, aircraft or other sources of disturbance could effectively lower the potential habitat value of areas that contain suitable and even abundant prey. Repeated and frequent disturbance will cause common scoter to fly and reposition to avoid the disturbance, thereby interfering with feeding, resting and incurring additional energetic costs. Thus it was necessary to quantify the location and occurrence of existing forms of anthropogenic disturbance that may impact upon common scoter in Liverpool Bay.

5.2 Methods

All spatial data were processed and analysed with ArcView GIS software using the model grid for reference (sections 2 and 3). The positions of the proposed windfarms were entered into ArcView as a map layer together with the tidal grid cells.

Commercial shipping intensity data was made available to us by Anatec UK Ltd through the COASTS database, and supplied as the number of ships (> 300 t) passing through each tidal grid cell per year. The COASTS database holds only data for vessels greater than 300 t (gross). The RV Prince Madog from which the flush distances were measured (section 4) is 390 t (gross). Hence the data represents vessels from 300 t up to super-tankers >> 90 000 t (gross). Vessels were assigned to each grid cell from the reported route taken by the vessel (port of embarkation, port of destination). Vessel routes are assumed to take the shortest possible linear distance other than to conform to the regulations imposed by navigational channels and separation zones (e.g. off the northern tip of Anglesey). Given the size of each of the model grid cells (3.7 x 3.35 km) and the known flush distance from a vessel of 390 t (1km – 2km), the grid cell size seems an appropriate scale at which to consider the extent of the disturbance created through each cell assuming vessels pass through the centre of that cell. The number of vessels that docked or embarked from each of the major ports around the North Wales and Lancashire coastline were extracted per month for the year 2003/2004 to determine any seasonality in the amount of potential disturbance from commercial shipping activity.

In addition to commercial shipping activities, fishing vessels from North Wales and Lancashire operate in Liverpool Bay and may generate additional disturbance for common scoter. These vessels will not appear in the COASTS database as most are < 24 m in length and << 300 t (gross). Larger fishing vessels such as beam trawlers of Dutch and Belgian origin fish in the Irish Sea but these are restricted to waters beyond 6 nautical miles from the shore. Detailed information of fishing activities in Liverpool Bay were ascertained for the period 1987 – 2002 from enforcement agency (Department of Environment, Food and Rural Affairs (DEFRA)) overflight data of direct observations of fishing vessels expressed as sightings per unit effort of observation (SPUE) (see Dinmore et al., 2003 for a full explanation of methods of data calculation and interpretation). These data were entered into the GIS ArcView software and interpolated to see to what extent fishing activities overlapped with the distribution of common scoter. The database includes fishing vessels of all types, but for the Northeastern Irish Sea this would primarily consist of otter trawlers, beam trawlers and scallop dredgers, although the latter are primarily confined to waters deeper than 20 m due to the location of scallop populations off the North of Anglesey and towards the Isle of Man. The data held within the database does not give information of routes taken by fishing vessels from their home port to fishing grounds, hence it is not possible to assess the possible disturbance caused by such activities, however it is likely to be highly variable as vessels from ports in the Northern Irish Sea target different fisheries according to market forces and movements of the target species.

The potential effects of disturbance by helicopter flights to and from oil and gas installations were also considered as these are likely to be regular and frequent for maintenance and personnel transfer.

Blackpool airport in Lancashire was the source of the flights to and from the oil and gas installations in the Irish Sea. Data were obtained from the SEA 6 report prepared for the DTI. The helicopter flight path is given as a corridor approximately 3 km wide.

5.3 Results

Although helicopter flights occurred directly across the main aggregations of common scoter off Blackpool and the River Ribble (Fig. 5.1), they were relatively infrequent occurring approximately once per day (one outbound and one inbound trip) for each installation. The low altitude of helicopter flights (300 – 600 m) is roughly similar to that used for the common scoter light aircraft surveys (500 m) which are known to flush birds at the water surface (P. Cranswick pers. Comm.). Nevertheless, the infrequent nature of these flights is likely to generate much less disturbance than the reported commercial shipping activities over the wider area of Liverpool Bay (see below).

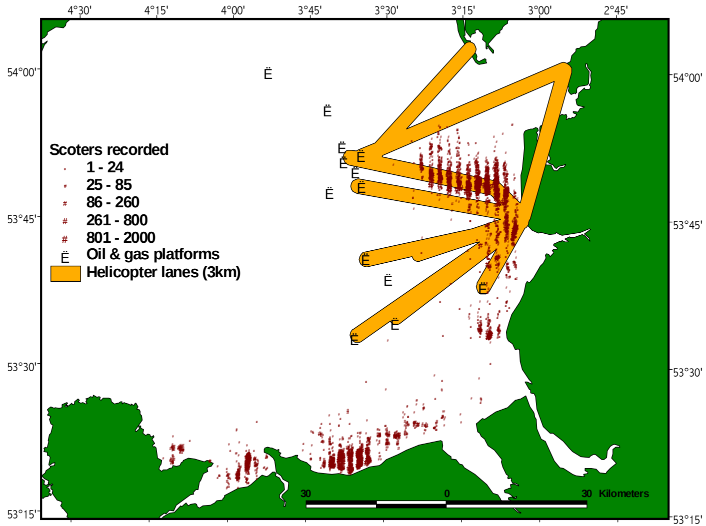


Fig. 5.1 Helicopter flight paths from Blackpool airport to oil and gas platforms (width 3 km) in relation to the distribution of common scoter observed during for the winter seasons 2002/2003 and 2003/2004. Helicopter flights occur approximately once per day at an altitude of 300 – 600 m.

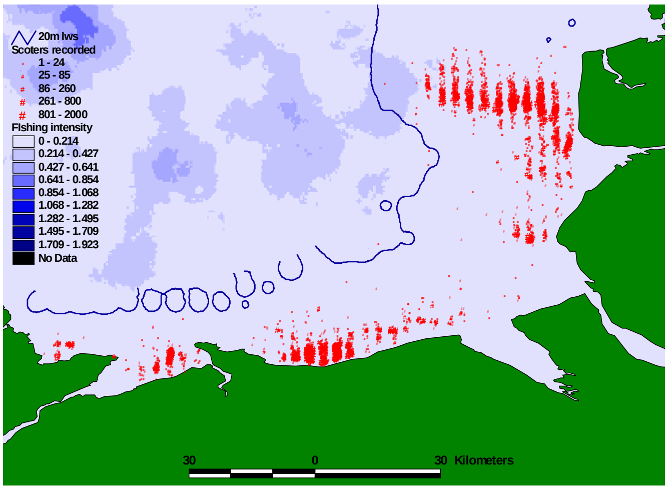


Fig. 5.2 The distribution of fishing effort in Liverpool Bay derived from DEFRA overflight data and the sightings of common scoter for the winter seasons 2002/2003 and 2003/2004.

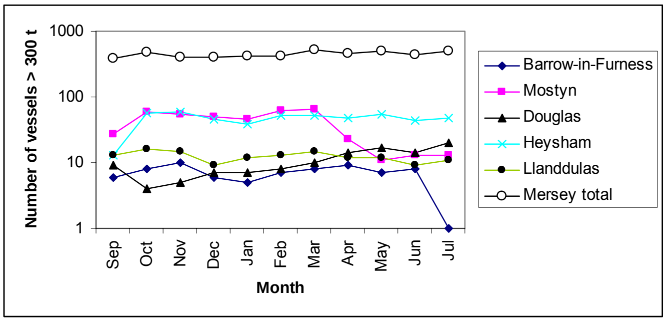


Fig. 5.3 Monthly figures for shipping activities at the main points in the northern Irish Sea. The y-axis is represented as a log scale. None of these trends deviated significantly from a slope of zero, hence the mean values give in Table 5.1 are an accurate representation of activity for each month.

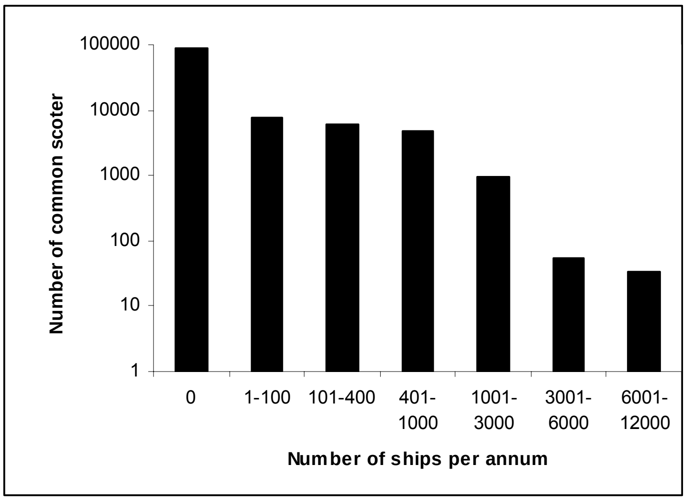


Fig. 5.4 Sum of common scoter observed during 8 overflights (2003/2004) for Liverpool Bay in relation to the number of ships > 300 t that passed through each 3.7 x 3.35 km cell defined for the behavioural ecology model

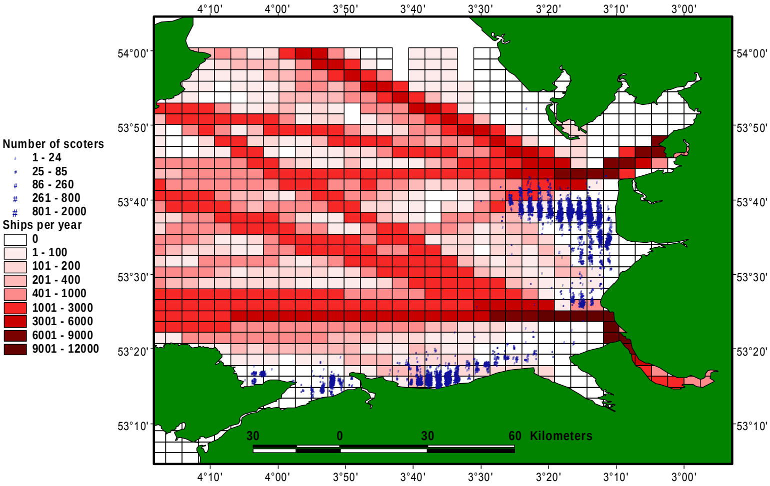


Fig. 5.5 The number of ships > 300 t that passed through each 3.7 x 3.35 km cell defined for the behavioural ecology model for the period September 2003 to July 2004. The number of common scoter sighted during 8 overflights for the period 2002/2004 is shown for reference.

The level of fishing activity in all areas in which common scoter occurred was extremely low, with only light fishing activity on the extreme western edge of Shell Flat. The majority of the fishing activities occurred much further offshore in the waters just to the south of the Isle of Man (Fig. 5.2).

Shipping activity in and out of the main eastern Irish Sea ports did not vary significantly through the period of September 2003 to July 2004 (all relationships non-significant with time P > 0.05). Thus there are no seasonal patterns in shipping activity that might be relevant with respect to fluctuations of disturbance to common scoter throughout the year. However, shipping activity was spatially aggregated at the 3.75 x 3.25 km grid scale such that c. 82% of common scoter observed through the period 2002/2004 occurred in cells that had zero shipping activities for ships > 300 t. The number of birds observed declined steeply with increasing levels of shipping activity (Fig. 5.4, Table 5.2). The distribution of common scoter differed significantly from an equal distribution of birds among all model cells (Table 5.2, $x^2 = 51173$, d.f. = 6, P <<< 0.0001).

Table 5.1 The mean number of vessels (> 300 gross tonnes) arriving and departing from the main ports in the northern Irish Sea for an area of coastline that extends from Point Lynas (Anglesey) to Barrow-in-Furness (Cumbria). Data were extracted from September 2003 to July 2004 (11 months).

Barrow-in-Furness	6.82	±	2.40
Mostyn	38.36	±	21.19
Douglas	10.45	±	5.13
Heysham	46.27	±	12.61
Llanddulas	12.45	±	2.30
River Mersey total	447.00	±	47.65

Table 5.2 Table of shipping activity for each 3.7 x 3.35 km represented as the number of vessels > 300 t passing through that a cell per annum. Only those cells selected for the behavioural ecology model have been analysed, any shipping areas with a depth greater than 25 m have been excluded. The sum of the number of common scoter observed over during the 8 overflights is also shown. These values are expressed as percentage in parentheses.

Ships per year per cell	Number of common scoter	Number of cells
0	90153 (82)	60 (48)
1-100	7777 (7)	23 (19)
101-400	6097 (5)	23 (19)
401-1000	4811 (4)	7 (5)
1001-3000	933 (1)	4 (3)
3001-6000	56 (<<1)	4 (3)
6001-12000	34 (<<1)	2 (1)

5.4 Discussion

The effect of human disturbance is often measured in terms of behavioural changes in response to human presence but from a conservation perspective such disturbance is important only if it affects survival or fecundity and hence a population decline (Cayford 1993; Gill et al. 2001; West et al. 2002). To demonstrate any such effect on common scoter populations through disturbance on their wintering grounds would be virtually impossible. However, common scoter as demonstrated, are extremely wary and it has been suggested that species showing the greatest avoidance require the greatest amount of protection (Klein et al. 1995). This though may not be true for species where the costs of moving to an alternative site are likely to be small (Gill et al. 2001). Wigeon *Anas penelope*, for example show a strong human avoidance (Tuite et al. 1984) but for this mainly herbivorous species often grazing on short swards with many nearby alternative feeding sites, costs are probably low. One could argue that this is the case for common scoter as upon disturbance there are plenty of areas of undisturbed sea to which they could fly and settle. On the other hand fitness costs may be high if there were few or no other nearby suitable feeding areas to which they can go. Furthermore, the additional expenditure of energy associated with each disturbance flight can in some instances lead to a substantial increase in daily energy expenditure and necessitates an increased foraging effort in order to compensate (White-Robinson 1982; Riddington et al. 1996).

Shipping activities

Most (82%) of the common scoter were observed in 48% of the model cells that had no shipping activity for vessels > 300 t, with 12% of the birds occurring in 38% of the cells that had light shipping activity. This perhaps suggests that common scoter avoid areas with activity associated with large vessels. Fishing activities did not occur in close proximity to areas in which common scoter were observed except for the extreme tip of Shell Flat off Lancashire. Most fishing activities were concentrated further offshore and consequently appear unlikely to have a significant influence on the distribution of common scoter.

Taking the direct observations of flush distance from section 4 quantified for the response of common scoter to a 390 t vessel, the 3.75 x 3.35 km model cells would be cleared of common scoter if this vessel steamed through its centre line. Presumably flush distances vary dependent upon factors such as the prevailing weather conditions, the speed of approach of a vessel, the angle of approach, the size (and even colour) of the vessel, human activity visible on the deck, and the fitness of the birds themselves. However, within the confines of the current study it is impossible to take such factors into account. It may be that along regularly used shipping lanes birds might become habituated to the presence of boats. However the lack of overlap between intensively utilised shipping lanes and common scoter suggests that this does not occur to a significant degree.

Helicopter disturbance

Helicopter disturbance seems to be relatively inconsequential as the main helicopter flight paths crossed some of the main aggregations of common scoter on Shell Flat. In the main, these flights occur at most once per day along each trajectory. Other forms of disturbance that are not accounted for within the study are the disturbance generated by pleasure craft such as sail boats and jet-skiis. The latter generate considerable noise and may affect areas much larger than their size would suggest. Nevertheless there is no available information to suggest the extent to which these activities might affect use of areas of the sea by common scoter. This perhaps requires further investigation as these activities are not currently measured.

Other potential sources of disturbance

Our ability to determine those sources of disturbance that influence the distribution of common scoter is limited by the availability of information on those sources of disturbance. The coastal zone is heavily utilised for recreational purposes and as such the effects of yachting and jet-skiing. The former is likely to be heavily concentrated around areas with marinas e.g. Menai Strait, Conwy, Rhos on Sea and Fleetwood, while jet skiing is likely to be focused on those areas with convenient launch facilities. Neither of these activities is currently recorded in a format suitable for incorporation in our considerations but might warrant further investigation in the future. Both activities have the potential to cause disturbance, yachts are highly visible due to their sails while jet-skiis have a noise disturbance envelope that can extend to multiple km.

6. Generic model description

6.1 Introduction

This section describes the individual-based model, MORPH, used to make predictions for each of the windfarm scenarios examined in this project. This model has been developed during the project, and replaces the models which existed at the start of the project. The original models have been tested on a wide range of sites and used to predict the effects of several environmental factors, including disturbance (West *et al*. 2002), shellfishing (Stillman *et* al. 2000, 2001, 2003; West *et al.* 2003; Caldow *et al.* 2004; Goss-Custard *et al*. 2004), habitat loss (Durell *et al*. 2005) and site quality (West *et al*. 2005) on the overwinter mortality of populations of waders and waterfowl. The development of the new model is an addition to the original project objectives which anticipated merely making a few modifications to one of the models that existed at the start of the project. The new model is based on the same fundamental principle as the previous models – that individuals behave in ways that maximise their own chances of survival and reproduction. It also tracks the location, behaviour and ultimate fate of each individual in the population, and incorporates variation in the foraging abilities of different individuals. However, the new model is much more flexible than either of the original models, and hence can be used to address a much wider range of environmental issues both within this project and beyond. For example, the previous models contained wader- or waterfowl-specific assumptions, and assumptions applicable to intertidal coastal areas but not others. The new model removes these limitations and contains virtually no species or system-specific assumptions. However, once parameterised, it can still be applied to specific species or systems.

The purpose of this section is to describe the general aspects of the model, applicable to any system. The specific details of the current system i.e. common scoter feeding on benthic prey in Liverpool Bay are described in sections 7 & 8. Here, the model is described using a standard protocol, designed by Grimm & Railsback (2005). The general protocol ensures that individual-based models are fully described in a way that is clearly understandable and would enable the models to be recreated by others. Clear communication of individual-based models has often been a problem in the past, which has limited the widespread use of some models (Grimm & Railsback 2005). The protocol has been used to avoid this problem. Model description is divided into the following sections: Purpose, Structure, Processes, Concepts, Initialisation, Input and Submodels. A general overview of the main elements of the model is initially presented (Purpose, Structure, Processes and Concepts), followed by a more detailed mathematical description (Initialisation, Input and Submodels). A number of technical modelling terms are used in this description, as these are required to describe the model unambiguously. However, each of these terms is defined when first used.

6.2 Purpose

The overall purpose of the model is to predict how environmental change (e.g. habitat loss, changes in human disturbance, climate change, mitigation measures in compensation for developments and changes in population size itself) affects the survival rate and body condition in animal populations. The model does this by predicting how individual animals respond to environmental change by altering their feeding location, consuming different food or adjusting the amount of time spent feeding. The central assumption of the model is that animals behave in ways that maximise their chances of survival. The model does not itself predict reproductive rate but its survival and body condition predictions can be input into other models that do make this prediction.

The model has been designed to be very flexible (hence the name MORPH), so that it can produce both general predictions (when parameterised in a very simple way), and predictions for specific systems (when parameterised using detailed system-specific data – as in the current study). The model can read in equations as parameters, and so can potentially represent a very wide range of species or systems.

6.3 Structure

The model itself contains only very general aspects of behaviour and ecology, applicable to a wide range of systems. The basic assumptions of the model are as follows.

Time progresses in discrete, fixed duration, time steps.

Space is divided into a number of uniform habitat patches, with fixed location and area.

Habitat patches contain a number of resources which can be consumed by foragers.

Resources contain components which are assimilated into foragers when resources are consumed.

Foragers remain at the same location during a time step, either on a patch or travelling between patches, but move between time steps.

Foragers alter their location and the food they consume in order to maximise their chances of survival.

The model defines the following five entities (*objects within the model*).

Global environment - State variables (*values used to describe the global environment*) which apply throughout the modelled system.

Patches - Locations with local, patch variables (*values used to describe patches*), containing resources and foragers. Foragers may experience travel costs when moving between patches.

Resources - The food consumed by foragers. Foragers can simultaneously consume one or more resources from a patch. Such collections of resources are termed *diets*.

Components - Elements within resources which foragers assimilate into their bodies.

Foragers - Animals which move within the system attempting to maximise their survival and body condition. One or more *forager types / species* may be present within the modelled system.

Table 6.1 lists the state variables (*values used to describe a model entity*) of each entity. The global state variables are the major driving variables in the model system. Patch variables may depend on these global variables. Patches contain one or more resources, which in turn contain one or more components. Foragers have a range of possible diets, which are simply a collection of resources. Foragers consume diets, from which they assimilate components. Components can either have positive, neutral or negative effects on foragers. Foragers are not forced to consume diets, but instead may occupy a patch and not feed.

Table 6.1 State variables used to describe model entities.

Entity	**State variable**	**State variable description**
Global	Global variables	Zero or more environmental variables which apply throughout the modelled system
Patches	Location	Central coordinates
	Size	Surface area / volume of patch
	Patch variables	Zero of more patch-specific environmental variables
Resources	Density on patch	Density of each resource on each patch
Components	Density in resource	Density of each component within each resource on each patch
Foragers	Forager type / species	Forager type / species to which forager belongs
	Forager constants	Zero or more forager-specific constants which remain constant throughout a simulation
	Forager variables	Zero or more forager-specific variables which can change throughout a simulation
	Location	Coordinates of forager's location
	Patch	Patch number being occupied by forager during current time step
	Diet	Diet number being consumed by forager during current time step (zero if no diet is being consumed)
	Proportion of time moving	Proportion of time moving between patches during current time step
	Proportion of time feeding	Proportion of time feeding during current time step
	Diet consumption rate	Rate at which diet is being consumed during current time step and averaged over previous and predicted for future time steps
	Component consumption rate	Rate at which a component is being consumed during current time step and averaged over previous and predicted for future time steps
	Component assimilation rate	Rate at which a component is assimilated into the body during current time step and averaged over previous and predicted for future time steps
	Component metabolic rate	Rate at which a component is metabolised / excreted from the body during current time step and averaged over previous and predicted for future time steps
	Component reserve size	Amount of a component within the body's reserves during current time step

6.4 Processes

The model defines the following processes (*the transfer of information or model entities between (other) model entities*).

Change in resource density. Changes in the density of a resource on a patch caused by consumption by the foragers and / or other factors.

Change in component density. Changes in the density of a component in a resource.

Forager immigration. The movement of foragers into the system.

Forager decision making. The optimal patch and diet selection of foragers and decisions to emigrate from the system.

Forager emigration. The movement of foragers away from the system.

Forager movement between patches. Movement of foragers between patches. Movement may have associated costs and may take more than one time step.

Forager diet consumption. The transfer of resource components into foragers when diets are consumed.

Forager physiology. Change in the size of a forager's component reserve due to the balance of consumption and metabolism.

Forager mortality. Death of foragers.

6.5 Concepts

The following concepts (*basic characteristics common to all individual-based models*) are represented in the model.

6.5.1 Emergence

The following phenomena emerge from the interaction between individual forager traits and global and patch variables, resource and component densities, and forager constants and variables.

Resource depletion. The amount of each resource consumed by foragers from each patch during each time step.

Forager distribution and diet selection. The location of each forager and its diet during each time step.

Proportion of time foragers spend feeding. Proportion of each time step each forager spends feeding.

Forager component reserve size. The amount of each component within each forager's reserves during each time step.

Forager mortality and emigration. The number of foragers remaining in the system after a given number of time steps.

6.5.2 Adaptation

Foragers adaptive traits (*behaviour through which foragers maximise their fitness (i.e. survival and reproduction)*) are their location and diet selection. During each time step, foragers select the patch /

diet combination which maximises their perceived fitness, or emigrate from the entire system if this has a higher perceived fitness than any patch / diet combination.

6.5.3 Fitness

A number of *fitness components* are assumed to affect the survival of animals and hence their overall fitness. Fitness components may have negative or positive effects on survival. Each fitness component has associated submodels (see below) to calculate the true probability of surviving the fitness component during a time step. The combined true survival probability for all fitness components is the product of the survival probabilities associated with each fitness component (see below). Each fitness component has a *fitness measure*, calculated using a submodel (see below), which animals use to assess the fitness consequences of different decisions. The combined fitness measure is the product of the fitness measures associated with each fitness component (see below). The forager selects the patch and diet combination (including no diet) which maximises its combined fitness measure, or emigrates from the system if this has a greater fitness measure than any of the possible patch and diet combinations. Once the forager has selected a patch and diet, the consequences of this decision are determined by true probability of survival. Both true survival probability and fitness measure submodels can depend on any combination of global, patch, resource, component or forager state variables.

6.5.4 Prediction

Foragers remember their foraging success during a given number of previous time steps. This memory is used to calculate average state variables over previous time steps (see Table 6.1 for a list of these variables). Foragers can also predict their future foraging success, over a given number of time steps, taking into account the time taken to move from their current location to a target patch. In making these predictions, the model assumes that foragers do not know the future values of any state variables, resource or component densities or the location of other animals. Instead, state variables, resource and component densities and the location of other foragers are all assumed to remain the same as in the current time step.

6.5.5 Interaction

Foragers interact within patches through the consumption of a shared resource (depletion competition). The number and / or density of other foragers within a patch can also affect any of a forager’s state variables, and fitness measures and true survival probabilities. These effects can be either positive or negative, depending on the submodels used. Increased competitor numbers or density can either increase consumption rate (facilitation) or decrease consumption rate (interference competition), again depending on the submodels used. Foragers can only interact within patches. The actual mechanisms of interactions within patches are not incorporated explicitly.

6.5.6 Sensing

The amount of knowledge foragers have can be varied. This can range from perfect knowledge of the complete system during the current time step, through complete knowledge of local patches, to no knowledge at all. Similarly, the amount of knowledge a forager has of its own state, both during the current time step and previous and future time steps, can be varied. Foragers base their decisions on the fitness measures associated with different patches and diets (or no diet). The fitness measure may or may not be related to the true probability of survival. Foragers will tend to avoid patches and diets with low fitness measures. Depending on the relationship between the true survival probabilities and fitness measures, this can mean that foragers avoid safe patches and diets (i.e. high true survival probability) because these are perceived as dangerous (i.e. low fitness measure), or select dangerous patches or diets because these are perceived as safe. The model does not explicitly represent any sensing mechanisms.

6.5.7 Stochasticity

The amount of stochasticity (*random variation in model predictions*) can be varied. Any state variables, except for patch size and location, and forager type / species can be stochastic. The probability of a forager (or the individuals within the forager (see below)) dying during a time step is a stochastic event unless the probability is zero or one.

6.5.8 Collectives

Collectives (*groups or aggregations of foragers*) are included in the model. These are represented by the number and / or density of foragers on each patch, and arise from the patch and diet selection of foragers. Collectives are not represented as social groups, instead each individual behaves independently albeit with its behaviour influenced by the number and / or density of competitors on different patches. Super-individuals can be incorporated, with each forager (super-individual) representing more than one individual. The number of individuals within a forager is set at the start of a simulation, but can decrease through time as some individuals within the forager die. In contrast, all individuals within a forager simultaneously immigrate to or emigrate from the system.

6.5.9 Scheduling

Time is represented using discrete time steps which are of constant duration. Figure 6.1 shows the sequence of events during each time step. Global events are processed first, followed by patch events and then forager events. Finally, results are displayed and saved. The order in which foragers are processed can either be random or based on the value of a specified forager constant. Once the order of foragers has been determined, foragers are updated one at a time during each time step (*asynchronous scheduling*). This means that all forager events (immigration, patch and diet selection, movement and emigration, diet consumption, resource depletion and forager mortality) are applied to one forager before the next forager is processed.

6.5.10 Observation

The results used to test the model depend on the particular system for which it is parameterised. All state variables can be displayed and saved during each time step.

6.6 Initialisation

The initial values of state variables are either read from a parameter file, created using random numbers, or calculated from state variables defined earlier in the parameter file. The sequence of random numbers is itself randomised at the start of each simulation so that replicate simulations using the same set of parameters will produce slightly different predictions. All global and patch variables are initialised at the start of the simulation. Forager state variables are initialised once the forager has immigrated into the system, and so foragers immigrating at different times may have different initial state variables.

6.7 Input

The particular data used to parameterise the model will depend on the particular system to which it is applied. However, Table 6.2 lists the basic set of parameters, which would be required for any system. Parameters can either be single values, values for each time step read in from a file, or an equation (submodel) to calculate values during each time step.

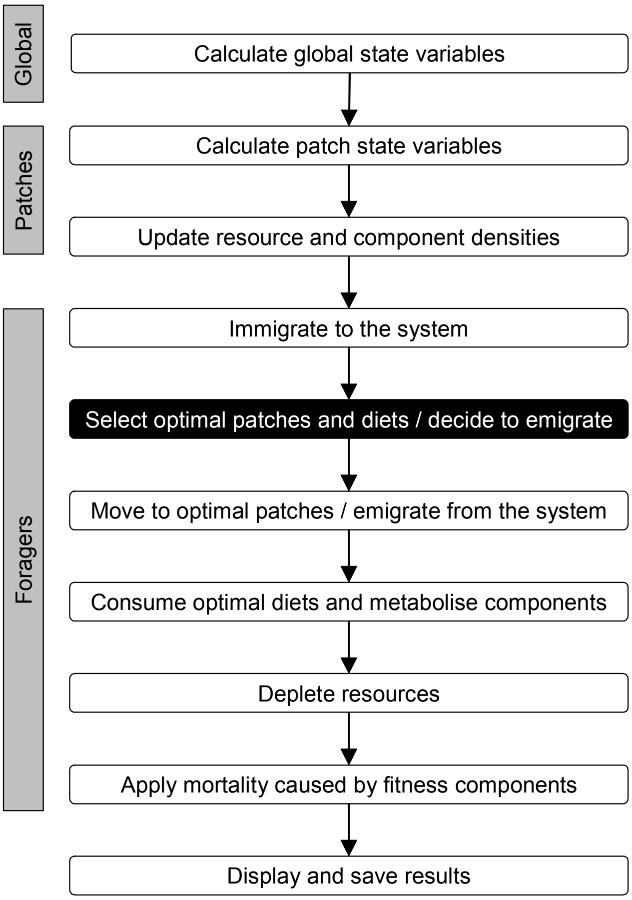


Figure 6.1 The sequence of events during each time step. The grey bars show the entity in which each event occurs. The black box indicates where foragers adaptive traits are executed to determine which patch and diet to feed on or whether to emigrate from the system. Forager events are either processed asynchronously. Foragers are only processed once they immigrate to the system, and are no longer processed after they emigrate or all their individuals have died. Patch and diet selection does not occur while foragers are moving. Components are metabolised while a forager is moving, unless moving is instantaneous.

Table 6.2 Basic set of parameter values / submodels required by the model.

Entity	Parameter
Global environment	Number and names of global variables
	Value / submodel for each global variable
Patches	Number and names of patches
	Size of each patch
	Location of each patch
	Value / submodel for each patch variable on each patch
Resources	Number and names of resources
	Initial density of each resource on each patch
	Submodel for change in density (excluding consumption by foragers) of each resource on each patch
Components	Number and names of components
	Value / submodel for density of each component in each resource on each patch
Diets	Number and names of diets
	Number and names of resources in each diet
Foragers	Number and names of forager types / species, and type / species of each forager
	Number and names of forager constants
	Value of each forager constant for each forager
	Number and names of forager variables
	Value / submodel for each forager variable
	Value / submodel for time to move between patches
	Number and names of diets consumed by forager type / species
	Rule to determine whether patches can be located
	Rule to determine whether fitness measure can be assessed on a patch
	Value / submodel for diet consumption rate
	Value / submodel for maximum diet consumption rate
	Value / submodel for assimilation efficiency of each component in each diet
	Value / submodel for rate of metabolising each component
	Value / submodel for target reserve size for each component
	Number of fitness components
	Value / submodel for fitness measure for each fitness component
	Value / submodel for true survival probability for each fitness component
	Value / submodel for expected fitness measure on patches on which fitness measure cannot be assessed
	Value / submodel for expected fitness measure of emigrating

6.8 Submodels

Many of the model’s submodels will be read in as equations from the parameter files. In these cases the particular submodels will depend on the specific system to which the model is being applied. These are termed parameter submodels in the follow sections. However, a number of submodels are incorporated into the model itself. The following sections describe the submodels used to represent each of the model’s processes.

6.8.1 Change in resource density

Resource densities change on patches due to (i) *non-depletion change* and (ii) *depletion* when foragers consume diets on a patch.

Non-depletion change is calculated at the start of each time step, excepting the first time step, using a parameter submodel which determines how resource density is updated at the start of each time step.

$$R = f\left(p_1, p_2..p_n\right)R_{previous} \tag{6.1}$$

where R = new resource density at start of current time step, $R_{previous}$ = old resource density at end of previous time step, $f\left(p_1, p_2..p_n\right)$ = a submodel containing n parameters. The submodel’s parameters may be any number of global or patch state variables.

After the resource density has been calculated at the start of each time step, the density of each diet is updated. Diets are simply a collection of resources, and so the density of a diet is simply the sum of all of the resources it contains.

$$R_{diet} = \sum_{r=1}^{N} R_r \tag{6.2}$$

where R_{diet} = diet resource density, r = resource number, N = number of resources in diet and R_r = density of resource r.

Depletion is incorporated by reducing the amount of a resource in a patch by the amount consumed by foragers. Foragers consume diets, rather than separate resources and so the model needs to calculate the amount of each resource consumed in the diet. The model assumes that resources are consumed in proportion to their relative density within a diet. The amount of a resource consumed within a diet is therefore given by.

$$E = E_{diet}\frac{R}{R_{diet}} \tag{6.3}$$

where E = amount of resource consumed (eaten), E_{diet} = amount of diet consumed, R = density of resource and R_{diet} = density of diet. The density of the resource on the patch is updated by assuming that depletion occurs uniformly throughout the patch.

$$R = R_{previous} - \frac{E}{A} \tag{6.4}$$

where R = new density of resource, $R_{previous}$ = previous density of resource before depletion, A = size (area / volume) of patch and E = amount of resource eaten.

Depletion occurs continually during a time step (as foragers are processed asynchronously). Diet densities are updated every time depletion occurs.

6.8.2 Change in component density

Component density within each resource on each patch is either read in as a single value which applies throughout the simulation or is read in as a parameter submodel to calculate values during each time step. Component density submodels can depend on global or patch state variables.

The density of a component within a diet is a weighted mean of the component densities within each of the resources contained in the diet.

$$C_{diet} = \frac{\sum_{r=1}^{N} C_r R_r}{\sum_{r=1}^{N} R_r} \tag{6.5}$$

where C_{diet} = density of component in diet, r = resource number, N = number of resources in diet, C_r = density of component in resource r and R_r = density of resource r.

6.8.3 Forager immigration

The probability of immigrating to the system for each forager type / species is read in as a single value which applies throughout the simulation or is read in as a parameter submodel to calculate values during each time step.

6.8.4 Forager decision making

Foragers in the model make three types of decisions.

Patch choice

Diet choice

Emigration from the system

The model uses the same submodel to determine how foragers make these decisions. The model's basic assumption is that foragers behave in order to maximise their fitness, which in turn is assumed to be measured as the probability of survival. Reproductive components of fitness are not considered directly as these are outside of the scope of the model. Model foragers test the fitness consequences of moving to different patches, consuming different diets, consuming no diet or emigrating from the system. The list of possible diets depends on the diets consumed by the forager type / species to which the forager belongs. Foragers select the combination which maximises their combined fitness measure.

Foragers do not necessarily have perfect knowledge of their survival probability when moving to different patches or consuming different diets. This uncertainty operates at two levels.

Ability to assess fitness measures

Accuracy of fitness measures (i.e. their relation to the true survival probability)

Ability to assess fitness measures. Figure 6.2 shows how the ability to assess the fitness measures associated with different decisions is incorporated. Foragers are assumed to be able to assess fitness measures associated with consuming different diets on their current patch. Other patches fall into one of three different categories. (1) Foragers may know the location of a different patch and be able to assess fitness measures on the patch. They can assess the survival consequences of moving to this patch consuming any diet, and know the values of all of the patch's state variables during the current time step. (2) Foragers may know the location of a patch, but not be able to assess the fitness measures associated with different diets. They cannot assess the survival consequences of consuming different diets, and are unaware of any of the patches state variables. However, they do have an expected fitness measure on this patch ($F_{expected}$), which is used to compare this patch with others. (3) Patches may be of unknown location, and so cannot be considered as potential locations to move to. Emigration from the system also has an expected fitness measure, which is used to determine whether emigration is the decision which maximises survival ($F_{emigrate}$).

Accuracy of perceived survival. For patches on which survival consequences can be detected, the following process is used to assess fitness measures, which may be unrelated to the true survival probability. Survival is assumed to be affected by a number of fitness components. Each fitness component has an associated submodel to predict the fitness measure given the forager's state (including average state over previous time steps) and any combination of global or patch state variables. The combined fitness measure is found from the product of the fitness measures associated with each fitness component.

$$F_{assessed} = \prod_{c=1}^{N} f_c \tag{6.6}$$

where $F_{assessed}$ = combined fitness measure for all fitness components; c = fitness component number, N = number of fitness components, f_c = fitness measure for fitness component c. $F_{assessed}$ is calculated for all possible combinations of patches and diets, including the option to occupy a patch but not feed. The forager selects the patch and diet combination which maximises either $F_{assessed}$ or $F_{expected}$ (depending on whether fitness can be assessed on the patch), or emigrates if $F_{emigrate}$ exceeds any of these values. In the event that more than one decision maximises survival, the forager takes a random option, but weighed by patch area, or remains in the system if $F_{emigrate}$ equals the probability associated with remaining in the system.

Once the forager has selected a patch and diet, it is allowed to move and consume its selected diet (see below). The consequences of this decision are then determined by true probability of survival.

$$S_{true} = \prod_{c=1}^{N} s_c \tag{6.7}$$

where S_{true} = true probability of surviving all fitness measures; c = fitness component number, N = number of fitness components, s_c = true probability of surviving fitness component c. The assessed fitness measure may or may not be related to the true probability. Foragers will tend to avoid patches and diets with low fitness measures. Depending on the relationship between these and the true survival probabilities, this can mean that foragers avoid safe patches and diets (i.e. high true survival probability) because these are assessed as dangerous (i.e. low fitness measures), or select dangerous patches or diets because these are perceived as safe.

6.8.5 Forager emigration and movement between patches

Foragers move when they emigrate from the system or change patches. Emigration is assumed to be instantaneous, with foragers leaving the system during the same time step in which they decide to emigrate. Movement between patches may or may not be instantaneous. When movement is instantaneous, foragers move to a target patch as soon as they decide to move and then spend the whole of a time step on the target patch. Otherwise, movement may take one or more time steps. If movement takes one or more time steps, foragers are assumed to reach a patch at the start of a time step. This means that they are able to respond to the local conditions on the patch (i.e. decide which diet to select or move to another patch), as these may not have been fully known when the forager initially decided to move to the patch. The time to travel between patches is calculated from a parameter submodel.

$$T_{move} = f\left(p_1, p_2..p_n\right) \tag{6.8}$$

where T_{move} = time to move between patches and $f\left(p_1, p_2..p_n\right)$ = a submodel containing n parameters. The submodel can depend on any global variables, the relative location of patches and any forager constants or variables.

For simplicity, the movement submodel assumes that movement always takes a whole number of time steps. The submodel checks that the relative values of movement time and time step length always result in movement time exactly equalling a whole number of time steps.

$$N_{timestep} = \frac{T_{move}}{T_{timestep}} \tag{6.9}$$

where $N_{timestep}$ = movement time in time steps, T_{move} = time to move between patches and $t_{timestep}$ = duration of one time step.

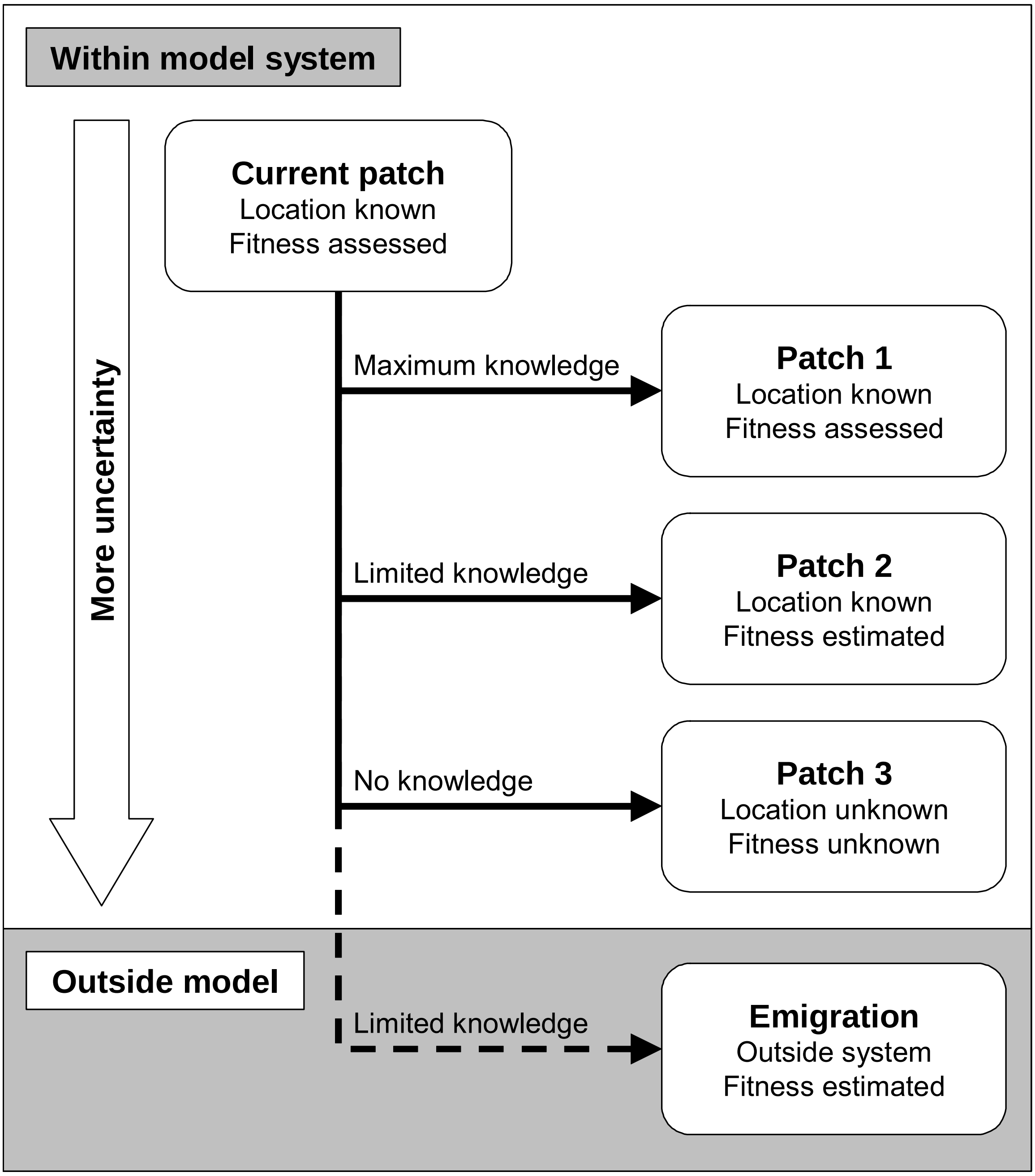


Figure 6.2 How uncertainty is incorporated into the model. Foragers are assumed to be able to assess the fitness measure associated with consuming different diets on their current patch. Other patches fall into one of three different categories. (1) Foragers may know the location of a different patch and be able to assess fitness measures on the patch (e.g. Patch 1). (2) Foragers may know the location of a patch, but not be able to assess the fitness measures associated with different diets (e.g. Patch 2). In this case the estimated fitness measure on the patch is used. (3) Patches may be of unknown location (e.g. Patch 3). Emigration from the system also has an expected fitness measure. Although, the figure shows increasing uncertainty associated with increasing distance between patches, this does not have to be the case.

While moving, forager's metabolise their component stores at a rate determined by the moving metabolic rate. The change in component reserve size while moving is.

$$C_{final} = C_{initial} - N_{timestep} T_{timestep} M_{moving} \tag{6.10}$$

where C_{final} = final component reserve size after moving, $C_{initial}$ = initial component reserve size and M_{moving} = rate of metabolising / excreting component while moving.
For simplicity, it is assumed that foragers cannot make any decisions while moving between patches, but can die while moving.

6.8.6 Forager diet consumption and physiology

A submodel parameter is read in to calculate the diet consumption rate of foragers of each forager type / species. The efficiency of assimilating each component from the resources in the diet to the body (i.e. the proportion of the component in the diet that is transferred to the body) is also read in as a submodel parameter. Both submodels can depend on any forager constant or variable, patch state variable or global variable. The rate of assimilating a component is calculated from.

$$I_{assim} = aC_{diet} I_{diet} \tag{6.11}$$

where I_{assim} = rate of assimilating component, a = efficiency of assimilating the component, C_{diet} = density of component in the diet and I_{diet} = rate of consuming the diet.
The amount of the component assimilated during a time step also depends on the proportion of time spent feeding during the time step. The proportion of time spent feeding can be limited in two ways.

Regulation of diet consumption rate

Regulation of component reserve size

Regulation of diet consumption rate. A submodel is used to calculate the maximum diet consumption rate ($I_{\max}$) during a time step. The maximum proportion of time that can be spent feeding ($P_{\max}$) is calculated from.

$$P_{\max} = \frac{I_{\max}}{I_{diet}} \qquad \text{if } I_{diet} > I_{max} \tag{6.12}$$

$$P_{\max} = 1 \qquad \text{if } I_{diet} \leq I_{max}$$

Regulation of component reserve size. If the forager were to feed for P_{max} of the time step, its component reserve size at the end of the time step would be.

$$C_{final} = C_{initial} + T_{timestep}\left(P_{\max} I_{assim} - P_{\max} M_{feeding} - (1 - P_{\max}) M_{resting}\right) \tag{6.13}$$

where C_{final} = final component reserve size at end of time step, $C_{initial}$ = initial component reserve size at start of time step, $M_{feeding}$ = rate of metabolising / excreting component while feeding and $M_{resting}$ = rate of metabolising / excreting component while resting. The model uses a parameter submodel to calculate the target component reserve size (C_{target}) during any time step. The required proportion of time needed to exactly match this target, or approach it as closely as possible is found by setting C_{final} to C_{target}, and P_{max} to P_{target} and rearranging the previous equation.

$$P_{target} = \frac{C_{target} - C_{initial} + T_{timestep} M_{resting}}{T_{timestep}\left(I_{assim} - M_{feeding} + M_{resting}\right)} \quad \text{if } \frac{C_{target} - C_{initial} + T_{timestep} M_{resting}}{T_{timestep}\left(I_{assim} - M_{feeding} + M_{resting}\right)} \leq 1 \tag{6.14}$$

$$P_{target} = 1 \quad \text{if } \frac{C_{target} - C_{initial} + T_{timestep} M_{resting}}{T_{timestep}\left(I_{assim} - M_{feeding} + M_{resting}\right)} > 1$$

where P_{target} = proportion of time that forager needs to feed for to match its target or approach it as closely as possible.
The actual proportion of time spent feeding depends on the value of P_{max} and the values of P_{target} for each component in the diet. The model attempts to exceed or match the target reserve size for each

component, with the constraint that the proportion of time feeding cannot exceed P_{max}. It does this by comparing the maximum value of P_{target} with P_{max}.

$$P_{feed} = \max\left(P_{target}\right) \quad \text{if } \max\left(P_{target}\right) \le P_{\max} \qquad (6.15)$$

$$P_{feed} = P_{\max} \quad \text{if } \max\left(P_{target}\right) > P_{\max}$$

where P_{feed} = proportion of time feeding during time step. The component store size at the end of the time step is then found from.

$$C_{final} = C_{initial} + T_{timestep}\left(P_{feed} I_{assim} - P_{feed} M_{feeding} - \left(1 - P_{feed}\right) M_{resting}\right) \qquad (6.16)$$

6.8.7 Forager mortality

A submodel parameter is read to calculate the probability of surviving each fitness component based on a forager's state, and any combination of global or patch variables. A uniform random number generator is used to determine whether each of a forager's individuals die as a result of any of the fitness components. In the event of two or more fitness components leading to the mortality of an individual, one is selected at random. When all the individuals in a forager die, the forager is removed from the simulation.

6.8.8 Prey intake rate

The prey intake rate achieved by a forager depends principally upon two factors; the density of prey resources available to it and the density of competitors around it. These two factors are often related in that patches with a lot of food resources may attract a lot of competitors. This in turn may result in a rapid rate of prey depletion in such patches such that the density of prey resources and hence achievable intake rate falls via depletion competition. The particular formulation of the sub model used to calculate prey intake rates in the case of common scoter as a function of resource density is described in section 7.2.9. The presence of high densities of conspecifics can also reduce the prey intake rate achieved by a forager through the other principal source of intraspecific competition i.e. interference (Stillman et al*.* 1996, 1997, 2002; Triplet et al. 1999; Yates et al. 2000). This form of competition may operate through direct kleptoparasitism i.e. theft of prey items, by reduced searching efficiency due to the need to avoid such encounters, or through reduced prey availability in the case of prey that respond behaviourally to the presence of their predators. The model is constructed such that the effects of this form of competition can also be incorporated. However, as there are no quantitative data on the magnitude or indeed of the existence of interference competition amongst common scoter, this competitive process is not included in the current version of the Liverpool Bay system (other than specifying a maximum limit to the number of common scoter that can occur in a given area (see section 7.2.7).

6.9 Summary

This section describes the general features of the new individual-based model (MORPH) developed during the project. The new model is much more flexible than its predecessors and is capable of making predictions for this particular system and indeed other systems that may be of interest in the context of other renewable energy development schemes including both onshore and offshore windfarm developments and tidal barrages. The specific details of how MORPH was set up to simulate common scoter feeding on benthic prey in Liverpool Bay and the influence on them of the presence of offshore windfarms are described in sections 7 and 8.

7. Literature review

7.1 Introduction

The model MORPH described in section 6 is coded in such a way that it has no system-specific features. It is entirely generic and has the flexibility to be applied to a very wide range of consumer-resource systems, subject to appropriate parameters being available. De Leeuw (1997i) developed an ecological energetic approach to elucidate the patterns in the distribution and patch exploitation of diving ducks wintering in a freshwater environment. De Leeuw (1997i) stated that "It would be a challenge to extend the approach to other trophic systems for example…to other diving duck species such as eider and black scoter feeding on bivalves in the marine environment." The literature review described in this section served, in combination with work described in sections 2-5, to enable us to use the model MORPH to do so.

7.2 Results of Literature review

In the course of the literature review in excess of 100 scientific papers and reports concerning the physiology, diet, energetics, foraging ecology and general behaviour of diving ducks were collated. This served four main purposes. The first objective was to build up knowledge of the way in which diving ducks forage in order to decide upon the way in which the model MORPH would need to be structured and to determine the particular parameters that it would need to incorporate. The second objective was to derive reasonable assumptions on which the model could be based with the justification of being derived from existing studies of diving ducks. The third objective was to derive values for the many parameters that the model would need. The fourth objective was to derive independent empirical data against which model outputs could be validated prior to conducting the novel scenarios.

During the literature review some c 1500 notes were made of points or parameter values that may have proven relevant to the final model. These were entered into an Excel database. Not all of these entries have proven to contribute directly to the model. For the purposes of brevity only those which have proven of direct relevance to the way in which the model MORPH operates, has been parameterised or has been validated, are discussed here. All of the relevant notes are presented in a series of appendices to this report.

Although may of the entries in the database refer directly to scoter, the majority do not. This reflects the inaccessible nature of the habitat in which the birds live during the winter months. Common scoter spend the majority of the year on the sea, often sufficiently far from shore not to be easily observed from land. Thus, in meeting each of the four principal objectives of the literature review it was necessary to utilise information derived from studies of other species of diving duck. Although this is not ideal, there is no alternative. In any case it is unlikely that any serious errors have been introduced by this necessary reliance on data derived from birds other than scoter.

The literature review yielded information concerning 16 key areas of the ecology of diving ducks and these are discussed in turn in the following sections. The appendix number in which the relevant notes from the database can be found is given in the heading to each section.

7.2.1 Foraging behaviour (appendix 1)

All previous applications of the model MORPH and its predecessors have concerned over wintering populations of birds foraging in intertidal or terrestrial habitats (Pettifor et al 2000; Stillman et al. 2000b, 2001, 2003; West et al. 2002, 2003; Caldow et al. 2004; Durell et al. 2005). All of these models have been based on the assumption that fitness maximisation by individual birds equates to the maximisation of instantaneous intake rate by which birds aim to minimise the risk of starvation. Generally, the models have addressed issues at the scale of single estuaries and have assumed that all birds have perfect knowledge of the potential rewards in all available patches at every point in time i.e. that they are ideal, and that because of the small spatial scale involved, are also free to reach any available patch at no travel cost. In other words birds are assumed to follow the ideal free distribution (Fretwell & Lucas 1970). The general result of these assumptions is that, subject to the intensity of interference competition and the magnitude of individual variation in susceptibility to interference and in foraging efficiency, birds tend to exhibit a positive numerical response i.e. the density of birds tends to be higher in places where the density of food is greater. This is generally the pattern that is observed in reality at a range of spatial scales. While all of these assumptions can be taken as reasonable in the contexts to which the model has been applied thus far, the question in the current context is whether the same assumptions can hold. Is the assumption that birds can update their knowledge of the potential rewards on all available patches with perfect precision on an hourly basis realistic given that the resources on the seabed are not readily visible and given the size of Liverpool Bay? In order to answer these questions and to formulate the assumptions on which the model of common scoter in Liverpool Bay should be based, the first task of the literature review was to collate information of the way in which diving ducks distribute themselves in a heterogeneous environment.

A number of studies have indicated that, as might be expected, diving ducks tend to aggregate in places where feeding is most profitable because their food is most abundant or because the water is shallower (e.g. Stott & Olson 1973; Pedroli 1982; Tome 1988; Giles 1989, 1990; Meissner & Brager 1990; Phillips 1991; Guillemette et al 1996; de Leeuw 1997h). De Leeuw (1997b) found that areas with highly profitable mussels received more attention from ducks. This could be ascertained at various levels of scale: lake, region, site and patch. He also found that ducks are not only able to recognise and to respond to differences in mussel density, but also to different quality over short distances. Several studies of diving animals provide support for the idea that these animals maximise their rate of net energy intake while foraging (Tome 1988; Phillips 1991; Mori & Boyd 2004). These studies suggest that a model of benthic feeding divers could justifiably be based on the assumption of maximisation of net rate of intake and perhaps that this can occur over a range of spatial scales.

A number of other studies contend that there is more to the distribution of diving ducks than this. Fox (2003) stated that there is more to habitat selection (of common scoter) than just benthic community and sediment type. Degraer et al (1999) suggested that a combination of food availability and the lack of disturbance, by fishing activities for instance, determine the spatial distribution of common scoter. The results of experimental manipulations of the foraging conditions presented to captive tufted ducks led Carbone & Houston (1994) to conclude that factors other than energetics influence the choice of foraging areas by diving ducks. They suggested that certain risks involved in diving at greater depths may exist which offset the otherwise greater energetic profitability of deeper patches in their experiments. Several other studies have indicated that diving ducks may distribute themselves equally between areas that provide (net) intake rates above some acceptable threshold level i.e. that they 'satisfice' rather than ' rate maximise'. For example, Lovvorn & Gillingham (1996) found that wild canvasbacks did not find high density loci and deplete them disproportionately, but appeared to feed in all loci encountered with profitable food densities. Guillemette et al (1996) found that the cumulative utilisation of most reefs of mussels by common eiders was proportional to their surface area. This suggests that eiders tend to deplete each patch equally during the winter. Brager et al (1995) suggested that certain sections of the common eider population probably seek habitats offering a stable but less profitable intake to improve their survival probability. De Leeuw (1997b) found that across lake Ijsselmeer the number of scaup bird days in a 2 x 2km grid cell correlated best with biomass in those cells where the probability of encountering mussels was at least 70% (i.e. >=7 out of 10 grab samples contained mussels). If cells with lower probabilities, or indeed all cells, were included, the relationship between bird days and cell biomass became weaker. In other words the distribution of scaup was less clearly related simply to the abundance of resources within a patch than it was to the abundance of resources within patches where there was some 'acceptable' probability of finding the profitable areas. Similarly, the number of scaup correlated well with the number of grid cells within an area that met the profitability criteria of having sufficiently high biomass (i.e. above the threshold density of 50gfw/sqm) and shallow depths. De Leeuw (1997b) concluded that the choice of a certain foraging area by a flock of several thousand birds is probably influenced by the average quality of the site rather than by peak densities which only a limited number of birds will experience in a patchy environment.

Although diving ducks may be able to respond to variations in the distribution or quality of the food supply at relatively fine spatial scales, the fine grain or first order patchiness of the food supply as perceived by the ducks cannot be exactly assessed because bottom samples, such as those taken by de Leeuw (1997b) or in the present study (see section 3) cover a much smaller area than a diving duck can scan in a single dive. Therefore diving ducks may perceive a more homogeneous distribution of benthos than expected from the variation in the bottom samples. Hence de Leeuw (1997b) concluded that considering larger scale variation at the level of patches is more appropriate for diving ducks. Accordingly, in one test of the ecological energetic model that he developed de Leeuw (1997b) defined grid cells of 2 x 2km with average densities of more than a certain threshold biomass density as a functional feeding unit which can sustain a flock of ducks for several days. Thus, the use of c 3.5 x 3.5km grid cells in the model MORPH and the use of average interpolated resource abundances across entire cells appears a reasonable basis on which to model the distribution of common scoter at the scale of Liverpool Bay.

De Leeuw (1997b) showed under-use of some rich patches by diving ducks within the Ijsselmeer. He attributed this to imperfect knowledge of the environment. Kirby et al (1993) noted that at least some flocks of common scoter appear to remain faithful to the same areas throughout the winter. Even in the Moray Firth where there are at least three alternative sites in close proximity, there has been no evidence of any regular interchanges (Kirby et al 1993). Such site faithfulness must contribute to imperfect knowledge at the wider scale and this may in turn lead to under-exploitation of rich areas. Kirby et al (1993) also noted that no regular dawn or dusk movements by common scoter have been described and noted that it is presumed that common scoter remain to roost in or close to their daytime feeding areas. This behaviour must also constrain the knowledge of the wider environment that birds can have.

In conclusion, much of the data concerning diving ducks suggests that although they may be able to respond to fine scale variation in prey abundance or quality within an area, their distribution at the spatial scale of Liverpool Bay may best be understood by considering variation in the average prey abundance over relatively large spatial units of the order of several kilometres. This is what has been done in the model MORPH. There is considerable evidence that diving ducks may distribute themselves across all areas that provide a level of intake, or probability of an acceptable intake, that exceeds some threshold value i.e. that they ‘satisfice’ rather than ‘rate maximise’. Thus, in the model of common scoter in Liverpool Bay it is assumed that the birds ‘satisfice’ rather than ‘rate maximise’. It is further assumed that common scoter remain on their daytime feeding grounds at night and that accordingly they have a relatively restricted radius of knowledge around their existing location. This is discussed more fully in section 8.6.5.

7.2.2 The diving sub-MODEL (appendices 2 & 3)

The literature review yielded only two studies in which the diving behaviour of scoter was studied in any detail. One of these (Dewar 1924) has been utilised in constructing the diving sub-model used in MORPH (see below). The other (Richman & Lovvorn 2003) yielded the functional response (section 7.2.9) but gave no information on the bird’s diving behaviour *per se*. Thus, in deriving the diving sub-model we have relied upon information gleaned from studies of many other species of diving duck and have assumed that scoter will follow the same general rules.

Common scoter, like all diving ducks, forage by diving underwater, and like most diving ducks, gather their food from the bottom substrate. They forage in so called ‘dive bouts’ during which they make repeated dives to the seabed, returning to the sea surface between dives. The duration of time between the beginning of one dive and the beginning of the next is often termed a ‘dive cycle’. Over the course of a diving cycle, diving ducks only gather food while on the bottom, the time spent travelling to and from the water surface and recovering between dives on the surface being essential but unprofitable components of their foraging behaviour. In order to determine the rate at which common scoter acquire food over the course of a dive cycle it is, therefore, necessary to be able to predict the duration of each dive cycle and to predict the duration of its four key components i.e: i) the time spent underwater, ii) the time spent travelling to and from the seabed, iii) the time spent foraging on the seabed and iv) the time spent on the surface between dives. The time spent recovering from a dive bout is included in the model in the proportion of each hourly time step that birds are assumed to rest i.e. not engaged in sequences of dive cycles.

Many studies of diving ducks have recorded the time that they take to descend to the bottom and to ascend to the water surface. Many studies have found that while birds descend by active propulsion, they ascend passively (Hawkins et al 2000) and often ascent occurs more quickly than descent. Many studies have noted that the relationship between return travel time and depth is strongly linear suggesting that rates of travel are approximately constant with respect to depth. Other studies of diving ducks have therefore assumed this to be the case (e.g. Beauchamp et al 1992). There are no empirical data on the speed at which common scoter swim between the sea surface and the seabed.

However, the literature review yielded 26 estimates of the speed with which ducks travel to and from the surface. Six estimates of the rate of ascent averaged 0.982 ms^{-1}. Sixteen estimates of the speed of descent averaged 0.774 ms^{-1}. The average of these two values was 0.878 ms^{-1} and this was assumed to be the speed at which common scoter travel to and from the seabed. The time that common scoter spent travelling to and from the seabed in any given grid cell at any point in time was thus determined from the water depth predicted by the tidal model and this assumed speed of travel.

Dewar (1924) presents a comprehensive set of empirical observations on the duration of the time spent underwater per dive in relation to water depth of a wide range of diving birds. When all the data are combined a highly significant positive relationship between total dive duration and water depth is apparent. This finding has been confirmed in numerous more recent studies (Stephenson et al 1986; Kramer 1988; Beauchamp et al 1992; Carbone & Houston 1994). Given this confirmation of Dewar's findings, this comprehensive dataset, which includes observations on scoter, has been used as the basis of calculations of dive durations with respect to depth in the model MORPH. Dewar's (1924) dataset comprised records of both benthic feeding ducks and pursuit feeding cormorants, grebes, divers, saw bills and auks. Given the potential difference in the behaviour of pursuit divers and benthic feeders, the data from pursuit divers was excluded from the analyses of the dataset used here. Dewar's dataset on benthic feeding species yields a highly significant relationship between the total time spent underwater per dive and the water depth (Fig 7.1). However, this dataset only extends to a maximum water depth of 6.7m. In the model it was necessary to predict dive durations in water over 20m deep. A simple extrapolation of the linear regression to a depth of 20m yielded a predicted dive duration of 120 seconds. This is well in excess of the maximum recorded dive duration of any bird recorded in Dewar's dataset (68s), of common scoter in Dewar's dataset (46s) and of the observed dive durations of common scoter in Liverpool Bay (63s) (see section 4). Thus, it was decided to constrain the predictive relationship to yield a maximum value of 60s underwater per dive. This was predicted to be achieved at a depth of 9m. Thus, in effect the model MORPH assumes that the dive duration of common scoter increases linearly up to an upper ceiling value at a depth of c 9m. This is in accord with the observations of Draulans (1982) who noted that the dive duration of tufted ducks increased up to a depth of 4m and then levelled off.

Dewar (1924) also presented data on the duration of time spent on the surface between successive dives in relation to water depth. When all the data are combined a significant positive relationship between surface time and water depth is apparent. However, this relationship, even when restricted to benthic feeding ducks, is far noisier than that between dive duration and water depth (Fig 7.2). Stephenson et al (1986) also noted that surface times are highly variable. However, other recent studies have confirmed the positive relationship between surface times between dives and water depth (de Leeuw 1997f; Carbone et al 1996). While divers are believed to rely predominantly on aerobic respiration, there is considerable evidence that they may combine aerobic and anaerobic respiration during extended dives (Carbone & Houston 1994; Carbone et al 1996). On the assumption that the rate at which a diver's body can take up oxygen from the air, or deal with the products of anaerobic metabolism, decline with increasing concentration of these materials in the body, Houston & Carbone (1992) Carbone & Houston (1994, 1996) and Carbone et al. (1996) developed models which predicted that the rate of increase of surface time durations as water depth increases should not be linear but should exhibit one or more rapid increases as various shifts in the bird's physiology occur. Carbone et al (1996) demonstrated that this is indeed the case in tufted ducks and pochard. In both cases, these birds exhibited a pronounced increase in the rate at which surface time increased with water depth at water depths (c 3m) at which the total time spent underwater per dive was far less (c 24s) than the estimated maximum aerobic dive limit of tufted ducks i.e. c 44s (Woakes & Butler 1983). In pochard, the rate of increase in the surface time with increasing water depth was c 3.5 times greater above the threshold depth value than below it (Carbone et al. 1996). Thus, in the model MORPH it is assumed that the rate of increase in surface time between dives increases linearly with water depth up to 4.5m according to the equation fitted to Dewar's dataset (Fig 7.3) and to increase faster than this between depths of 4.5 and 9m, the depth at which the total dive duration was limited to 60s. This yielded a maximum surface time between dives of 82s. This served to mimic the likely decrease in the efficiency with which diving ducks can achieve metabolic equilibrium as they approach limits to their aerobic (or anaerobic) capacity.

The maximum time per dive that common scoter could spend on the seabed foraging in a given grid cell at a given point in time was calculated in the model by deducting the predicted total travelling time from the predicted total time spent underwater per dive. With the assumed speed of travel and dive duration function described above, foraging time per dive initially increased with water depth (up to a depth of 10m) and then declined to 0 seconds at a depth of c 25m (Fig 7.3). Several studies have noted that the increase in foraging time with depth is indeed non linear, either increasing to an upper asymptote (Carbone 1995; Carbone et al 1996), or declining again as depth increases further (Carbone & Houston 1994). Initially as the water depth increases, the travel time increases and so the diver must increase the size of its oxygen stores to allow for more foraging time, in order to reduce the number of trips between the surface and the foraging site. As depth increases further and the diver approaches its maximum dive duration, foraging time must decrease to compensate for increasing travel time (Carbone & Houston 1994). The diving model used in MORPH is therefore consistent with the models of Houston & Carbone (1992) and Carbone & Houston (1994). The result of all of these calculations is that the proportion of dive cycle that is devoted to foraging decreases steadily with increasing depth and approaches 0 at c 25m (Fig. 7.3). This is consistent with the findings of Carbone (1995) and Carbone et al (1996).

Thus, in the model MORPH, the time that common scoter spend in all four phases of the dive cycle are calculated as a function of water depth on the basis of relationships derived from and consistent with existing studies. It is unfortunate that the lack of direct studies of the diving behaviour of common scoter means that scoter-specific information has contributed very little to this dive-model and that the validity of the dive model cannot be tested against independent empirical data concerning the behaviour of common scoter. However, given the current state of scientific knowledge concerning the diving behaviour of ducks there is no alternative but to proceed on the basis described above. Some confidence in the validity of this approach can be gained from the consistency between the maximum recorded dive depths of common scoter (*circa* 20m) and the predicted decline in the proportion of time available for feeding to a value of near 0 at depths over 20m. It can only be hoped that by being based on the best available information concerning other benthic feeding ducks, the dive model is as good an estimate of the behaviour of common scoter as it is possible to obtain at present.

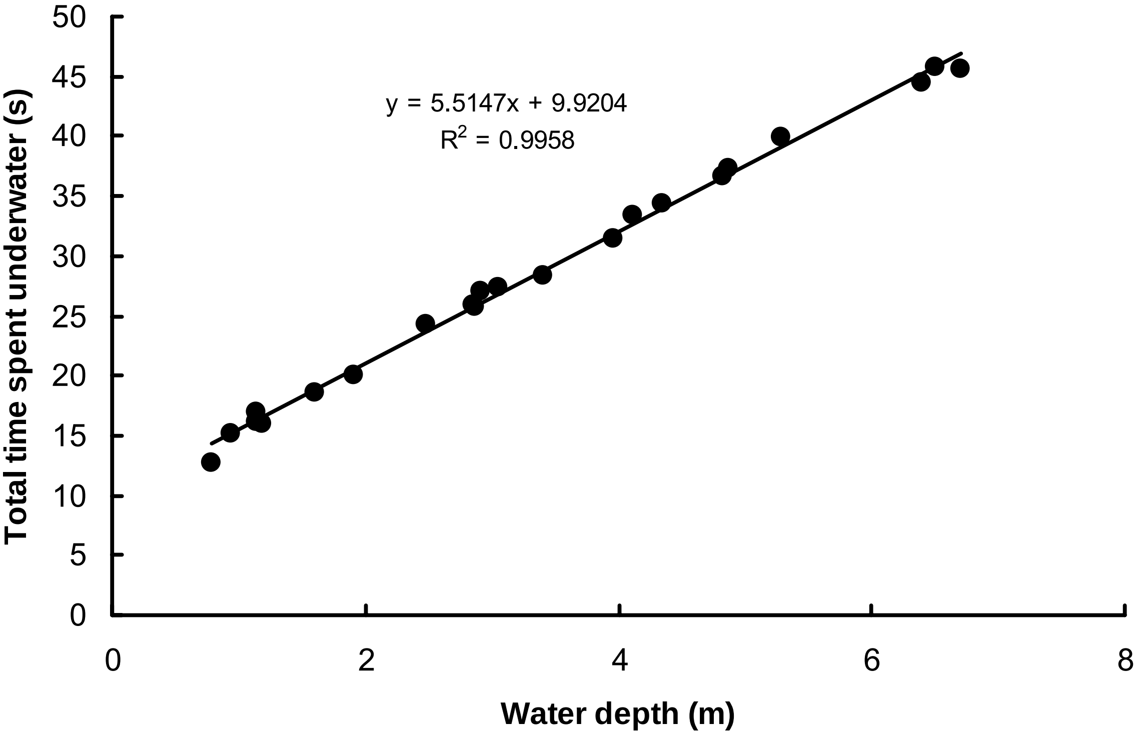


Figure 7.1. Relationship between the total length of time spent underwater per dive by benthic feeding ducks and the water depth in which the bird was diving (data derived from Dewar (1924)).

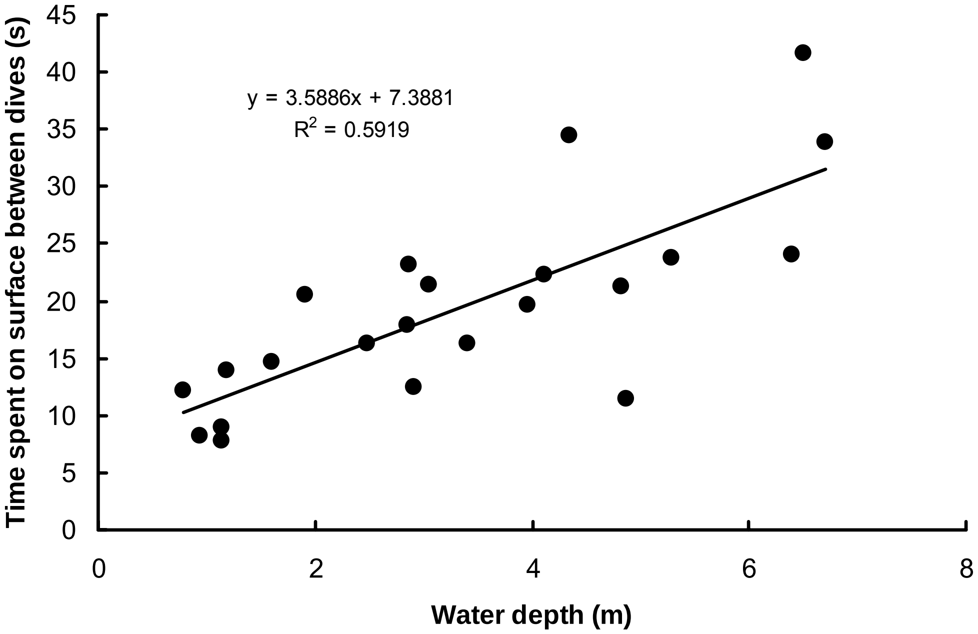


Figure 7.2 Relationship between the total length of time spent on the surface of the water between successive dives by benthic feeding ducks and the water depth in which the bird was diving (data derived from Dewar (1924)).

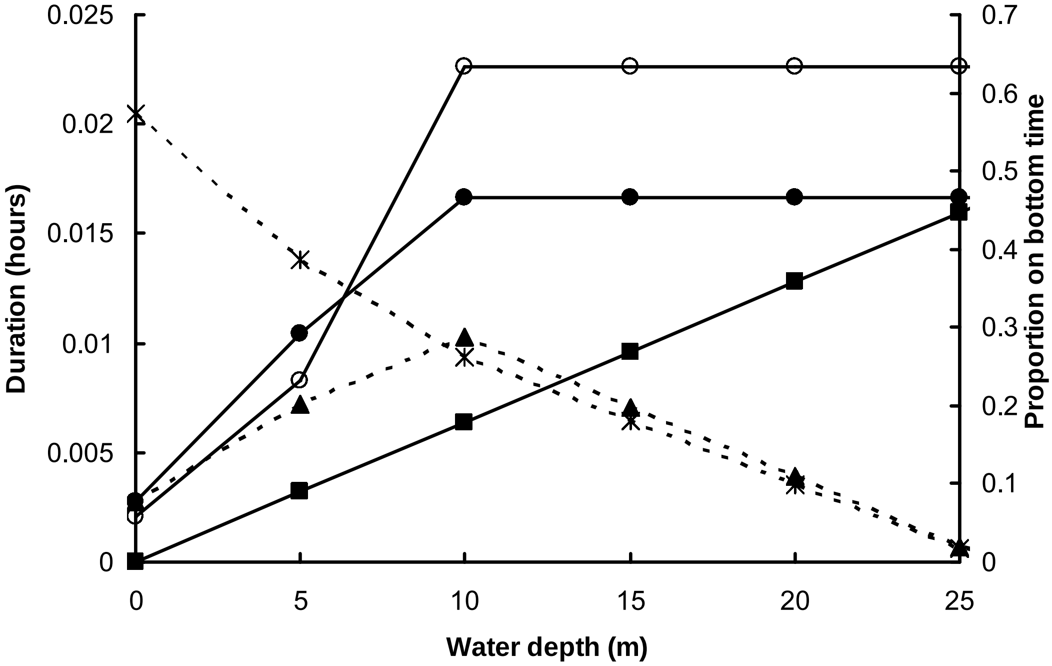


Figure 7.3 The diving sub model within the model MORPH is based on the relationships between the depth of water and: i) the total time spent underwater per dive (filled circles), ii) the time spent on the water surface between dives (open circles), iii) the time spent in transit between the surface and the seabed per dive (filled squares), iv) the time spent on the seabed per dive (filled triangles) and v) the resultant proportion of a dive cycle that is spent feeding on the bottom (asterisks).

7.2.3 Day/night feeding activity (appendix 4)

Eleven papers made reference to the tendency of diving ducks to feed by day or by night. In general it would appear that ducks such as tufted duck and pochard that feed in freshwater habitats feed principally at night (Pedroli 1982; de Leeuw 1997a) in contrast to sea ducks which feed principally during the day (Cramp & Simmons 1977; Goudie & Ankney 1986; Kirby et al 1993; Guillemette 1998; Systad et al 2000; Systad & Bustnes 2001). All references to the foraging behaviour of scoter (with one exception (Durinck et al (1993))) state that scoter of all species are diurnal feeders (Cramp & Simmons 1977; Goudie & Ankney 1986; Kirby et al 1993). Guillemette (1998) concluded that common eiders in winter forage mostly during the day and that night foraging if any is rare. They stated that night feeding is related to the digestion constraint and ingestion of a large bulk of shell material associated with eating large molluscs. Systad & Bustnes (2001) concluded that Steller's eiders are most likely to feed during daylight and twilight, but that they also fed during darkness. Guillemette (1998) noted that although some authors have stated that eiders and sea ducks in general are diurnal feeders, none has presented evidence to support this. Durinck et al (1993) did provide evidence that common scoter can feed at night. He noted that birds were found drowned in fishing nets set on the bottom and laid out overnight. Thus, it would seem that diving ducks in general and scoter in particular are able to feed at night but under most circumstances may not do so. Given that they almost certainly feed by touch on the seabed rather than visually it is unclear why this should be the case. Pedroli (1982) noted that most species of diving ducks (feeding in freshwater habitats) feed during the night and rest during the day. In the great number of cases nocturnal feeding by these ducks was attributed to human disturbance on feeding grounds, during the day, mostly near the shore (Pedroli 1982). On the assumption that diurnally feeding scoter may also respond to reduced feeding opportunities (due for example to increased daytime disturbance by windfarm maintenance traffic) by feeding at times that they normally do not, night-feeding may be a behavioural response similar to the daytime response noted by Pedroli (1982).

It was decided that in the first instance, simulations would be conducted under the assumption that common scoter only fed during daylight. This assumption is consistent with a precautionary approach. However, in recognition of the possibility that diurnally feeding common scoter may respond to reduced daytime foraging opportunities by foraging at night, simulations were repeated in which common scoter were allowed to feed at night too. The differences between the predictions under these two assumptions indicate the extent to which any predicted consequences of windfarm development on common scoter may be offset if their behavioural response to environmental change is to feed at night as well as during the day.

7.2.4 Depletion (appendix 5)

Twelve studies made reference to the rate at which diving ducks deplete their resources. All studies record that predation by diving ducks reduces the abundance of their prey. However, the magnitude of this effect appears to vary considerably between studies. The absolute lowest value amounted to only 3% of the biomass or stock being consumed. The absolute maximum value equated to 70% of the food stocks being removed. The average of the minimum values recorded was 21%, the average of the mean values recorded was 31% and the average of the maximum values recorded was 47%. Such variation may stem from variation in the way in which the food supply is defined and the spatial scale over which the depletion is measured. Many studies demonstrate that depletion tends to be most pronounced in those locations where it is most profitable for the birds to feed i.e. areas with initially high densities of food and/or shallow water (Nillson 1972; Draulans 1982; Nehls & Ketzenberg 2002). Several other studies note that depletion of such areas leads to shifts in either the diet or the distribution of the ducks over time and that depletion of resources may in fact be the principal driving factor in the changing distribution of diving ducks (Lovvorn 1989; Guillemette et al 1996; de Leeuw 1997b; Sekiya et al 2000; Guillemette & Larsen 2002). Only one study referred specifically to depletion by scoter. Stott & Olson (1973) noted that, superficially it appeared that the food resource had not been severely depleted by the scoter population. However, they also cite Glude (1967) who found that an increase in the number of scoter in a coastal shellfish area of Washington caused a reduction in numbers of commercial soft shelled clams. Thus, in scoter as in other sea ducks there appears to be variation between studies in the extent to which they deplete their resources. However, given that depletion would seem to be an important factor in the distribution of many species of sea duck the model, as in all previous applications concerning predation by birds on over-winter shellfish stocks, takes into account that consumption by scoter will result in a reduction in the remaining resources on a day to day basis through the winter.

7.2.5 Diving depth (appendix 6)

Eighteen studies made reference to the water depth in which diving ducks have been recorded. The data presented in Dewar (1924) is discussed above in the context of the construction of the diving sub-model. Of the other 17 studies, 11 refer to the diving depths of scoter. The absolute minimum value recorded for common scoter is 1m and the absolute maximum value is 30m. The average of the minimum values given is 4.5m, the average of the mean values given is 9.6m and the average of the maximum values given is 14.2m. The variation between the depths in which scoter are recorded foraging reflects to a large extent variation in the water depth in the location where the study was conducted. For example studies in the breeding season in e.g. Iceland where depths of 1-3m are considered normal probably relate to birds foraging in shallow freshwater lakes. Similarly, the low maximum recorded depth in the Kattegat in spring (9.4m Fox 2003) probably reflects the shallow water in this area. However, the general picture that emerges is that common scoter usually forage in water shallower than 20m and only very occasionally forage in deeper water. The diving sub-model (section 7.2.2) predicts that the proportion of time that scoter can spend foraging on the seabed per dive cycle declines to virtually 0 at 25m. There is, therefore, consistency between this model and the independent observations of foraging scoter. It is, therefore, assumed in the model that areas of Liverpool Bay in which the water is always deeper than 20m are not habitat that the scoter can exploit. Thus, all tidal grid cells where the depth of water is predicted by the tidal model (see section 2) to exceed 20m at low water spring tides were excluded from the model.

7.2.6 Individual variation (appendix 7)

Individual variation in the intake rate of foraging animals arises largely from variation in two individual characteristics: i) foraging efficiency, their intake rate in the absence of conspecifics, and ii) susceptibility to interference, the immediate and reversible detrimental effect on their intake rate caused by the presence of competitors (Goss-Custard & Durell 1987, Sutherland 1996, Goss-Custard & Sutherland 1997, Caldow et al 1999, Stillman et al 2000a). There are no data on the extent to which common scoter differ from one another in their efficiency as foragers. Indeed there is very little information on this matter in diving ducks in general. Tome (1988) compared the slopes and intercepts of the energy gain functions among individual ruddy ducks within a patch density and found no difference in slopes or intercepts. However, in terms of optimal foraging efficiency (i.e. when birds chose to leave patches) Tome (1988) found that this differed between individual ruddy ducks - some birds behaved closer to optimality than others. In studies of tufted duck Draulans (1984, 1987) found that among 4 captive ducks the most profitable size class of mussel varied between 12.5-15mm and 20-22.5mm. Draulans (1984, 1987) concluded that this variation can only stem from variation in the speed with which different birds handled mussels of different sizes.

In contrast to diving ducks, there is good experimental evidence of considerable variation in the feeding efficiency of captive dabbling ducks (Fritz et al 2001; Durant et al 2003). However, perhaps the best example of the quantification of the variation in feeding efficiency between individual birds feeding on bivalve prey is that of colour-ringed oystercatchers feeding on intertidal mussel beds (Goss-Custard and Durell 1987). In this case, the standard deviation in feeding efficiency around the population mean value is around 12.5% of the mean value (Stillman et al 2000b). Given the paucity of data concerning common scoter and the fact that tufted duck when feeding on mussels exhibit individual variation in their feeding efficiency, much as oystercatchers do, the model assumes that the variation in feeding efficiency amongst common scoter feeding on benthic bivalves is of the same magnitude as that of oystercatchers feeding on benthic bivalves. Thus, the feeding efficiency of each individual within the population of common scoter is drawn from a normal distribution, with a mean of one and a standard deviation of 0.125.

7.2.7 Interference (appendix 8)

Observations of displacement of one individual by another and of aggression between foraging diving ducks have been made in the case of canvasbacks (Lovvorn 1989; Hohman 1993) and common eider (Ashcroft 1976; Nehls & Ketzenberg 2002).These observations are consistent with the existence of intraspecific interference. Although interspecific aggressive behaviour is rarely observed in free living ducks the segregation of different species might well be a result of interference competition (de Leeuw

1997i). De Leeuw (1997i) also suggested that intraspecific interference competition can also explain the tendency for segregation between males, females and juveniles within species of diving duck. Thus, although the underwater foraging that characterises diving ducks means that with the exception of Ashcroft (1976) there is very little direct evidence of interference amongst foraging diving ducks (i.e. a negative effect of density on the rate of food intake) or of the role of social status in this form of competition for access to resources, there are observations of several species of diving duck that are consistent with the existence of interference. The lack of quantitative data concerning the strength of interference in diving ducks (i.e. the slope of the interference function) meant that it was not possible to use any such values in the model. However, the effects of interference typically are only observable (i.e. result in a decline in intake rate) once the density of competitors has exceeded some threshold value (Stillman et al 1997). Thus, it was assumed in the model that above some threshold density of common scoter, the intake rate of all individuals would be reduced to such an extent that it would be more profitable to feed elsewhere. In the model this was achieved simply by setting an upper limit to the density of common scoter in a grid cell. This ceiling was set at 4,140 birds per grid cell. This was the maximum observed count of common scoter in any one grid cell on any of the 8 over flights. The maximum density used in the model is therefore consistent with the maximum density of common scoter at the spatial scale relevant to the model.

7.2.8 Diet and size selection (appendices 9 & 10)

Eighteen publications made reference to the food of common scoter, velvet scoter or surf scoter. These included two compilations of information (Cramp & Simmons (1977) and Fox (2003)). In total these papers yielded 429 records in the database. Of these, 351 records related to the diet of scoter in marine or brackish habitats and referred to a particular taxonomic group of prey (Table 7.1). 63% of these records referred to bivalves. This percentage varied between the three scoter species being higher in the common scoter (67%) than in either velvet scoter (55%) or surf scoter (58%). 82% of the records that related to prey items in the diet of scoter in general referred to bivalves. This very crude analysis of the dataset clearly indicates that molluscs in general and bivalves in particular are the most important type of prey for scoter, especially common scoter. However, this is a very crude analysis, based as it is simply on counts of the number of times information of interest concerning a given species was presented in a paper and was thus entered in the database.

The literature review yielded 8 quantitative analyses of the diets of common scoter. The results of these studies are summarised in Table 7.2. It is clear that in all studies, the importance of molluscs in general and bivalves in particular is even more pronounced than in the simple analyses of the literature review database described in Table 7.1. In every study the % value for the occurrence of molluscs (however measured) exceeds 90% and that for bivalves exceeds 88%. Fox (2003) concluded that the local distribution and abundance of scoter is likely to be strongly influenced by the local abundance and availability of bivalves. As a consequence of these findings we have assumed that bivalves are the only prey resources of any significance that are exploited by common scoter in Liverpool Bay.

The literature review yielded a total of 30 species of bivalves within the diet of common scoter. Fox (2003) stated that scoter take the most abundant bivalve mollusc species known to be present in the substrate in areas where the birds feed. Common scoter diet appears simply to reflect local abundance, the major constituents of the benthic communities dominating the diet in most studied situations (Fox 2003). The most noted instance of such behaviour concerns the exploitation of a wrecked cargo of horse beans off the German coast at the end of the 19th century which fed 1000 common scoter for over 4 weeks (Cramp & Simmons 1977). Several other studies indicate that sea ducks often concentrate on feeding on one or a few locally abundant resources and will ignore other potential prey items which under other circumstances they have been recorded to feed upon (Lovvorn et al 2003; Richman & Lovvorn 2004). Thus, we assume that all bivalve species found in the survey of Liverpool Bay are potential prey of common scoter.

Several studies report data concerning the size-selection of bivalves by diving ducks. Some studies report diving ducks preferentially selecting smaller prey size classes within the total prey population available to them (Draulans 1982; Bustnes & Erikstad 1990). In contrast Lovvorn et al (2003) report that spectacled eiders consume intermediate-large prey items in preference to small ones. Other studies report that common eider switch between selecting small and large prey items at different times of year (Nehls 1995; Hamilton et al 1999). Fox (2003) stated that it is difficult to differentiate between the hypotheses that scoter select for specific prey sizes or simply take prey in proportion to their availability. In all cases, size selection has been explained by differential handling times, effects on meat/shell ratios on nutrient gain relative to passage rates or as a means of avoiding the risk of ingesting prey that are too large (Lovvorn et al 2003) . In many instances size selection appears to be inconsistent with simple maximisation of gross energy intake. Rather, in many instances, minimisation of the intake of indigestible shell seems to be the factor influencing size-selection (Bustnes & Erikstad 1990; Bustnes 1998; Hamilton et al 1999). It is likely that in all cases size selection patterns, and changes in this over time, can be explained by the maximisation of the net rate at which the birds gain energy from the ingested material, taking into account all the relevant factors. Given the variation in the size selection patterns observed in the literature and that diving ducks seem capable of altering their size selection preferences over time in subtle ways (Nehls 1995; de Leeuw 1997g; Hamilton et al 1999), the model assumes for simplicity that scoter do not exhibit prey size preferences within the overall range of prey sizes that they consume but consume prey of differing sizes in proportion to their abundance.

Nine studies, including the two compilations of information by Cramp & Simmons (1977) and Fox (2003), provided quantitative data on the size of hard prey consumed by scoter. Across these studies the absolute minimum and maximum sizes of hard prey (i.e. excluding one value of 120mm for Arenicola spp.) consumed by common, velvet and surf scoter were as follows: 3mm, 5mm and <10mm respectively and <50mm, 52mm and <50mm respectively. Entries in the database listed as ‘scoter’ i.e. non species specific gave minimum and maximum prey sizes of 6mm and 38mm respectively. Fox (2003) concluded that the presence of large numbers of very small prey items in one sample collected from birds in the Danish Baltic suggested that there is no obvious lower critical threshold that limits prey size since none of the abundant prey was found to exceed 10mm. In contrast, Fox (2003) concluded that there is likely to be an upper limit to the size of hard prey taken. Thus, in the model, there is no lower limit to the size of the bivalves that the scoter can include in their diet. The proposed upper limit for all three scoter species (in the region of 50mm) encompassed all of the bivalves sampled with the exception of large razor clams. Given that these elongate clams are likely to be ingested lengthways, the limited width of the gape or throat may not constrain the maximum length of these prey that can be consumed. We assume that common scoter can consume all the size classes of bivalves found in the benthic survey of Liverpool Bay, including the larger razor clams. Given the scarcity of individuals of this size this is unlikely to be a source of error in the model.

Table 7.1 Summary of the number of entries in the database referring to different prey types in the context of the diet of scoter.

Prey Taxa	Scoter species				
	common scoter	velvet scoter	surf scoter	Scoter spp.	Total number of entries
Annelida	6	5		1	12
Bivalvia	116	69	11	27	223
Crustacea	18	15	4	2	39
Echinodermata	4	6	2	1	13
Pisces	4	6			10
Gastropoda	19	18	2	1	40
Mollusca	7	6		1	14
Total number of entries	174	125	19	33	351

7.2.9 Functional response (appendix 11)

The rate at which a consumer consumes food is often strongly related to the density of resources available to it. The relationship between these two variables is termed the functional response of the consumer to its food. Because of the underwater foraging behaviour of diving ducks their functional responses have seldom been studied. The literature review yielded only 24 published estimates of either the functional response or the intake rate achieved by diving ducks. Only 16 of these were expressed in units of prey items consumed per second on the bottom and 6 of these were single values of intake rate rather than functional responses. Of the 10 equations in the correct format, only 4 concerned ducks feeding on benthic bivalves. These were all presented in a single publication

(Richman & Lovvorn 2003) and were derived from velvet scoter feeding on *Macoma balthica*. As is typical of many functional responses, these all described a Type II curve (Fig. 7.4). The precise shape of the curves varied with the size of the prey items and the depth to which they were buried in the sediment (Fig 7.4). The functional response used in the model used the average of the gradients and asymptotic values of these 4 relationships.

Table 7.2 Summary of the findings of the 8 quantitative studies of the diet of common scoter. N birds denotes the number of individual birds examined. Values represent the percentage of the diet comprising each prey type as assessed by the method listed in the last column. Methods: i) % of birds found to contain items of the taxa in question, ii) % of total number of items identified from all birds sampled, iii) % of volume of gut contents, iv) % of weight of gut contents

Reference	N birds	Mollusca	Bivalvia	Gastropoda	Crustacea	Annelida	Echinodermata	Pisces	Method
Madsen 1954	219	95.9	93.2	10.9	10.9	12.8	0	0	i)
Nilsson 1972	13	100	100	0	0	0	0	0	ii)
Stott & Olson 1973	42	99	98	1	1	0	1	0	iii)
		100	100	12	21*	0	0	0	i)
Bourne 1984	16	94	88	12	56*	0	6	0	i)
Stempniewicz 1986	52	93.9	93.9	0	0	0	0	6.2	iv)
		100	100	0	0	0	0	19.2	i)
Goudie & Ankney 1986	15	100	>95	<5	0	0	0	0	iv)
Meissner & Brager 1990	157	100	100	0	0	0	0	0	iv)
Durinck *et al* 1993	125	100	100	0	0	0	0	0	ii)

* refers to barnacles probably ingested incidentally with mussels *Mytilus edulis*

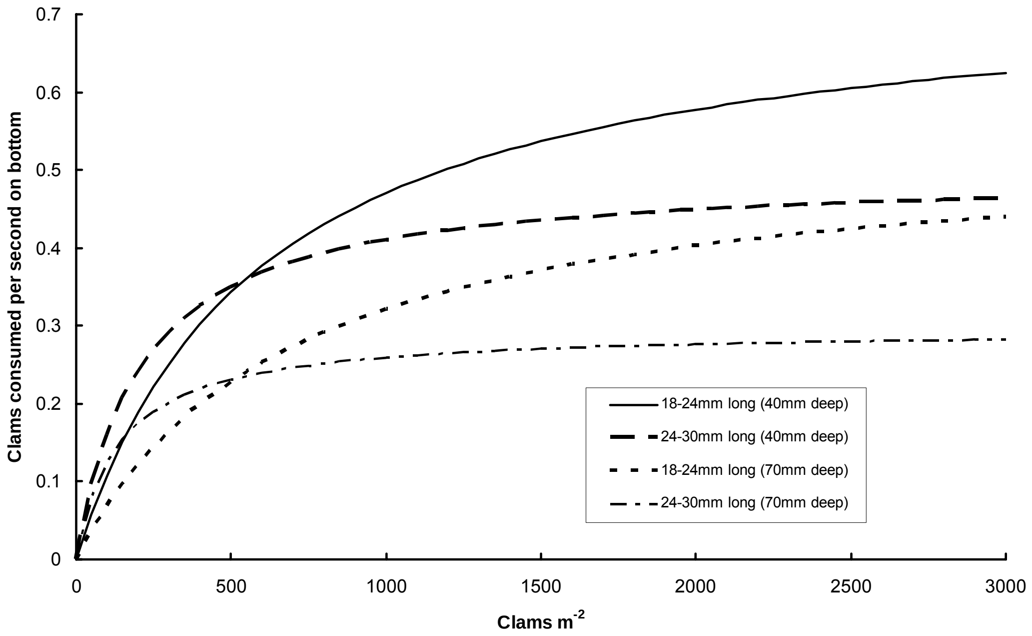


Figure 7.4 Relationship between the rate at which velvet scoter consume Macoma spp. and the numerical density of clams buried in the sediment. Four relationships are shown which differ in the size of the clams offered to the scoter and the depth to which they were buried in the sediment. Data from Richman & Lovvorn (2003).

7.2.10 Energetics

7.2.10.1 Constraints on food intake rates (appendix 12)

In many circumstances the rate at which a bird can find food resources does not limit the rate at which it can assimilate energy. Often, constraints on the rate at which the digestive tract can process food and the physical capacity (i.e. volume) of the digestive tract can limit the rate of energy assimilation. Guillemette (1998) noted that the ingestion rate of shells by common eider is approximately twice as high as the defecation rate and concluded that energy assimilation is constrained by digestion in this species. De Leeuw (1997h) noted that the rate of food processing by scaup is apparently the factor that limits crude intake rate over a period of several hours. This problem is particularly true in animals which, like diving ducks, ingest food which has a considerable indigestible component e.g. the shells of bivalves. The general problem for these birds is thus not to find food (fast enough) but to locate prey with sufficient energy density to fulfil the daily requirement (Bustnes 1998). Furthermore, there is also often a physiological limit to the rate at which the metabolic machinery can operate and this too may impose a constraint on the rate at which energy can be assimilated.

Twelve papers provided values concerning the meal sizes, gut capacities, gut processing rates or maximum daily rates of energy expenditure of diving ducks. Bourne (1984) gives the gut capacity of scoter as 80g fresh mass. De Leeuw (1997h) gives a value of 90g for the gut capacity of scaup. Given the similarity of these values and the wealth of other information concerning the foraging behaviour and diving energetics of scaup provided by De Leeuw (1997a), it is assumed that the value of 90g presented by de Leeuw is a reasonable approximation of the gut capacity of common scoter.

De Leeuw (1997h) observed that the maximum crude intake rate of captive scaup feeding on freshwater mussels *Dreissena polymorpha* was 220g of fresh mass h^{-1}. On the basis of this figure he estimated the throughput time of mussels to be 25 minutes. This is similar to the 30-40 minute throughput time of black duck eating mussels (Grandy 1972 cited in Bustnes & Erikstad 1990). Based on the proportion of the mussels comprising dry flesh, shell and water, the energetic content of the dry flesh and an assumed assimilation efficiency (see below for these values), this 220g of fresh mass equated to a maximum energy assimilation rate of 105 kJ h^{-1} i.e. 29 J s^{-1}. However, the captive birds used in this study had a mean mass of 995g in comparison with a typical over-winter mass of wild scaup of 1300g (de Leeuw 1997i). Scaling these values up in proportion to the extra mass of wild scaup yields a maximum crude intake rate of 287g of fresh mass h^{-1} and a maximum energy assimilation rate of 137 kJ h^{-1} i.e. 38.2 J s^{-1}. Given that common scoter target masses reached 1330g (section 7.2.15), these values were used as the two constraints to the rate at which scoter could consume food and hence the proportion of time that they could spend engaged in active dive bouts over the course of an hour. Although these two values are related, they only yield the same constraint to the number of prey items which can be consumed per hour under the condition that the characteristics of the prey match those of the prey in the study from which they were derived. In the model these two constraints were both converted to the number of prey items consumed per hour.

De Leeuw (1997g) noted that zebra mussels comprise c 56% water, 6% dry flesh mass and 38% shell. Thus, the proportion of the wet matter that comprises flesh in this species is on average 9.7%. The website "http://www.awi-brmerehaven.de/Benthic/Ecosystem/FoodWeb/ Handbook/navlog" gives an overall figure of 0.087 to convert the wet mass of marine bivalves to shell free dry mass. This is very similar to the value of 0.097 given by De Leeuw (1997g). The resource components considered in the model are the flesh dry mass and the shell dry mass per individual prey. The ratio of these varies between size classes and resource types (see section 8.6.4). However, on the basis of the figures described above, it is assumed for simplicity that the total dry mass components of all bivalve resources in the model comprise 40% of their total mass, the other 60% comprising water. Thus, in converting the 287g of fresh mass h^{-1} limit to the birds' intake rate into the maximum allowable number of prey items consumed, the sum of the weighted dry mass per individual prey item in the diet is multiplied by 2.5.

7.2.10.2 Assimilation and storage efficiency (appendix 13)

Only two studies provided data on the efficiency with which diving ducks digest their bivalve prey. Because diving ducks ingest bivalve prey whole, both of these provided values in which the digestive efficiency was calculated for whole bivalve prey. However, in order to take account of the fact that the flesh: shell ratio differs between size classes of prey and between prey types defined in the model (see section 8.6.4) the model treated both flesh and shell as separate resource components (see section 8). Thus, these whole-prey values were not useful. The efficiency with which dry bivalve flesh material is assimilated is 0.85 (Kersten & Visser 1996). This value has been used in the models of de Leeuw (1997i) and Stillman et al (2000b) and is also used here. However, in diving ducks some of the assimilated energy must be used to crush the bivalves' shells in the gizzard and to then digest the material. In captive eiders feeding on *Mytilus edulis* Nehls (1995) found that 8-28% of the assimilated energy at thermoneutrality was used for crushing the mussel shells in the gizzard and a further 19% of the assimilated energy was used for digestion. At low ambient temperatures, however, these additive costs were approximately halved due to the fact that some of the heat generated by these energy consuming activities offset the increased thermoregulatory demands of the birds. On the basis of these figures de Leeuw (1997g) assumed that in winter, scaup eating the much smaller *Dreissena* mussels, utilised, like eider, 9.5% of the energy assimilated to digest their food in winter but only 4% of the assimilated energy to crush the shells of their prey. These values are assumed to apply to common scoter, and results in a final assimilation efficiency of 0.735. There is a further loss in the process of the conversion of assimilated energy to stored mass. This has a value of 0.88 (Kersten & Piersma 1987). This value has been used in the models of de Leeuw (1997i) and Stillman et al (2000b) and is also used here.

The model assumes that no energy is assimilated from the dry mass of shell that birds ingest.

7.2.10.3 Energy density of food and body reserves (appendix 14)

Thirteen studies presented values of the energy density of the prey of diving ducks. Again, many of these referred to the energetic density of whole animals (including shells), or did not refer to bivalves or were presented in units that were inconsistent with those needed for the model. Only 6 studies yielded 8 values for the energy density of the dry flesh of bivalves. These values ranged between 16.37 kJ g dry flesh $mass^{-1}$ to 22.5 kJ g dry flesh $mass^{-1}$. The average value of 18.94 kJ g dry flesh $mass^{-1}$ was used in the model.

The energy density of bird's fat reserves is 39.3kJ g^{-1} (Kersten & Piersma 1987). This value has been used in the models of diving ducks developed by de Leeuw (1997i) and of waders by Stillman et al (2000b), and is also used here.

7.2.10.4 Basal metabolic rate

De Leeuw (1997e) presents several directly measured estimates of the basal metabolic rate of tufted ducks (2.8-2.9 J s^{-1}). The allometric equation (eqn 5.5) of Kendeigh et al*.* (1977) for non-passerines in winter yields a value of 2.8 J s^{-1} assuming a mean mass of 596g for tufted ducks (as also presented by de Leeuw (1997e)). On the basis that this allometric equation predicted the observed BMR of tufted ducks correctly, the same equation was used to predict the BMR of common scoter. Because fat is metabolically inactive tissue, BMR correlates best with lean body mass (Piersma et al 1996). Thus, assuming an average adult lean mass of 728g (see Appendix 19), the resultant value for the BMR of common scoter was 3.2 J s^{-1} or 11.54 kJ h^{-1}.

7.2.10.5 Energetic costs of diving

The energetics of diving by ducks has been the subject of a huge number of research studies. The literature review covered a reasonable number of these but was far from exhaustive. Many of the studies are concerned with extremely detailed quantification of the physiology and hydrodynamics of diving and have involved the experimental measurement of factors such as: heart beat rates, blood flow patterns, rates of oxygen consumption, leg beat frequencies, and assessment of forces such as inertia, body drag and buoyancy. Many investigations have used such information to estimate the rates of work done and energy expended by diving ducks while descending, while on the bottom, while ascending and while on the surface between dives and to assess how the costs of these different phases of diving are influenced by environmental factors such as the depth to which the ducks dive and the temperature of the water. However, the ‘dive cycle’ as a whole has been shown to be a more appropriate metabolic and temporal unit for developing an understanding of the behaviour of divers (de Leeuw 1997e). Even so, de Leeuw (1997e) pointed out that even the average metabolism over a series of dives, including recovery metabolism during breathing intervals between dives may not account for all the metabolic costs of diving. In many instances it has been shown that the body temperature of divers declines after a series of dives and that the metabolic rate may be elevated for more than 1 hour as animals subsequently recover from heat loss or anaerobic metabolism while underwater (de Leeuw 1997e). De Leeuw (1997e) noted that three types of diving costs can be distinguished with reference to the time frame over which measurements are made: i) the metabolic rate during submergence, ii) the average metabolic rate over the dive cycle (MR_d) and iii) the costs of diving as the excess costs over resting costs, including both recovery from heat loss or anaerobic metabolism after a series of dives and all surface activity associated with diving, such as grooming and preening. De Leeuw (1997e) defined the latter as the excess diving costs (EDC) which in contrast to i) and ii) includes the whole period of elevated metabolism due to diving activity and can be applied to entire dive bouts rather than to single dives in a bout.

If full recovery from diving takes place within a dive cycle, the energy expenditure per second spent underwater in excess of the resting rate can be estimated from the difference between (MR_d) and the resting metabolic rate (RMR) allowing for the proportion of time spent underwater. However, if full recovery is postponed until after a dive bout, the time frame over which MR_d is measured will be too short and EDC will be underestimated. De Leeuw (1997e) found that in three studies this was indeed the case, and the underestimation was most pronounced at lower temperatures, demonstrating that conventionally measured MR_d may be a poor estimate of the increase in thermoregulatory costs due to diving in small endothermic divers. In general, the thermoregulatory component of diving costs seems to be underestimated in metabolic studies (de Leeuw 1997e). On the basis of this analysis and experiments on captive tufted ducks (see below), de Leeuw (1997e) concluded that in general, the usual practice of measuring metabolic costs only during diving activity (i.e. i) or ii) above) is insufficient to estimate the total costs of diving. From an ecological perspective, EDC is the most informative measure of diving costs, as it translates directly as the contribution of diving to an animal’s daily energy budget. It is, therefore, the most appropriate measure of diving costs in the current context. Thus, the very large numbers of studies which have examined in great detail the physiology and hydrodynamics of diving have not in general been used to derive the parameters used in the model MORPH. Accordingly the results of these studies, although examined during the literature review process are not discussed further here. The calculations of the energetic costs of diving in the model MORPH are based on the approach proposed by de Leeuw (1997e).This is discussed below.

De Leeuw (1997e) conducted experimental trials with three captive tufted ducks diving in a tank to reach food suspended on trays near the bottom. He measured the birds' oxygen consumption while resting (absorptive, thermoregulating ducks (at water temperatures probably below the thermoneutral zone)) (RMR) and while diving. MR_d over entire dive bouts was calculated as:

$$MR_d = VO_{2totaldivebout} / (\sum t_{dive} + \sum t_{surface}) \qquad (7.1)$$

where $\sum t_{dive}$ and $\sum t_{surface}$ are the total underwater and surface durations during a dive bout. The energy investment in diving (EDC), expressed as the extra oxygen consumption over and above the resting rate per second spent underwater, was calculated over the period from the first dive in a bout until the bird's metabolic rate had returned to the resting level after the dive bout had finished:

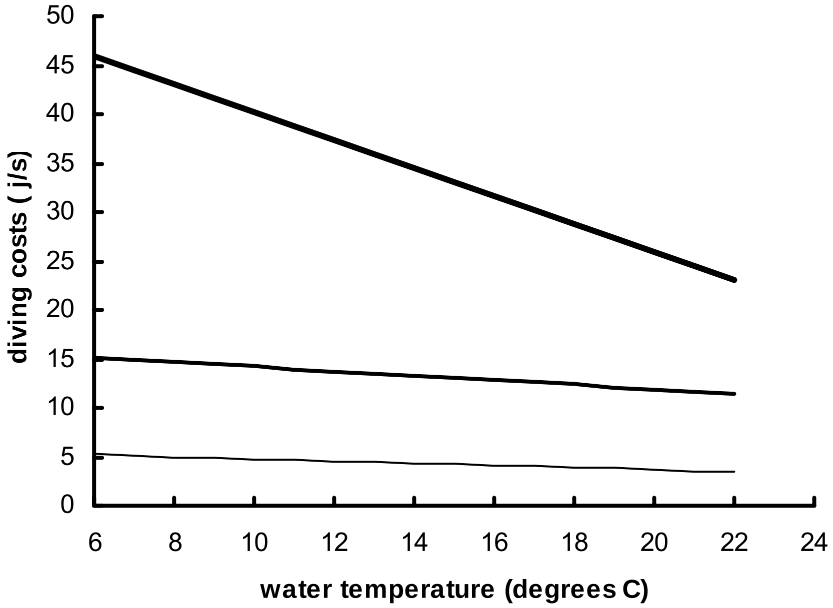
$$EDC = (VO_{2total} - VO_{2rest} * t_{total}) / \sum t_{dive} \qquad (7.2)$$

De Leeuw (1997e) found that the birds' RMR and EDC decreased significantly with increasing water temperature, whereas the MR_d although declining did not do so significantly. These findings confirmed de Leeuw's (1997e) analysis of the difference between these two measures of the costs of diving i.e. that during a diving bout the extra energy is used mainly to overcome hydrodynamic forces (which will be little affected by water temperature) whereas the thermoregulatory costs of being underwater (which will be temperature dependent) are largely paid after a series of dives.

These results of de Leeuw's (1997e) experiments on tufted ducks were used as a basis to derive the costs of diving in the model MORPH. Using the equation presented by de Leeuw (1997e) for RMR as a function of water temperature (Fig. 7.5a), the predicted RMR values were divided by the measured BMR of tufted ducks and the resultant values of the RMR: BMR ratio were regressed against water temperature (Fig 7.5b). The ratio declined from 1.8 at a water temperature of 6 degrees to 1.45 at a water temperature of 15 degrees (the max and min used in the model of Liverpool Bay). The ratio reached a value of 1 at a temperature of 27 degrees. The RMR: BMR ratio predicted from the regression equation was used to multiply the scoters' BMR (see above) to yield their maintenance metabolic costs at a given water temperature. Using the equations presented by de Leeuw (1997e) for RMR and for EDC as a function of water temperature (Fig 7.5a), the predicted value of EDC was divided by the predicted value of RMR and the resultant values of the EDC: RMR ratio were regressed against water temperature (Fig 7.5b). This ratio declined from 8.6 at a water temperature of 6 degrees to 7.8 at a water temperature of 15 degrees. The EDC:RMR ratio predicted from the regression equation was used to multiply the common scoter predicted RMR to yield the extra metabolic costs due to diving, over and above the maintenance costs at any given water temperature. De Leeuw (1997i) proposed that the hydrodynamic costs of diving in winter fattened ducks should be taken to be 3% greater than the values derived from the near lean ducks used in his experiments. Thus, in the model the EDC is multiplied by 1.03. The overall metabolic costs while diving actively involved the summation of the maintenance metabolic costs (RMR) over a period of feeding time plus the extra diving costs (EDC) incurred during the proportion of that feeding time which was spent underwater (given that even when actively feeding only a fraction of a diving bout is spent underwater).

The use of de Leeuw's model as a basis for the model of the energetics of diving by common scoter in the model MORPH is based upon the assumption that scoter and tufted duck dive in the same way. In fact Lovvorn & Jones (1991a) noted that large bodied sea ducks (scoter and eiders) had buoyancies 22-28% above values predicted by a common linear regression equation with respect to mass. Thus, scoter and eiders have larger respiratory or plumage air volumes relative to body mass and this probably affects the mechanics and energy costs of diving (Lovvorn & Jones 1991a). Indeed, Lovvorn & Jones (1991a) also noted that scoter and eiders are the only species amongst those that they studied that often (scoter) or always (eiders) use their wings as well as feet in propulsion during descent. Thus, scoter do not propel themselves in the same way as tufted ducks and may incur different energetic costs of doing so. Nonetheless, these differences in mode of propulsion and buoyancy will only affect the energetic costs of overcoming hydrodynamic forces. De Leeuw's (1997e) results indicate that in relatively small endothermic divers such as ducks, these costs may, over the time scale of a dive bout and subsequent recovery period, be relatively minor in comparison with the energetic costs of overcoming heat loss while diving in cold water. Thus, given that de Leeuw's approach appears to be the best way to deal with this aspect of the energetic costs of diving, it is this approach that is used here.

a)



b)

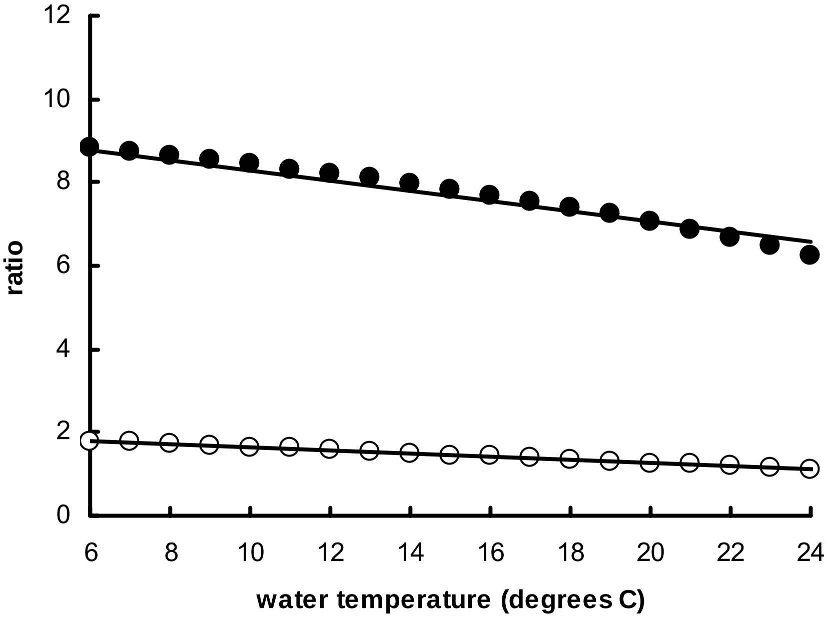


Figure 7.5 a) Excess diving cost (EDC) (thickest line) and metabolic rates during diving activity (MR_d) (thin line) and while resting on the water (RMR) (thinnest line) in relation to water temperature for three tufted ducks. Regression equations are: EDC = 54.6 – 1.43x, $p<0.0001$, $MR_d = 16.5 – 0.23x$, P = 0.26, RMR = 5.88 – 0.11x, $P < 0.0001$. After de Leeuw (1997e). b) Relationships between the EDC: RMR ratio (filled circles) and the RMR: BMR ratio (open circles) of tufted ducks and water temperature – derived from the data in a). The solid lines depict linear regressions through the predicted ratio values: EDC:RMR = 9.4717 – 0.1153x, $r^2 = 0.980$, RMR: BMR = 2.0276 – 0.0379x, $r^2 = 1.000$.

7.2.10.6 Energetic costs of heating food

In addition to calculating the metabolic rate while resting and while underwater, the calculation of the overall rate of energy metabolism while feeding required a third component to be calculated: the energetic costs of heating food. De Leeuw (1997g) found that the high daily energy expenditure of tufted ducks in winter (>4*BMR) was primarily explained by the costs for thermoregulation and heating up the mass of the ingested bivalves from ambient water temperatures to the core body temperature of 41°C. The increase in the maintenance costs with decreasing water temperature were addressed in the model MORPH by inclusion of the water temperature dependent RMR: BMR ratio (see above). However, it was still necessary to take into account the fact that common scoter like tufted ducks must heat up the mass of food that they consume. The additional cost of compensating the cooling effect of the cold food mass passing through the body was calculated in the same way as by de Leeuw (1997g). The caloric value to heat up the food from ambient water temperatures to a body core temperature of 41°C, was calculated by assuming a specific heat of 4.2 $J\ g^{-1}\ {}^{o}C^{-1}$ for the water content of the prey (assumed to be 60% of the ingested mass (i.e. 1.5 times the ingested mass of dry flesh plus dry shell material)) and 0.8 $J\ g^{-1}\ {}^{o}C^{-1}$ for the calcareous shell (c 40% of the food mass) (see de Leeuw 1997g). The small proportion of the total ingested mass that comprises dry flesh can be safely neglected in this context (de Leeuw 1997g).

The total rate of metabolism while feeding actively comprised the sum of three components: i) the maintenance metabolic rate * the duration of the feeding period, ii) the extra costs of diving over and above maintenance costs * the time spent underwater and iii) the costs of heating up each gram of food ingested * the fresh mass of food consumed.

7.2.10.7 Energetic cost of resting

The rate of metabolism while a bird was resting i.e. while not engaged in dive bouts was taken to be equivalent to the first of the three components described above i.e. the RMR.

7.2.10.8 Energetic cost of flight

De Leeuw (1997i) calculated the energetic costs of flight for tufted duck and scaup from the equations of Masman & Klaassen (1987). The values he calculated were 68 $J\ s^{-1}$ for tufted duck (weighing 1000g on average) and 84 $J\ s^{-1}$ for scaup (weighing 1300g on average). On the assumption that these ducks all have very similar wing morphology and an average mass of 1100g for a common scoter, a value of 73 $J\ s^{-1}$ (or 264 $kJ\ h^{-1}$) was interpolated for common scoter.

7.2.11 Response to human activities/ structures (appendix 15)

There are remarkably little data on the response of scoter to sources of human disturbance. Cramp & Simmons (1977) note that common scoter are generally rather wary, more so than the velvet scoter, and are more willing to take to the wing than the latter. In an analysis of the vulnerability of various species of seabird to the adverse effects of offshore windfarms Garthe & Huppop (2004) classified common scoter as having the highest possible vulnerability index score in the case of their response to disturbance by ship and helicopter traffic. This was also the score attributed to velvet scoter. Of the 26 species examined, the scoter had higher scores in this regard than any other species. These scores were derived from the results of extensive surveys at sea from boats and from species' reactions to aerial surveys as well as to over-flying aeroplanes and helicopters in coastal waters. The classifications were modulated by experts (Garthe & Huppop 2004) so it would appear that in spite of the paucity of data, scoter are generally believed to be highly sensitive to sources of human disturbance such as boat and low-level aerial traffic. Thus, the distribution and frequency of shipping and helicopter traffic in the Liverpool Bay area have been included in the model as part of the baseline conditions with which scoter currently have to contend (see sections 5 & 8.6.2). The cumulative effect of windfarms may depend on this existing background level of disturbance to the birds.

Windfarms can be considered as a potential and concentrated source of disturbance (Guillemette & Larsen 2002). It has been concluded that disturbance to resting/foraging birds is the main problem related to wind farms, whereas collisions are likely to be a minor concern in most circumstances (Guillemette & Larsen 2002) (see below). To date, the only research concerning the direct effects of offshore windfarms on sea ducks has been conducted in Denmark where a number of offshore windfarms have been constructed during the last decade.

Guillemette & Larsen (2002) conducted a number of post-construction experiments to elucidate the effects of the Tunø Knob wind farm on common eider. They found little evidence for negative impacts

– in three out of four tests they could not detect any effect at all. In terms of the distribution of eiders on the sea surface they found that variation in eider numbers was almost entirely explained by the amount of food present and that the wind turbines did not play any role in the exploitation pattern of eiders during the winter (Guillemette & Larsen 2002). At the same study site, Guillemette et al (1998) conducted studies on the distribution of eider over a larger spatial scale and found different trends in numbers at different spatial scales. However, they rejected the explanation that this reflected a negative effect of the windfarm and concluded that the patterns in eider distribution were again driven by the distribution of their food supply. Thus, studies at Tunø Knob suggest that at least small wind farms have no noticeable effect on eiders. However, Guillemette & Larsen (2002) note that the results from this system cannot be readily applied to other sites or species. For example, they state that scoter have a different flock structure to eiders and seem to be more easily disturbed than eiders. Furthermore, large wind farms may create impacts that are not detectable in small wind farms such as that at Tunø Knob.

Since the research at Tunø Knob, the National Environmental Research Institute (NERI) in Denmark has conducted intensive research on the effects of two other offshore windfarms in Danish coastal waters – one in the Baltic (Nysted) and one on the Danish North Sea coast (Horns Rev) (Petersen et al 2004; Christensen et al 2004; Kahlert et al 2004a,b; Petersen 2004). These studies have combined surveys of sea ducks on the sea surface and radar tracking of the paths taken by birds in flight.
At Horns Rev, no common scoter were observed within 1.5km of the wind farm. Assuming an even distribution both prior to and following the erection of the windfarm, common scoter were encountered significantly less than expected within the wind farm area as well as the 2 and 4km zones around it. The degree of avoidance increased markedly from pre to post construction in the windfarm area itself and within the 2km and 4km zones around it. The reason for the change in avoidance of the windfarm by common scoter is unknown. Disturbance effects from the wind turbines are one possible reason. Disturbance from increased human activity associated with maintenance of the wind turbines could be another. The results of pre and post construction surveys of sea ducks indicated a change in the distribution of common scoter out to a distance of approximately 8km from the windfarm. Petersen (2004) concluded that such an effect cannot be explained purely as a result of the visual stimulus of the turbines at such long range. Petersen (2004) suggested a supplementary explanation involving the patchiness of the habitat exploited by the ducks. Changes in the distribution of the birds' food resources in the study area (between years) could play a role in the observed shift in common scoter distribution.

Analyses of the radar tracking of flocks of birds in flight showed that the majority of flight tracks at Horns Rev either changed their orientation and passed around the windfarm, most reacting 400m from the farm (north side) or 1000m (east side), or disappeared from the monitoring screen altogether. The loss of tracks on the radar screen reflects an avian behavioural response to the wind farm by approaching birds. Thus, few bird flocks actually entered the windfarm. Those that did enter headed almost parallel with the turbine rows. Thus it is expected that collisions may be very rare. Since the most pronounced change in the direction of recorded flight tracks occurred at c400m from the outer turbines (north side) or 1000m (east side) these distances may represent the general extent to which flying birds avoid such structures. However, although the most rapid change in the average direction of flight tracks occurred at these distances, another point of note is that at which the number of flight tracks first begins to decline with increasing proximity to the windfarm i.e. 1.5-2km (approaches from the north) and 2km (approaches from the east). Thus, 2km may in fact be the distance at which flying flocks of seabirds respond to wind farms. Regarding common scoter in particular, a total of 10 (out of 36,000) common scoter was recorded in the windfarm itself. These few observations suggest that common scoter actively avoided the windfarm.

At Nysted, analyses of daytime flight track data revealed that the standard deviation of track directions at distances closer than 3000m to the windfarm in 2003 was more than twice that compared to the baseline years and that this was even more pronounced at distances closer than 1000m. The standard deviation of the migration orientation also increased significantly during the night time at distances closer than 1000m to the windfarm. These results support the hypothesis that migrating birds show a response to the windfarm, specifically reacting by increased lateral avoidance. This means that after the wind turbines were erected in 2003, a flock of birds that approached the windfarm was significantly less likely to pass into it compared to baseline years. Even those birds entering the windfarm are not necessarily at risk from collision since the tracks clearly showed that many water birds moved along the open corridors between the rows of turbines. Observations at this site in spring revealed that track densities immediately to the east of the windfarm area were significantly lower in spring 2004 (operational phase) compared to spring 2001, 2002 (baseline) and 2003 (construction phase). This supports the results obtained in autumn 2003 when the flight behaviour of the birds at their approach to the wind farm area suggested that birds avoided the windfarm area to some extent. Further support for this conclusion could also be derived from the fact that track densities in the reference area further east of the farm was maintained at a relatively high level throughout the entire study (2001-2004). Hence the results from spring 2004 support the conclusions from autumn 2003 when there were strong indications that part of the migrating water birds showed an avoidance response to the windfarm.

The results of surveys of sea ducks on the sea between 1999 and 2004 around Nysted revealed that in general the distribution pattern in spring 2004 (post construction) resembled the general pattern observed in previous years. This was the case for common scoter, common eiders and long-tailed ducks. No common scoter and very few eiders or long tailed ducks were observed within the area of the windfarm in spring 2004. However, in the case of both the eiders and long-tailed ducks, which occurred in sufficient numbers for an analysis to be conducted, the selectivity index for the windfarm area itself recovered during the operational phase compared to the construction phase and returned to baseline levels- i.e. an effect could no longer be detected. However, the reduced selectivity for the 2km and 4km zones that was apparent when the windfarm was under construction continued to get worse or did not improve (depending on the method of analysis employed).Thus, usage of these areas distant from the windfarm was still lower than under pre-construction, baseline conditions. Thus, a significant effect on the distribution of both eiders and long-tailed ducks at the wider spatial scale could be detected. An analyses of the increase in the cumulative percentage of long-tailed duck sightings with increasing distance from the windfarm during baseline years and during and after construction revealed that up to a distance of c7km, the proportionate distribution of birds post construction (2004) was not clearly different from the highly variable patterns apparent in the preceding 4 years. However, in spring 2004, the cumulative % of birds seen up to a distance of 20km increased more slowly than in any previous year. However, given that an effect on the distribution of sea ducks up to a range of 8km from Horns Rev was deemed to be unlikely to be purely as a result of the visual stimulus of the turbines (Petersen 2004) it is also unlikely that this result from Nysted can be explained in this way either. Again, changes to the distribution of the birds' food resources between years may be the ultimate explanatory factor.

Thus, in summary, the findings from the Danish studies indicate that flying birds in general and sea ducks in particular respond behaviourally to the presence of windfarms at distances of between 1000 and 3000m by altering their flight tracks such that only a few birds fly directly through windfarms. Those that do, appear to fly along the 'corridors' between rows of turbines. In combination, these behavioural responses result in the probability of collisions with windfarms being much lower than would otherwise be the case. Studies at Tunø Knob failed to find any evidence that the distribution of eiders within close proximity to the windfarm was affected by the presence of the turbines. Apparent effects at a larger spatial scale may have reflected unknown changes to the distribution of the birds' food resources. Nonetheless, at both Horns Rev and Nysted there would appear to be some evidence that sea ducks tend to exhibit avoidance of windfarms. At both sites common scoter were not seen within the windfarm and at Horns Rev none were seen within 1.5km of the windfarm. At both sites, larger scale effects could be detected at distances of up to 2km, 4km and even up to 8km (Horns Rev) or 20km (Nysted). However, the lack of benthic data precludes testing of the hypothesis that it has been changes to the distribution of the birds' food resources rather than the avoidance of the turbines that has led to these results. In the light of these results, it has been assumed in the model that as a worst (justifiable) case scenario, avoidance zones of 2km radius around windfarms should be simulated to explore the potential consequences of habitat loss due to windfarms.

7.2.12 Proportion of time spent feeding (appendix 16)

Of all the papers and reports compiled in the literature review, only 4 contained any data on the length of time for which wild diving ducks forage in winter. Two of these only provided data on the proportion of the day spent actually underwater and did not distinguish between birds on the water's surface between dives in an active dive bout and those that were not feeding at all. Thus, only two papers gave information on the proportion of time that sea ducks spend engaged in actively foraging, as opposed to resting i.e. in the same form as the model output files. When measured in this way, Guillemette (1998) found that the proportion of daylight hours spent actively feeding by common eiders declined from 0.528 in mid-winter to 0.430 in late winter and to 0.282 in spring. Goudie & Ankney (1986) found that the proportion of daylight time spent actively feeding varied as a function of body size; it did not differ between common eiders 0.57 and common scoter 0.585 but was greater in the two smaller species i.e. Long-tailed ducks (0.83) and harlequin ducks (0.685). Thus, on the basis of this sparse information it might be expected that the proportion of daylight hours spent feeding by common scoter should be in the range of 0.4 to 0.6 but may decline to lower values in spring. These values were used to validate the model's predictions of the birds' feeding behaviour under baseline conditions.

7.2.13 Daily consumption of food (appendix 17)

The literature review yielded very few estimates of the daily food consumption of wintering diving ducks. Bourne (1984) noted that daily ingestion rates have not been determined for scoter although they have been for common eiders. Citing previously published data, Bourne (1984) noted that Belopoloski (1957) calculated the daily consumption of eiders to be 300g of whole molluscs i.e. 15-20% of body mass. Bourne (1984) noted that Swennen (1976) considered this figure too low and found that eiders consume about 60% of their body mass per day in whole clams. Bourne (1984) used these figures to estimate the daily consumption of whole clams by surf scoter and velvet scoter, based on their respective body masses. Bourne (1984) estimated that if scoter consume 60% of the body mass per day in the form of fresh whole clams that they would consume 672g (surf scoter 1120g body mass) and 1008g (velvet scoter 1680g body mass). Given that common scoter are given an initial target mass of c1000g and that this increases to c1300g, the expected daily consumption of fresh bivalves can be expected to be in the range of 600g-780g. Guillemette et al (1996) and Guillemette (1998) present a variety of figures for the daily food consumption of common eiders. These range between 1781g in spring and 2098g in late winter. The average of the various values quoted equate to 90% of the bird's average body mass (assuming a value of 2200g Cramp & Simmons 1977). Thus, an upper limit to the daily consumption of common scoter may be estimated as 0.9*1300g i.e. 1170g. De Leeuw (1997h) found that the daily food consumption of freshwater mussels by captive but free-diving scaup and tufted ducks was 2240g fresh mass and 1607g fresh mass respectively. Given the body masses of these birds (scaup – 800g, tufted ducks - 600g) these values are extremely high. This may reflect the low water temperatures in de Leeuw's outdoor freshwater facilities i.e. 3^{o}C and the poor nutritional quality of their mussel prey. Thus, on the basis of the data available from free-living sea ducks the most likely range for common scoter daily food consumption is between 600g and 1170g fresh mass (including the shells). These values are used to validate the model's calculations of the common scoter daily food consumption.

7.2.14 Maximum daily energy expenditure (appendix 18)

Drent & Daan (1980) concluded that the maximum daily work capacity of birds during the breeding season (generally assumed to be the most energy demanding period for most birds) is approximately 4 * BMR. In the vast majority of studies of the daily energy expenditure (DEE) of free-living birds the calculated DEEs have indeed been below this critical value. However, Nehls (1995) gives a value of 4.3*BMR as the DEE of common eiders in winter. De Leeuw (1997b) give a value of 4.2*BMR for tufted ducks in winter while de Leeuw (1997h) estimated the DEE of scaup in winter to be 1063kJ day^{-1}. This is equivalent to approximately 3.8*BMR. Thus, it would seem that all diving ducks in winter expend energy at a rate that is close to or slightly in excess of the proposed critical threshold of 4*BMR. De Leeuw (1997g) attributed this to the energetically costly mode of foraging employed by diving ducks coupled with the relatively poor nutritional quality of the material that they consume i.e. whole bivalves. There are no empirical measurements of the daily energy expenditure of common scoter. However, on the basis of the published studies of other species of diving duck it is likely that the upper limit to the DEE of common scoter is around 4.3 * BMR i.e. 1190kJ day^{-1}. This value has been used as a ceiling value as a means of validating the model's calculations of daily energy expenditure.

7.2.15 Body mass/ body condition (appendix 19)

All the data concerning the seasonal variation in the body mass of common scoter and their starvation mass was derived from the compilation of data presented by Cramp & Simmons (1977) and the study of Durinck et al (1993). In March, April and May, common scoter weigh more than their average over winter mass (averaged over the months October-April) and considerably more than they do in

July/August. The average starvation mass for an adult male common scoter in winter is 752g whereas that of an adult female is 703g. Deducting these values from the mean masses recorded in the dataset yielded the mass of body reserves carried by male and female common scoter at various times of year. Assuming that the winter (October-April) values presented in Cramp & Simmons (1977) occur in early January, the masses of body reserves (i.e. recorded total mass – starvation mass) were regressed against days since 1st August. This yielded a positive linear relationship between mass of body reserves and date (Fig. 7.6). The day to day values generated by this equation served to set an increasing target body reserve mass for common scoter over the course of the model run i.e. birds in the model were continually attempting to increase their body reserves.

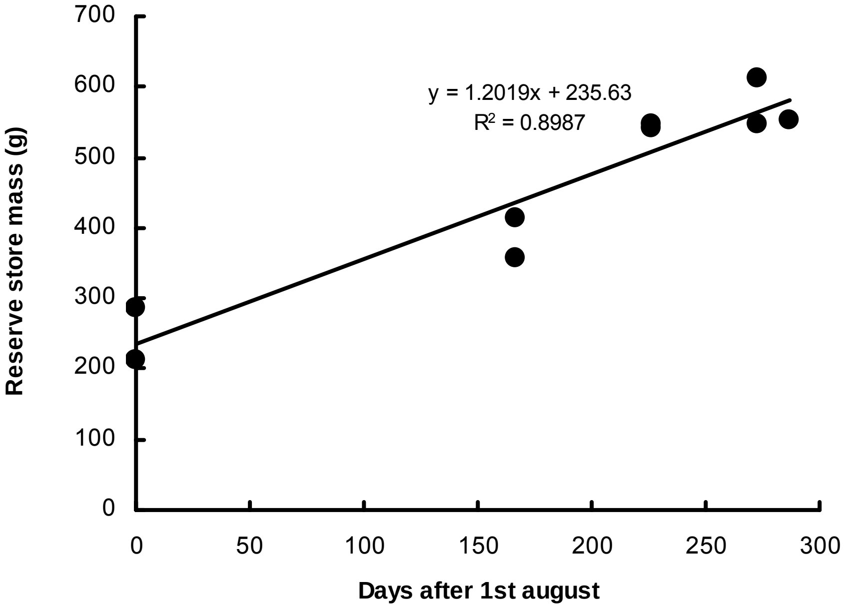


Figure 7.6 Seasonal variation in the mass of body fuel reserves carried by common scoter.

The linear relationship fitted to this data is, however, dependent upon the assumption that the values given as being measured between October and April by Cramp & Simmons (1977) are valid in early January. There is consequently a large gap in the data between the July-August values and the values taken to apply in January. Lovvorn (1989) found that the body mass of canvasbacks is typically low and declines in winter when it is cold and they eat mostly clams. Studies on body mass change suggest that diving ducks are often in a negative energy balance during the coldest months when they rely on their fat reserves (de Leeuw 1997g). Guillemette et al (1992) noted that “body mass (and reserves) in ducks in winter is positively correlated with the probability of survival”. Hohman (1993) stated that overwinter and annual survival probabilities of waterfowl may be influenced by their relative body mass in winter. Thus, empirical data from wild diving ducks suggests that decreases in mass are quite likely to occur in mid winter. Given this information, and the lack of precise autumn and winter data for common scoter, the linear increase in the target mass of common scoter assumed in the model is likely to be an upper limit that may in fact be unobtainable. Thus, in comparisons of the model’s output with the upper limit target (see section 9.3.4), failure of birds in the model to reach the assumed target mass does not indicate a failure of the model – rather the lack of data on which to base the birds’ targets, and may in fact be closer to reality.

7.2.16 Over-winter survival (appendix 20)

There is very little hard data on any aspect of the population ecology of sea ducks (Kirby et al. 1993). Relatively little is known about winter mortality rates. However, Guillemette et al (1992) state that “We have no difficulty imagining that starvation could be a major cause of natural mortality in wintering (common) eiders”. Richman & Lovvorn (2003) found that very nearly half of the annual mortality of adult female spectacled eiders appears to occur in the non-breeding period when the ducks are at sea. They concluded that regardless of the mechanism, a major limitation on the population is adult mortality much of which occurs away from the breeding area. Boyd (1962) estimated from a small sample of recoveries that the annual survival of common scoter was around 77% i.e. 23% mortality

(Fox et al 2003). Garthe & Huppop (2004) citing the work of Krementz et al (1997) give the annual survival of common scoter as 77.3%. Fox et al. (2003) analysed an extensive historical capture-mark-recapture dataset of female common scoter in Iceland. They calculated the annual survival of adult female common scoter to be 78% i.e. 22% annual mortality. On the basis of these figures the over-winter mortality of adult female common scoter may be estimated as 0.46 * 22% i.e. 10.12%. Common scoter have a male-biased sex ratio (1.2 – 2.0 males: 1 female) on the breeding grounds (Fox et al 2003). Observations of common scoter in Liverpool Bay also reveal a male-biased sex ratio (see section 4.3), the average ratio over the winter being 2.7 males: 1 female. Assuming that common scoter eggs hatch with an equal sex ratio, the most likely explanation of this biased sex ratio in the population as a whole is that the annual mortality of males is lower than that of females. Thus, it is necessary to correct the annual mortality of females (22%) to that for the population as a whole in order to produce a figure against which the model output can be compared.

By means of simple arithmetic it is possible to apply an annual mortality of 22% to females and some other value to males and to determine the overall sex ratio that would result across the whole population, assuming that common scoter do not live beyond around 20 years (17 years being the maximum recorded longevity of an adult female common scoter (Fox et al 2003)). Assuming simply that the annual mortality of males is half that of females i.e. 11%, results in an overall sex ratio in the population of 1.84 males to 1 female i.e. within the range noted by Fox et al (2003). On the assumption that males like females suffer half of their annual mortality during the winter the resultant estimate of over winter mortality for female common scoter is 10.12% and that for males is 5.06%. Given that the population in Liverpool Bay is male biased, the weighted over-winter mortality of common scoter in Liverpool Bay can be estimated at around 6.4%. This value has been used as a guideline against which to validate the model output under baseline conditions.

8. Development and parameterisation of Liverpool Bay/ common scoter model

8.1 Introduction

This section describes the particular details of the version of the model MORPH that was created in order to simulate the over-wintering common scoter population of Liverpool Bay and to predict the effects on it of a range of alternative offshore windfarm development scenarios. The creation of this version of MORPH is based upon the work described in the preceding sections. Table 8.1 lists the state variables (values used to describe a model entity) of each entity, and clarifies whether the values are derived from Liverpool Bay itself, from general literature concerning common scoter and their prey or from literature concerning other species.

8.2 Study region

The study region with which this project is concerned covers the coastal sea area from Red Wharf Bay on the eastern corner of Anglesey to Fleetwood on the Lancashire coast (Fig 8.1). The seaward limit to the geographic region included in the model was determined by excluding grid cells within which the predicted water depth exceeded 20m at low water of spring tides i.e. by excluding all areas of the sea where the water is permanently deeper than 20m. This criterion was selected on the basis of: i) the predictions of the diving sub-model that the proportion of time that a common scoter can spend on the seabed per dive cycle diminishes to near 0 in waters deeper than 20m (see section 7.2.2) and ii) the literature review concerning diving depths of common scoter (see section 7.2.5). The western boundary of the study area along the coast of Anglesey and the northern boundary on the Lancashire coast were defined by the observed distribution of common scoter i.e. all but one outlying cell off Barrow in Furness in which common scoter were observed during overflights were included in the model. The northern boundary to the study area was also constrained by the limits of the benthic survey. The study region encompasses the location of the existing windfarm at North Hoyle, the consented locations for windfarms at Rhyl Flats and Burbo Bank and the proposed locations for windfarms at Shell Flat and Gwynt-y-Mor.

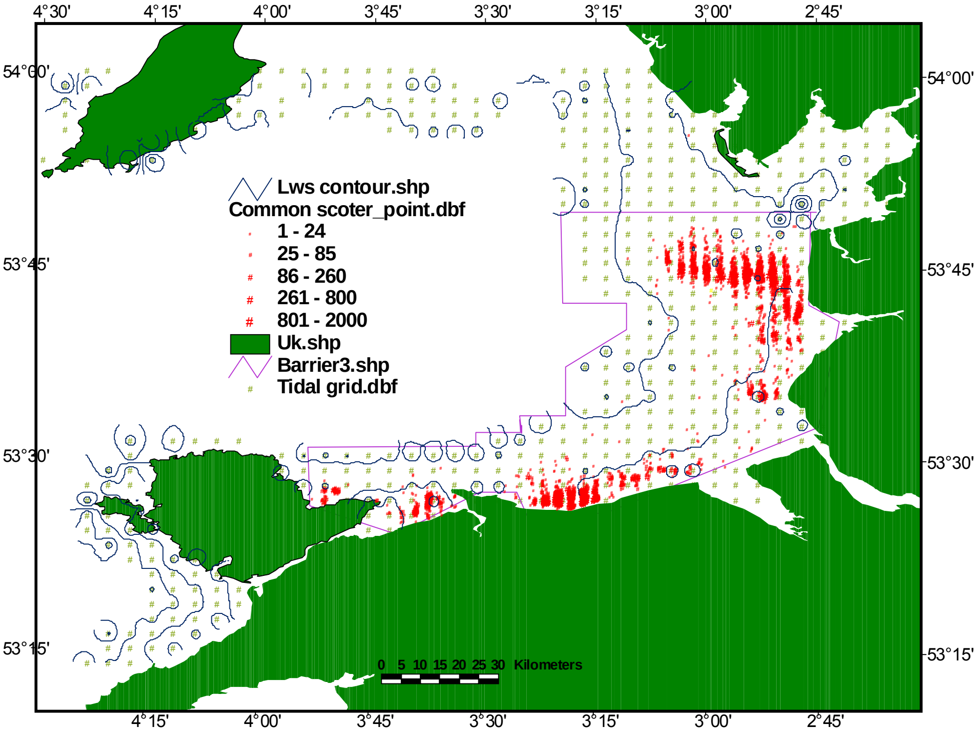


Figure 8.1 Geographical location of the study region. The centre of each tidal grid cell is shown by a pale green dot. The grid cells included in the model all lie within the purple bounded area (the original boundary of benthic resource abundance interpolations) and include only those within this

area that are also inshore of the outer bathymetric contour. Further restrictions on the set of grid cells included in the final model are discussed in section 8.6.3.. The red dots denote the distribution of common scoter as seen on 8 overflights conducted between August 2002 and March 2004.

8.3 Issues

The construction and presence of offshore windfarms in shallow coastal waters have the potential to affect over-wintering common scoter populations in a number of different ways. Broadly, these can be summarised as: i) direct mortality due to collision of birds in flight, ii) alteration to the seabed foraging habitat, iii) habitat loss due to avoidance of the structures and associated maintenance traffic and iv) increased energy expenditure due to altered flight paths around farms. In this report we are concerned solely with the third of these mechanisms. The reasons for this are outlined below.

There is as yet little evidence to suggest that sea ducks are subject to increased mortality due to collisions with offshore windfarms. Indeed, the results of recent research in Denmark reveals that migrating birds, including sea ducks, often alter their flight paths to avoid such structures, or, if they do not do so, often fly along the corridors between rows of turbines (see section 7.2.11). Thus, under most circumstances (except perhaps in poor visibility) birds appear to have behavioural responses to minimise the probability of collisions with wind turbines.

The laying of cables and the construction of foundations for individual turbines will alter the seabed at the precise locations where these structures are sited. This may have implications for the availability of benthic food to common scoter in those precise locations. However, the extent of the area of seabed that is physically occupied by the foundations of the turbines and the associated under-water cabling is likely to be negligible. This is especially so if the area occupied by these structures is compared with the area of the sea surface around windfarms which sea ducks may choose to avoid. Danish studies (see section 7.2.11) have revealed that the distribution of several species of sea duck including common scoter may be altered up to distances of at least 2 - 4km around a windfarm. Thus, the loss of habitat due to the physical alteration of the seabed is likely to be insignificant compared to the loss of habitat due to the behavioural avoidance of visible man made structures. Common scoter are very wary of shipping and are easily put to flight (see section 7.2.11). Thus, habitat loss due to the disturbance caused by windfarm maintenance traffic is also likely to be a major consideration.

Danish studies (see section 7.2.11) have indicated that birds alter their migration paths in order to fly around windfarms. Thus, there is evidence that the flight costs of birds flying in the vicinity of windfarms is likely to increase. However, the increase in the energy expenditure due to this behaviour is likely to be insignificant in the context of the overall cost of a migratory flight. Of more concern in the context of an overwintering population is whether windfarms represent a barrier to the daily/ tidally driven movement of birds to and from feeding areas such that birds have to fly further on a day to day basis throughout the winter. At present, there is very little information on the extent to which common scoter fly between different areas of Liverpool Bay on a daily basis. There are anecdotal records of movements at dawn and dusk but the limited range of the radar with which such observations have been made mean that the distance and destination of such flights remain largely unknown. Given this uncertainty, it was decided that it was not practical at this point in time to address the issue of the increase in flight costs that common scoter might incur were they to make circuitous flights around windfarms.

Thus, in this report we are concerned solely with what existing knowledge of common scoter behaviour suggests is the most serious potential consequence of offshore windfarms, namely habitat loss due to the avoidance of man made structures and activities - specifically the avoidance of the turbines themselves and the associated maintenance boat traffic.

8.4 Data collection

The data used to parameterise the model, and to validate it, were derived by a combination of: i) the development of a tidal model of Liverpool Bay (section 2), ii) fieldwork and laboratory analyses to characterise the benthic food resources of common scoter in Liverpool Bay (section 3), iii) studies of the behaviour of common scoter in Liverpool Bay (section 4), iv) existing data concerning the frequency and distribution of shipping and helicopter activity (section 5) and v) a review of in excess of

100 scientific papers and research reports on the foraging ecology and energetics of diving ducks (section 7).

8.4.1 Patches

The modelled region of Liverpool Bay was divided into a grid of contiguous patches of sea. The sizes of these cells were determined by the resolution of the tidal model of Liverpool Bay (section 2).

8.4.2 Resources

Data concerning the early autumn numerical abundance of the principal prey of common scoter i.e. bivalve molluscs and the seasonal change in the abundance of these resources in the assumed absence of predation by common scoter were collected by sampling over a large number of stations across Liverpool Bay in August 2003, and repeated visits to a number of these stations in December 2003 and April 2004 (section 3).

8.4.3 Components

Two resource components which influence the energetic profitability of consuming a given size and type of bivalve, and which may influence the birds' patch choices, are considered in the model i.e. the dry flesh mass content and the dry shell mass content of a prey item. Values for the dry mass content of both flesh and shell of different size classes of different types of bivalve were derived by processing samples gathered during the survey of Liverpool Bay. Values for the energy content of the dry flesh mass of bivalves and the efficiency with which this energy is first assimilated across the gut wall and then stored as body reserves were collated from the literature (section 7.2.10.2 & 7.2.10.3).

8.4.4 Foragers

Overflight surveys of common scoter in Liverpool Bay were conducted in August, November and December 2002, January, February and May 2003 and in February and March 2004. The seasonal change in numbers apparent in these counts and the interpolated peak count were used to determine the total population size used in the model and the timing of the arrivals in autumn - early winter and of the departures in spring (section 8.5.4).

8.5 Data analysis

8.5.1 Patches

The grid cells used by the tidal model (section 2) measure 1/30 of a degree of latitude by 1/20 of a degree of longitude i.e. they extend over 3.35km west to east and 3.70km north to south. Thus, each grid cell covered an area of 12,395,000 m^2. The proportion of each grid cell that comprised sea as apposed to land (in coastal cells) and hence the true area of sea surface and hence seabed was derived from the GIS of Liverpool Bay. The central coordinates of each patch were used to define the location of each patch in space and hence the distances between each patch and every other patch in the model.

8.5.2 Resources

On the strength of the literature review (section 7.2.8) the only benthic prey resources included in the model are bivalve molluscs. A total of 21 species of bivalves were commonly recorded in the benthic samples collected in Liverpool Bay (Tables 3.2 & 3.3). The distribution of many of these was patchy at a range of scales (section 3). Given the patchy nature of the species' distributions and that the diet of common scoter has been shown to include a very large number of different bivalve species i.e. they seem to feed on whatever happens to be abundant locally, it was decided to aggregate bivalve species into three prey types that may differ considerably in their profitability as food resources i.e. i) elongate bivalves (*Pharus* spp, *Phaxas* spp. *Ensis* spp), ii) thick, solid-shelled bivalves (*Nucula* spp., *Spisula subtruncata*, *S.elliptica*, *Chamelea* spp., *Donax* spp., *Dosinia*, spp. *Corbula* spp., *Acanthocardia* spp.) and iii) thin, brittle shelled bivalves (*Abra* spp., *Fabulina* spp., *Lutraria* spp., *Mysella* spp., *Tellimya* spp. *Mactra* spp., *Thracia* spp., *Thyasira* spp., *Macoma* spp., *Moerella* spp.). The proportion of dry flesh to shell mass varied with length within bivalve types (see section 8.6.4).

Within a bivalve type, individuals of differing size often occurred in different places within Liverpool Bay (section 3). Given these facts, each of the three prey types was split into several prey type size classes. Thus, elongate bivalves were split into 6 size classes and each of the other two prey types were split into 4 size classes. Each size class of each prey type represented one resource upon which the common scoter could feed in the model. Thus, there were 14 resources available to common scoter in the model.

The model assumes that the common scoter do not distinguish between the 14 resources as different dietary options but rather that they comprise a single diet and are consumed in proportion to their relative numerical abundance within a given patch. Nonetheless, the relative profitability of each of the resources and their relative abundance in each grid cell influences the net energy gain that can be achieved there and hence influences the patch choice decisions made by the common scoter in the model.

The results of the August 2003 survey of Liverpool Bay were used to define the starting numerical density of each resource in each patch in the model. The results of the repeat sampling of selected monitoring stations, where overflight data suggested common scoter were scarce, were used to determine the change in the abundance of each resource between August and December and between December and April in the assumed absence of predation by common scoter. These figures were used to yield estimates of the proportionate daily survival rate for each resource in the early and late winter. The mean of these two values was used to incorporate the day to day change to the numerical abundance of the birds' resources over time that was not due to the depletion by the birds themselves.

8.5.3 Components

Samples of elongate, thick and thin bivalves were measured (maximum length) and processed to determine the dry flesh mass and shell mass of individual bivalves (section 3.2). The relationships between dry masses and length of each of the three types of bivalve were derived by first transforming both variables and regressing $\log_e$DM (flesh or shell) on $\log_e$length. Using appropriate back-transformation correction procedures (error mean square/2) the resultant equations were used to estimate the flesh and shell dry masses of bivalves belonging to each of the 14 resources. The value of length used to derive these estimated values of dry mass corresponded to the midpoint of the size range of each resource. Values for the energy content of the dry flesh mass of bivalves and the efficiency with which this energy is first assimilated across the gut wall and then stored as body reserves were collated from the literature (section 7.2.10.2 & 7.2.10.3).

It is assumed that birds do not assimilate any energy from the dry shell component of each resource. Although water is also not a resource component from which foraging common scoter gain any energetic benefit, the model included a measure of the water content of the various resources because the gut capacity of the birds is dictated by the volume of fresh prey mass that they ingest, not by the volume of dry matter from which they extract energy and nutrients. Data in the literature was used to derive a value for the proportion of total fresh mass that comprised dry mass (section 7.2.10.1). This was used to derive the value of a factor in the model that was used to estimate total fresh mass consumption from the consumption of dry flesh and shell mass.

8.5.4 Foragers

The common scoter population in Liverpool Bay fluctuates over the course of the 'over-wintering' period between August and May (Fig 8.2a). On the basis of the assumption that numbers change linearly with date between overflights these empirical data were used to derive a phenology for the common scoter population in Liverpool Bay (Fig 8.2b). Thus, the number of common scoter is assumed to build up steadily between early August and mid February and then to decline steadily between then and the end of May.

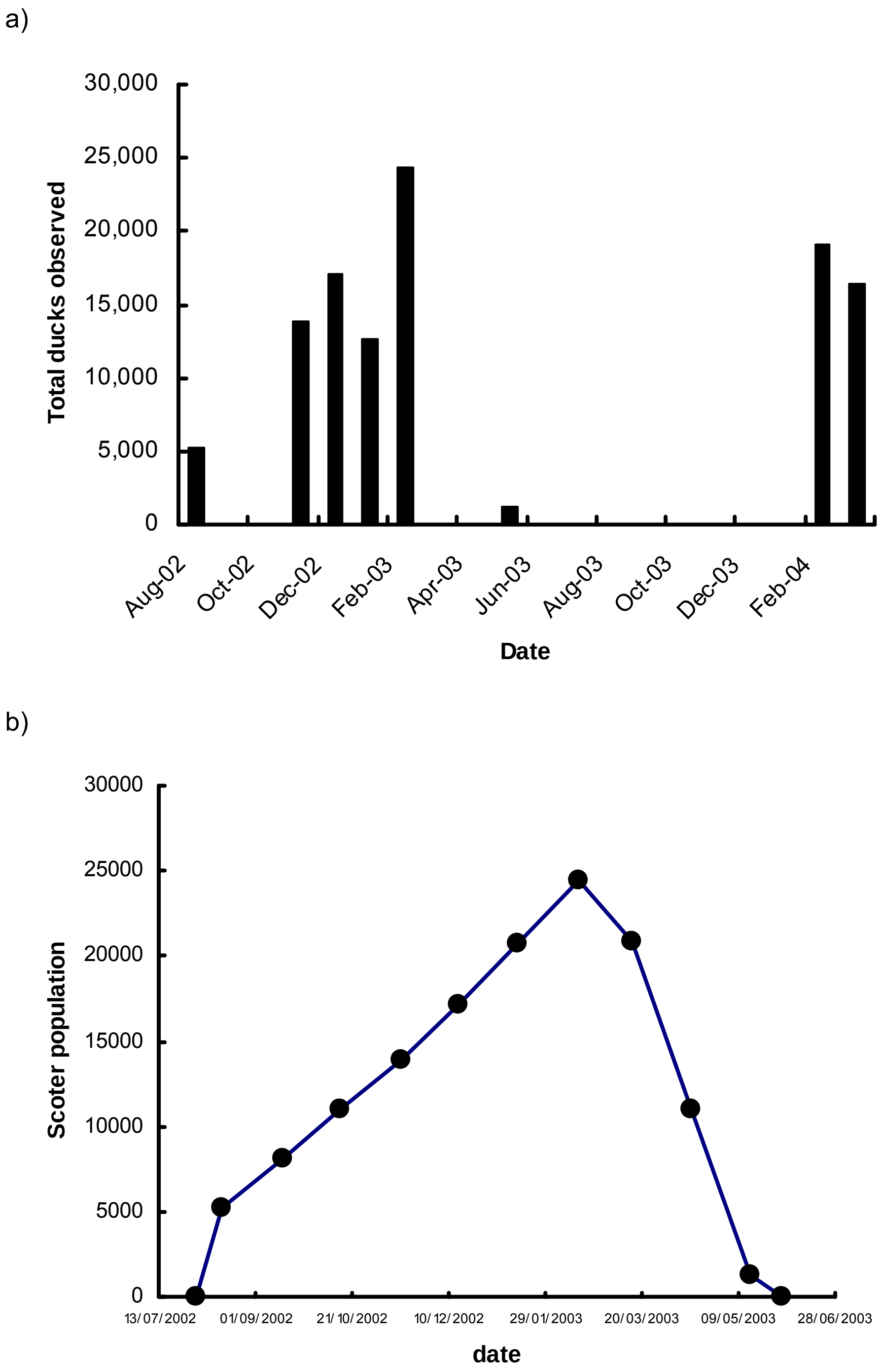


Figure 8.2 a) The total number of common scoter observed on each of 12 over flights of Liverpool Bay between August 2002 and February 2004. b) The phenology of the common scoter population in Liverpool Bay derived from the over flight data.

8.6 Model variables

8.6.1 Global variables

Five global variables were used in the model: Day, Time, Daylength, Daylight and Water temperature. These global variables take the same value on every patch at a given point in time. Day 1 was taken to be the 1st of August and a model simulation covered the period from then until 31st May by when all common scoter leave Liverpool Bay. Each day was divided into 24 one hour time steps. The annual maximum and minimum day length (sunrise to sunset) at Blackpool was derived from data held on the website http://aa.usno.navy.mil/cgi-bin/aa_rstablew.pl. Using a simple cosine function, these maximum and minimum values were used to calculate the duration of daylight on each day. Assuming, for simplicity, symmetry of sunrise and sunset around noon, predicted day length was used to ascribe each time step to occur either in darkness or daylight. A value for the average sea surface water temperature in each month in Liverpool Bay was fitted by a 2nd order polynomial regression equation (Fig 8.3) and this equation was used to predict the day to day changes in water temperature across the whole of Liverpool Bay.

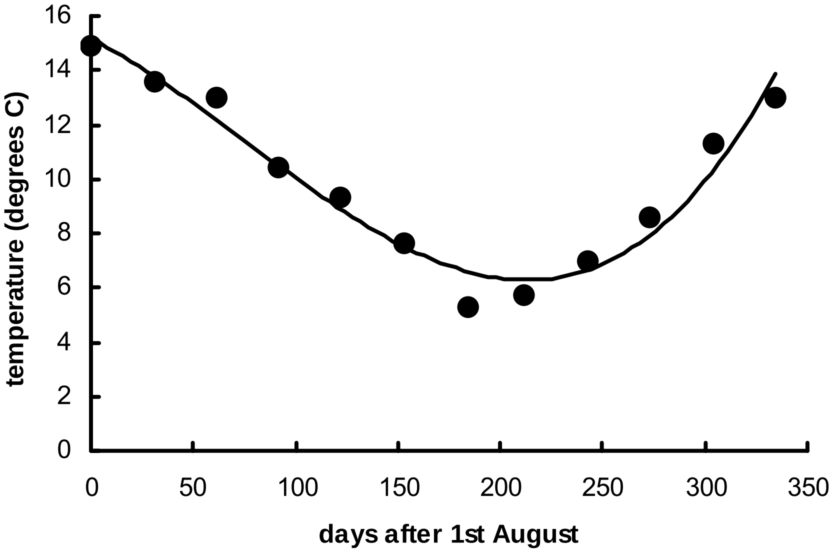


Figure 8.3. Monthly mean values for the sea surface water temperature in Liverpool Bay and a fitted 2nd order polynomial trendline.

8.6.2 Patch variables

There were a total of 206 grid cells within the geographic boundaries of the study region (Fig. 8.1). The location of each patch in the model was determined from its central grid coordinates. Patch locations were used to determine the distance required to fly between each. Each grid cell covered an area of 12,395,000 m^2. The proportion of each grid cell that comprised sea as apposed to land (in coastal cells) and hence the true area of sea surface and hence seabed in such cells was derived from the GIS of Liverpool Bay. The depth of the water in each patch at each hourly time step throughout the modelled period was predicted by the tidal model of Liverpool Bay (section 2).

In addition to the water depth, which varies naturally between patches, there are several variables mediated by mankind which may also already influence the suitability of an area of sea for common scoter and hence their existing distribution within Liverpool Bay. These are the frequency of shipping activity and the frequency of low-flying aircraft, notably helicopters flying to and from existing offshore gas and oil installations. Thus, two patch variables were defined to denote the extent to which each patch was affected by each of these factors.

Data on the spatial variation in the frequency of shipping activity within Liverpool Bay (ships >= 300 tonnes only) were incorporated into the GIS (section 5). The GIS was interrogated to yield a value for the intensity of shipping activity within each tidal grid cell. These values were expressed as ships per annum. To be consistent with the hourly time step used by the model these values wee converted to the units of ships per hour assuming no seasonal, diurnal or tidal variation in shipping activity. The model assumes that a grid cell is either entirely available to common scoter during a particular one hour time step or it is entirely unavailable. Thus, in the model a value is drawn at random from a uniform distribution of values between 0 and 1 for each grid cell on each time step. If the resultant random value exceeds the frequency of ships ascribed to that cell, it is deemed to contain a ship during that time step and to be unavailable to the birds. Otherwise, a grid cell is assumed to be available. In effect, the model assumes that on average a ship passes through the centre of a grid cell, disturbs all birds within a zone of approximately 1-2km around its path and that disturbed birds will not return to the area within an hour. Cells with a frequency of shipping traffic of 1 ship per hour or more are effectively permanently unavailable to the birds.

Data on the principal routes used by helicopter were incorporated into the GIS (section 5). The GIS was interrogated to yield the proportion of each grid cell that overlapped each of the helicopter routes which are 3km in width (section 5). Given the resolution of the grid cells (3.35*3.7km), helicopter routes seldom completely encompass a grid cell. More often the routes overlap some fraction of a cell. A conservative approach would be to assume that a cell has to be 100% within the flight path boundaries in order to be rendered unavailable. This would effectively assume a far smaller flight path width than the 3km intended. A precautionary approach would be to assume that if any part of a cell falls within the flight path boundaries then it is unavailable to the birds. This would effectively assume a far greater flight path width than the 3km intended. Thus, the model assumed that in order for a cell to be rendered unavailable to common scoter due to helicopter activity, 50% or more of a cell would have to overlap a given flight path. On average, this should mean the effective exclusion distance around the centre line of a given route within the model is the same as that intended based on the empirical data i.e. 3km.

In order to simulate the possible effect on common scoter of the presence of offshore windfarms a further patch variable was defined to denote whether each patch was affected by this factor. The existing location (North Hoyle) and planned locations of the other 4 windfarms within the study area were incorporated into the GIS. The GIS was interrogated to yield the proportion of each grid cell that overlapped each of the windfarms, assuming buffers of either 0km or 2km as appropriate (see section 10.3.3). Again, the model assumed that that in order for a cell to be rendered unavailable to common scoter, 50% or more of a cell would have to overlap a given windfarm or the surrounding buffer zone.

8.6.3 Resources

The initial numerical density of each resource on each patch was derived from various analyses of the August 2003 extensive sampling survey of Liverpool Bay (section 3). In summary, the sampling station data were analysed and used to derive the interpolated numerical abundance of each resource at each point within each grid cell. These interpolated values were used to derive the mean numerical abundance of each resource in each grid cell.

Examination of the output of this interpolation exercise revealed that a few sampling stations at which benthic bivalves were particularly abundant resulted in predictions of relatively high prey abundance over quite extensive areas. This was particularly the case when such ‘hot spots’ fell at the edge of one cluster of sampling stations and distant from the next nearest cluster. Two such examples occurred at Red Wharf Bay and to the south of the proposed Burbo Bank windfarm site. In both cases, large areas of relatively high resource abundance were generated by the interpolation procedure. The design of the sampling programme (which was focused on the existing distribution of common scoter) meant that in neither case was there any empirical data to verify the interpolations. Given the lack of common scoter in these areas and the lack of empirical data to validate the predictions of abundant food supplies, it was decided that interpolations of the numerical abundance of prey resources should be constrained to only those patches within a 2.5km radius of a sampling station. This restriction resulted in 115 patches being ‘included’ in the model. The other 91 patches were ‘excluded’ from the model by setting the initial numerical abundance of each resource to 0. Although this effectively removed a large area within which common scoter could in principle feed, the 115 usable patches within the model still encompass all of the areas which currently hold the vast majority of the common scoter population (circa 30 grid cells), and a further 80-90 grid cells that are little used by the birds at present. Thus, even with the restriction imposed by our precautionary approach to predicting the distribution of potential resources, the model still contains a far larger area of sea than that currently exploited by the Liverpool Bay common scoter population.

Given the large number of resources and patches, a tabulation of all of the values for resource densities used within this report is not practical.

Analyses of the numerical abundance of each of the 14 resources at each of sampling stations sampled in August 2002, December 2002 and April 2003, at which common scoter abundance was estimated (on the basis of the overflight data) to have been low, allowed an estimate to be derived of the average over-winter proportionate daily survival rate of each of the 14 resources (section 3). These values were assumed to apply throughout the study area.

8.6.4 Components

The quantity of dry flesh and of dry shell matter in bivalves belonging to each size class of each prey type i.e. of each of the 14 separate resources, was estimated from analyses of the bivalves collected from throughout Liverpool Bay (Fig. 8.4). As the analyses indicated that within many resources these values differed between samples collected from Shell Flat and from Llanddulas, region specific values were used in the model.

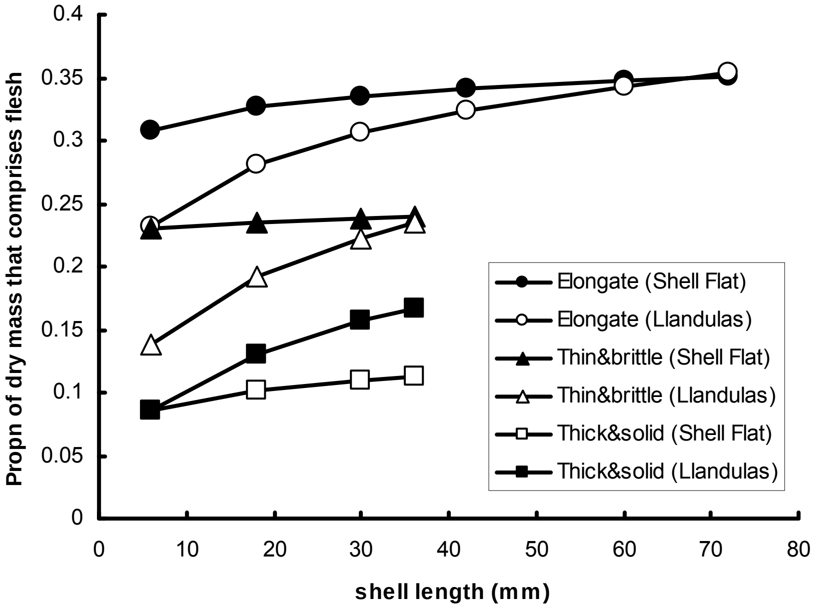


Figure 8.4. The proportion of dry mass that comprises flesh (as opposed to shell) as a function of bivalve length in each of the three prey types in two different areas of Liverpool Bay (Shell Flat and Llanddulas).

8.6.5 Foragers

The model was run with 1000 ‘super-individuals’ each representing 30 real birds i.e. the peak population simulated was of 30,000 birds (see section 10.3.1).

8.6.5.1 Forager constants

The model defined four forager constants i.e. characteristics ascribed to each forager which remain constant throughout a simulation. These are: foraging efficiency, dominance, the maximum density of competitors that can be tolerated within a grid cell, arrival day, and departure day. These are described in the following sections.

8.6.5.1.1 Feeding efficiency

The feeding efficiency of each individual within the population of common scoter is drawn from a normal distribution of scores, with a mean of one and a standard deviation of 0.125 (see section 7.2.6).

8.6.5.1.2 Dominance

The dominance of each individual within the population of common scoter is drawn at random from a uniform distribution of scores between a minimum of 0 and a maximum of 1. This value was used to determine the order in which individuals were processed in each time step (see below).

8.6.5.1.3 Interference

A degree of interference between common scoter was included in the model simply by setting an upper ceiling to the density of common scoter that could occur within a grid cell. This was set at 4,140 birds per grid cell. This was the maximum observed count of common scoter in any one grid cell on any of the 8 overflights. Thus, the maximum density of common scoter allowed in the model is consistent with the maximum density of common scoter observed at the spatial scale equivalent to the resolution of the model (see section 7.2.7). As, there are no empirical data on which to base an estimate of the strength of interference suffered by common scoter and how this varies with dominance status it was not possible to calculate directly the extent to which the intake rate of individual common scoter would be reduced by interference in a given patch. In most previous applications of the model MORPH it is on this basis that sub-dominant individuals within a population suffer disproportionately from the consequences of interference. In the present case it was necessary to devise an alternative way in which the effects of interference could be distributed unevenly between individuals of differing social status. This was achieved by processing birds in decreasing order of dominance score such that the individuals of lower status were more susceptible to being excluded from the best cells by the maximum density limit. This procedure served to mimic the effects of interference competition tending to act consistently on the less dominant individuals within the population.

8.6.5.1.4 Arrival and departure dates

The arrival day of each bird in the population was defined by an analysis of the overflights conducted between August 2002 and February 2004 (section 8.5.4).The arrival day of each bird was drawn from a uniform distribution between 1st August and 15th February. Thus, the number of birds in the model increased steadily from early August to reach a peak in mid-February. The departure date of each bird in the model was drawn from a uniform distribution between 15th February and 31st May. Thus, the population size in the model declined steadily from mid-February until the end of May. The arrival and departure dates of individual birds were independent of each other such that a bird could in principal arrive on the 1st of August and depart on the 31st of May or conversely arrive on the 14th of February and depart on the 16th of February. Although the rates of population turnover in Liverpool Bay are unknown such extremes in the duration of stay by individuals are unlikely. Nonetheless, as arrival and departure dates of birds in the model are not correlated with any characteristic that might affect their survival chances e.g. foraging efficiency, this simplification has no significant effect on the predictions of the model while enabling the seasonal variation in the population size within Liverpool Bay to be replicated without unnecessary complexity.

8.6.5.2 Forager variables

The model defined four forager variables i.e. characteristics ascribed to each forager which vary in space and time depending upon where and when it forages. These four variables are the time per dive that is spent: i) underwater, ii) travelling between the sea surface and the seabed, iii) on the surface before the next dive and iv) foraging on the seabed. Together these four variables constitute the diving sub-model. This is described in full in section 7.2.2.

8.6.5.3 Rate of acquisition of energy

The rate at which a bird can acquire resources over a period of time depends upon the length of time for which the resources are available to it during that time and the rate at which they can consume resources while the resources are available to them. In the context of benthic feeding diving ducks this translates to: i) the proportion of a dive cycle that is spent on the bottom and ii) the rate at which prey are consumed while on the bottom. The way in which the first of these components is derived is described in section 7.2.2. The way in which the second of these components is derived is described in section 7.2.9.

In many circumstances the rate at which birds can find food resources does not limit the rate at which they can assimilate energy. Often, constraints on the rate at which the digestive tract can process food and the physical capacity i.e. volume of the digestive tract can limit the rate of energy assimilation. This is particularly true in animals which, like diving ducks, ingest food which has a considerable indigestible component e.g. the shells of bivalves. Furthermore, there is also often a physiological limit to the rate at which the metabolic machinery can operate and this too may impose a constraint on the rate at which energy can be assimilated. Thus, two potential constraints, namely: i) the maximum rate at which they can assimilate energy and ii) the maximum rate at which their guts can process fresh mass of prey are included in the model. The way in which the values of these two constraints are derived is described in section 7.2.10.1. In the model these two constraints were both converted to the number of prey items that could be consumed per hour as follows

To determine the maximum rate at which bivalves could be consumed by a common scoter in a given grid cell at a given point in time, the weighted average of the flesh dry mass per bivalve across all the resources present was calculated. This was then multiplied by the assumed energy density of the dry flesh and the assumed assimilation efficiency to yield the energy assimilated per prey item consumed in that grid cell. The maximum energy assimilation rate constraint value was then divided by this value to yield one possible constraint to prey item consumption rate. To determine the value of the alternative constraint set by the physical capacity and processing rate of the digestive tract, the sum of the weighted averages of the flesh dry mass and shell dry mass across all 14 resources was calculated. This was multiplied by 2.5 to yield the average fresh mass per prey item consumed in a grid cell (section 7.2.10.1). The maximum crude intake rate of fresh mass per hour constraint value was divided by this value to yield the second possible constraint to common scoter hourly rate of prey item consumption. The lower of these two constraints was taken to be the limiting factor. Which of these two factors operated varied in space and time depending upon the relative abundance of the different resources present and their respective dry flesh: dry shell mass ratio.

8.6.5.4 Body reserves

The only source of mortality in the model is starvation. A bird is assumed to starve when it reaches its starvation mass i.e. its body mass reserves fall to 0. In order for the model to determine whether any given common scoter reaches this point is has to be able to track the rate at which birds accumulate energy reserves from the food that they consume and the rate at which they metabolise energy. It is the balance between these two rates that determine whether an individual duck gains or loses mass and ultimately whether it survives or dies. The way in which the birds in the model acquire and expend energy is described in section 7.2.10.

A bird’s body mass is assumed to comprise two principal components: i) its core structural mass and ii) its body reserves. The model assumes that birds can either build up their reserves if their energy intake exceeds their energy requirements or they can deplete their reserves if their energy requirements exceed their energy intake. The model assumes that a bird dies when its reserves run out and its body mass falls to its core structural i.e. starvation mass.

The data from the literature review were used to generate an equation describing a linear increase in the body mass of common scoter throughout the period between August and May (see section 7.2.15). The day to day values generated by this equation served to set an increasing target body mass for common scoter over the course of the model run i.e. birds in the model were continually attempting to increase their body reserves.

8.6.5.5 Movement between patches

For simplicity, the model assumes that when birds fly between grid cells, they take a whole number of time steps to do so. With an hourly time step this means that a bird must fly for 1, 2, 3 etc whole hours, depending upon the distance involved. Common scoter fly at 75 km h^{-1} (Christensen *et al* 2004). Thus, if the distance between two grid cells was less than 75km the model assumes that the common scoter can move between them at zero cost. However, beyond this distance birds must fly for one (or more) full hour(s) and incur the costs of doing so. In order for birds to consider a grid cell further than 75km from their current location as being a feeding location in which they might fare better than in their current location, it was necessary for birds in the model to estimate their predicted fitness (i.e. body mass reserve – see below) in each grid cell over more than one time step into the future. This was necessary so that birds could offset the costs of flying to a distant cell (which would take at least one full time step) against the reward that could be gained during the subsequent hour of foraging once the distant cell had been reached. Without this ability to look beyond the current time step birds would never move to locations further than 75km away because their fitness will always be lower at the end of the current time step (due to the energetic costs of flying for one hour) than it would be were they not to move. The model assumes that the birds predict their future fitness over the current plus one future time step i.e. over a 2 hour interval.

8.6.5.6 Fitness and survival

Foragers are assumed to be able to assess fitness measures associated with consuming different diets on their current patch. Other patches fall into one of three different categories. (1) Foragers may know the location of a different patch and be able to assess fitness measures on the patch. They can assess the survival consequences of moving to this patch consuming any diet, and know the values of all of the patch's state variables during the current time step. (2) Foragers may know the location of a patch, but not be able to assess the fitness measures associated with different diets. They cannot assess the survival consequences of consuming different diets, and are unaware of any of the patch's state variables. However, they do have an expected fitness measure on this patch ($F_{expected}$), which is used to compare this patch with others. (3) Patches may be of unknown location, and so cannot be considered as potential locations to move to (see section 6.8.4).

The model assumes that common scoter can know the location of and can assess the fitness measures and hence the survival consequences of moving to all grid cells within a radius of 37.5km of their current location (category 1 above). This assumes that the birds have perfect knowledge within a radius of half an hour's flight time. However, the model assumes (for speed of calculation) that common scoter cannot assess the fitness measures or the survival consequences of feeding in any cell within their radius of knowledge where the numerical density of bivalve prey is 0 (category 2 above). Their expected fitness in such cells is assumed to be 0. The model assumes that cells beyond this radius of a bird's current location cannot be located as a potential foraging location (category 3 above). They can, however, move across the entire study region in a number of 'leaps' made over a number of successive time steps.

The literature suggests that common scoter, like most sea ducks are primarily diurnal feeders (see section 7.2.3). Thus, the model assumes that the rules described above apply only during the hours of daylight. The model assumes that at night common scoter cannot locate grid cells other than their current one. This means that during the hours of darkness, common scoter remain at the location at which they ended the day. This constraint was relaxed in those simulations in which night feeding was permitted (see section 11.4). In these simulations, birds behaved in the same way at night as by day.

The model assumes that there are two components to the fitness of common scoter. The first of these relates to the fact that a common scoter's biological fitness must depend in some way on its physical body condition. The second acknowledges that the behaviour of common scoter in the wild indicates that they perceive man-made structures and activity to be deleterious to their biological fitness i.e. they fly away from boats and avoid man-made structures (see section 7.2.11). As described in section 6.8.4, the combined fitness measure is found from the product of the fitness measures associated with these two fitness component. The values of the two fitness component measures are ascribed to each grid cell in the following way.

In most previous applications of the behaviour-based model MORPH (and its predecessors) the study region over which it has been applied has been comparatively small. Most previous applications have considered birds foraging within the well-defined boundaries of an estuary e.g. the Exe estuary (Stillman et al 2000b), the Wash (Stillman et al 2002), the Burry Inlet (West et al 2003), the Menai Straits (Caldow et al 2004) and the Seine estuary (Durell et al 2005). All of these previous applications have concerned wading birds foraging on intertidal habitats. Because of the relatively small spatial scale considered and because the foraging habitat is visible to the birds it has been taken to be a reasonable assumption that birds have the ability to assess their potential fitness at all possible foraging locations with more or less perfect precision. Moreover, because these birds simply walk across their foraging grounds it has been assumed that the cost of foraging is the same everywhere and hence that birds maximise their fitness by simply maximising the gross rate of energy intake while feeding. Under these assumptions, birds in these previous versions of the model have been allowed to move at zero cost between all available foraging locations and to move on an hour-to-hour basis to wherever they can achieve the highest gross rate of energy intake. This simple rule is less justifiable in the current context and a different rule has been employed in allowing birds to assess the value of the first fitness component (section 7.2.1).

In the first, instance the birds' ability to assess their potential fitness is constrained to only that fraction of the study region within a specified radius of their current location (as described above). Second, it is assumed that because the foraging habitat is not visible to the birds on the sea surface it is unrealistic to expect them to be able to assess the energy gain that they can achieve with perfect precision at all locations within the specified radius of knowledge. Rather, it is assumed that birds 'satisfice' i.e. choose at random amongst those cells where their estimated fitness exceeds some threshold value (see section 7.2.1). In effect, this assumes that common scoter cannot reliably distinguish with precision between the qualities of these locations. Third, it is assumed that because the energetic cost of foraging per unit of energy gained differs between places (due to variation in water depth and relative resource densities) fitness should be assessed not simply on the gross rate of energy consumption but upon the final store of body reserves achieved at the end of a time step. This measure of fitness integrates all of the component parts of the energetic budget and is equivalent to birds maximising the net rate of energy gained. The model assumes that the birds' preference will be to feed in any of the cells within its radius of knowledge where the mass of body reserves it will have at the end of a time step is equivalent to that at the start of the step plus an amount equivalent to the quantity of mass that was lost during one hour of resting the preceding night. This rule ensures that diurnally foraging birds by preference forage in those locations where the return is in excess of that required to maintain their body mass over the course of an hour and also to offset one hour's worth of resting energy expenditure at night. By feeding in these locations birds can gain mass over a 24 hour period. If no cells meet this criterion the model assumes that birds will then choose to feed only amongst those cells where their body mass store at the end of the step will exceed that at the start. Under these circumstances birds may lose mass over a 24 hour period because they cannot offset the costs incurred while resting at night. Under the circumstances in which no cell within a bird's radius of knowledge meets even this lower threshold, the model assumes that the birds will remain where they are. Thus, the model assumes that the birds do have some ability to discriminate between places of widely different quality. However, because of the nature of this study system this level of knowledge is far lower than has been assumed to be realistic in most previous applications of the model.

The second fitness component, which is used to multiply the value of the first in order to calculate $F_{assessed}$ (the combined fitness measure for all fitness components) (see section 6.8.4), is assumed for simplicity to take a value of 0 or 1. As described above (section 8.6.2) the model assumes that a grid cell is unavailable to a bird when a source of disturbance is present within that cell during a time step and, in the case of helicopter routes and windfarms, the proportion of the area of that cell which overlaps the area that will be disturbed by that source of disturbance given its location (windfarm) or path (helicopters) exceeds 0.5. Within a grid cell the model is not spatially explicit and so cannot ascribe different areas to fall within e.g. a windfarm structure as opposed to another part that falls within a helicopter path. For simplicity the model assumes that all the various factors that may disturb common scoter from an area within a cell are mutually exclusive in space and so sums the proportion of the cell affected by each factor that operates within it at a given point in time. If the sum of these values exceeds 0.5, the model assumes that common scoter assess the value of the second fitness component to be 0, otherwise it is assumed to be 1.

When the two fitness component values are multiplied to derive the combined fitness measure, the resultant value is either that of the first fitness component or 0. This ensures that birds never visit cells when sources of disturbance are present, but may do so at other times. Amongst the cells that are not disturbed, it is the birds' measure of the first fitness component that determines where they forage, given the rules described above.

The consequences of birds' patch choice decisions (or the decision to fly from one patch to another for a whole time step) are determined by the true probability of survival in the chosen location (section 6.8.4). Given that starvation is the only source of mortality considered in this model, the survival probability associated with the first fitness component is dependent upon the bird's body mass. If a bird's body mass exceeds the starvation mass at the end of a time step the survival probability associated with the first fitness component is set to 1, otherwise it is set to 0 because the bird would starve. Although the decision of birds as to whether to forage in a cell is influenced by the presence or absence of factors that disturb them it is assumed that these factors, even if present, do not directly result in mortality. Thus, regardless of the 0/1 value ascribed to the second fitness component associated with disturbance, the survival probability associated with this fitness component is always set to 1. Thus, when the two survival probabilities are multiplied together to yield S_{true} (i.e. the true probability of surviving all fitness measures) (see section 6.8.4) the resultant value depends solely on the first fitness component. Birds' probability of survival in a location at a given point in time depends solely on whether or not they will starve there during that time step or not.

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Table 8.1 State variables used to describe model entities. The number of patches in the model (206) coupled with the number of resources (14) and components (2) means that it is not practical to present each of the actual parameter values used in the model in a tabular format of this kind.

Entity	State variable	Description	Value	Source of information
Global	Global variables	Day	Day 1 = 1st August, Day 304 = 31st May	Based on seasonality of common scoter, presence within Liverpool Bay (see section 8.5.4)
		Time	01-24 hours per day	N/A
		Day length	21 June 17.07h, 21 December 7.45h	Based on sunset and sunrise times at Blackpool (section 8.6.1)
		Daylight	0 or 1 dependent upon above	Based on sunset and sunrise times at Blackpool (section 8.6.1)
		Water temperature	Max 1st August 14.9°C, Min 1st Feb 5.3°C	Liverpool Bay sea surface temperature data (section 8.6.1)
Patches	Number	Number of patches	206	The number of tidal grid cells within the study area
	Location	Central coordinates	Decimal degrees of latitude and longitude	Determined by spatial resolution of tidal model of Liverpool Bay
	Size	Surface area / volume of patch	Default = 12,395,000 m^2.	Determined by spatial resolution of tidal model of Liverpool Bay. Reduced areas of cells abutting coast generated by GIS of Liverpool Bay
	Patch variables	Water depth	Depth in meters	Determined by predictions of tidal model of Liverpool Bay
		Wind farm	0, 0.25, 0.5. 0.75, or 1	Proportionate overlap of each cell with windfarms derived from GIS of Liverpool Bay.
		Shipping	Ships per hour	Anatec UK Ltd commercial shipping data for Liverpool Bay
		Helicopters	Helicopters per hour	DTI data on helicopter routes and frequency of traffic in Liverpool Bay
		Included	0/1	Used to include/exclude cells from different model runs
Resources	Number	Number of resources	14	A result of the classification of all species of bivalves found in benthic survey of Liverpool Bay into three types and the division of each of these into a number of size classes.
	Initial density	Initial density of each resource on each patch	Numbers per m^2.	Derived by interpolation based on the results of the benthic survey of Liverpool Bay in August 2003
	Change in density	Change in density with time	Proportionate daily change in numerical abundance of each resource	Derived from analyses of the change in numerical abundance of resources between repeat surveys of the benthos in Liverpool Bay in August 2003, December 2003 and April 2004.

Components	Density in resource	Shell Dry Mass	g of shell dry mass per individual prey item within each resource type	Derived from relationships between dry shell mass and length of each of the three principal bivalve types collected from Liverpool Bay (see section 8.6.4)
		Flesh Dry Mass	g of flesh dry mass per individual prey item within each resource type	Derived from relationships between dry flesh mass and length of each of the three principal bivalve types collected from Liverpool Bay (see section 8.6.4)
Foragers	Forager type / species	Number of forager types	1	No distinction made between sexes and ages of common scoter within the population as no quantitative data available concerning other ways in which they differ that are of relevance to susceptibility to depletion/interference competition.
	Maximum number of foragers	Number of super-individuals	1000	1000 chosen to reduce noise between replicate runs while enabling all scenarios to be explored within time available
	Individuals per forager	Individuals per forager	30	This is the value needed to yield a model population of 30,000 common scoter in line with JNCC recommendations (section 10.3.1).
	Forager constants	Foraging Efficiency	A value drawn at random from a normal distribution with mean of 1, st. dev. of 0.125, min of 0, and max of 1000	Based on data on mussel-feeding oystercatchers (see section 7.2.6).
		Dominance	A value drawn at random from a uniform distribution with a min of 0 and a max of 1.	Based on an assumed linear dominance hierarchy found in other species of birds.
		Arrival Day	A value drawn at random from a uniform distribution with a minimum of day 1 and a maximum of day 198	Based on an analyses of the seasonal variation in overflight count data in Liverpool Bay (see section 8.6.5.1.4)
		Departure Day	A value drawn at random from a uniform distribution with a minimum of day 198 and a maximum of day 304	Based on an analyses of the seasonal variation in overflight count data in Liverpool Bay (see section 8.6.5.1.4)
		Maximum common scoter density	0.000334 scoter m^{-2} i.e. 4,140 birds per grid cell	Derived from the maximum observed count of common scoter in any one tidal grid cell on any of the 8 overflights of Liverpool Bay between August 2002 and February 2004. (see section 8.6.5.1.3)

	Forager variables	Underwater time per dive (hours)	if(WaterDepth>9.08,(60/3600),else((9.920+5.515*WaterDepth)/3600))	Relationship with water depth derived from published study of several diving ducks (Dewar 1924), including common and velvet scoter but constrained to a maximum value based on maximum dive durations for common scoter in published data and in Liverpool Bay observations. (see section 7.2.2)
		Travel time per dive (hours)	((2*WaterDepth)/0.87)/3600	Based on published values of the speed of underwater swimming by ducks other than common scoter (see section 7.2.2)
		Surface time per dive (hours)	if(WaterDepth>9.08,(81.56/3600),elseif(WaterDepth>4.5, ((23.54+(3.589*3.53*(WaterDepth-4.5)))/3600), else((7.388+3.589*WaterDepth)/3600)))	Basic relationship with water depth derived from published study of several diving ducks (Dewar 1924), including common and velvet scoter. Steeper relationship at greater depths derived from studies of tufted ducks and pochard (see section 7.2.2 for references). Maximum value constrained to be that predicted to occur when diving at depths of c 9m when maximum dive duration predicted to be reached.
		Foraging time per dive (hours)	if((UWTPDive-TravTPDive)>0,UWTPDive-TravTPDive,else 0)	Derived by subtraction of predicted time spent travelling to and from seabed from predicted total time spent underwater
	Location	Coordinates of forager's location		Defined by the central coordinates of the patch in which bird is located
	Patch	Patch number occupied by forager during current time step		Defined by the sequence number of the patch in which the bird is located i.e. 1 – 206.
	Diet	Number of diets	1	Literature concerning scoter, especially common scoter, suggests that bivalves are by far the most important dietary component (see section 7.2.8)
		Number of resources in each diet	14	Literature concerning scoter suggests unlikely to discriminate between bivalve types but that their diet is dictated by whatever is locally abundant. (see section 7.2.8)
	Proportion of time moving	Proportion of time moving between patches during current time step	0 or 1	For simplicity model assumes birds move for whole time steps.

	Proportion of time feeding	Proportion of time feeding during current time step	0 - 1	Calculated on basis of relative values of achievable diet consumption rate in a patch during a time step and the maximum diet consumption rate allowed.
	Diet consumption rate	Bivalves eaten per second on the bottom as a function of the numerical abundance of bivalve prey (bivalves m^{-2})	0.52 * MixedDietDens / (405+MixedDietDens)	Functional response equation derived from studies of captive velvet scoter feeding on buried bivalve prey (see section 7.2.9).
	Maximum diet consumption rate	Maximum number of bivalves that can be eaten per hour	Minimum of: 1) (137.4/(0.85*18.7*Mixed Diet Flesh Dry Mass Dens), 2) 287.4/(2.5*(Mixed Diet Flesh Dry Mass Dens + Mixed Diet Shell Dry Mass Dens)))	Two constraints based on: 1) maximum energy assimilation rate (137.4 kJ h^{-1}) and 2) maximum crude intake rate (287 g fresh mass h^{-1}) are both derived from studies of captive scaup feeding on freshwater mussels (see section 7.2.10.1) The value of assimilation efficiency (0.85) is derived from published studies of captive oystercatchers eating bivalves. The value of energy density of bivalve flesh (18.7 kJ g dry flesh $mass^{-1}$) is the average of several published values for bivalves. The value of 2.5 is used to calculate the fresh mass ingested from the dry mass on the assumption that the dry mass makes up only 40% of total bivalve mass. This is based on published figures for freshwater mussels (see section 7.2.10 for details)
	Component consumption rate	Rate at which each component is consumed during current time step		Calculated from the diet consumption rate and the weighted resource component densities within a patch and time step.

	Component assimilation rate	Flesh Dry Mass	0.88*0.73525*(18.7/39.3)	The value of 0.88 defines the efficiency with which assimilated energy is converted into stored energy reserves and is derived from published studies of wading birds. The value 0.735 defines the proportion of the energy content of the dry flesh material that is ingested which is assimilated across the gut wall and available for conversion to stored energy reserves (taking into account losses due to costs of crushing bivalve shells and digesting the food in the first place). This value is derived from published studies of the energetics of captive bivalve-feeding common eider ducks. The value of energy density of bivalve flesh (18.7 kJ g dry flesh mass^{-1}) is the average of several published values for bivalves. The value of the energy density of birds' energy (i.e. fat) reserves (39.3 kJ g^{-1}) is derived from published studies of wading birds (see section 7.2.10 for details)
		Shell Dry Mass	0	It is assumed that common scoter do not acquire any energy from the shell component of their bivalve prey. No published study on diving ducks has suggested otherwise.
	Component metabolic rate	While engaged in active foraging (g h^{-1})	(((2.0276-0.0379 * Water Temp) * 11.54) + (1.03 * ((9.4717 - 0.1153 * Water Temp) * (2.0276 -0.0379 * Water Temp) * 11.54) * (UWTPDive / (UWTPDive + SurfTPDive))) + ((41 –Water Temp) * ((0.8 * Shell Dry Mass Cons Rate) + (4.2 * (1.5 * (Flesh Dry Mass Cons Rate + Shell Dry Mass Cons Rate)))) / 1000)) / 39.3	The calculation of the energetic cost of foraging is split into three components: i) the rate of metabolism while resting on the surface, ii) the excess diving costs over and above the resting metabolic rate while underwater and iii) the costs of heating the food ingested while foraging. The first two of these rely upon an estimate of the basal metabolic rate of common scoter (11.54 kJ h^{-1}). This is derived from a published allometric equation. The other coefficients used in calculation of the first, second and third components are based on analyses of the experimental results of work on captive tufted ducks and scaup. The assumption that this is how the energetic expenditure of foraging diving ducks should be calculated is based on a detailed study of the energetics of captive tufted ducks and scaup (see section 7.2.10 for details).
		While not actively foraging (g h^{-1})	(2.0276 - 0.0379 * Water Temp) * 11.54 / 39.3	This is the same as the first component described above.

		While moving between patches (i.e. flying) (g h^{-1})	264 / 39.3	The value of 264 kJ h^{-1} was interpolated between published estimates for the cost of flight of tufted duck and scaup which were themselves calculated from published equations for the cost of bird flight (see section 7.2.10.8). The value of the energy density of birds' energy (i.e. fat) reserves (39.3 kJ g^{-1}) is derived from published studies of wading birds (see section 7.2.10)
	Component reserve size	Initial reserve size (g)	728 + 235.63	728g is the average of the published starvation masses of adult male and female common scoter. 235g is the mass of body reserves estimated to be carried by an average adult common scoter in early August based on an analysis of published common scoter body mass data. (see section 7.2.15)
		Seasonal change in target reserve size	728 + (235.63 + 1.2019 * TheDay)	The values of 728g and 235g are as described above. The value of 1.20 g day^{-1} is the estimated daily rate of increase in the mass of common scoter body reserves derived from a linear regression through published common scoter body mass data (see section 7.2.15).

9. Model calibration and validation

9.1 Introduction

Prior to conducting any of the windfarm scenario simulations that are described in section 10 and the results of which are presented in section 11, it was necessary to construct and parameterise the model MORPH as described in sections 6, 7 and 8. Having done so, it was then necessary to run the model under 'baseline' conditions and establish whether or not it was behaving realistically by comparing the model's outputs with independent empirical data derived from the literature concerning the foraging behaviour and mortality of common scoter. The results of the calibration and validation stages in the modelling process are presented in this section.

To conduct the calibration and validation exercise, the model MORPH was parameterised to simulate the current environment, as experienced by common scoter in Liverpool Bay. As described in the previous section, a precautionary approach to predicting resource abundances distant from benthic sampling stations constrained birds in the model to 115 patches. However, this still presented the model birds with very large areas which could be used by common scoter but which are little (or never) used in reality. In addition, the model incorporated the existing frequency and distribution of shipping and helicopter activity and the presence of the North Hoyle windfarm. For the purposes of calibration and validation, the model was run using the default values for all the various parameters and assumptions, variations to which were explored in the full simulations described in sections 10 and 11.

9.2 Model calibration

When the model was run as described above, a substantial proportion of the population was predicted to forage consistently on the Burbo Bank area and in the area to the east of the site originally proposed for the Southport windfarm i.e. off the mouth of the Ribble estuary (Fig. 9.1). The over flight data indicates that these areas are seldom, or in the case of the former virtually never, used by ducks in reality (Fig. 8.1). Clearly, there are abundant benthic food resources for common scoter in these areas (Fig. 3.6). However, for some reason, the existing common scoter population does not utilise them. There are a number of possible explanations for this discrepancy between the model and reality. For example, if common scoter are relatively site faithful (see section 7.2.1), birds that feed off the north Wales coast or off the Lancashire coast between Fleetwood and Lytham St Anne's may never visit these areas. It is also possible that these areas are underexploited because, at the scale of Liverpool Bay, the common scoter population is well below that which the total resources within the bay can support. Alternatively, there are numerous environmental factors which might render these areas unsuitable for common scoter but which are not included in the model. One example might be the activity of small ships or even recreational activity such as jet skis. Whatever, the reason for the discrepancy, the inclusion of these areas in the model clearly presented the model birds with highly suitable areas that they do not use in reality. This may mean that the birds in the model are presented with a far 'easier' environment than that which they currently encounter. In the context of model validation, this may mean that the amount of time that birds devote to foraging and their mortality may be artificially reduced in the model. To avoid this it was decided that it was necessary to exclude these two areas from the model. Thus, for the purposes of validation, 11 grid cells around the Burbo Bank area and 5 grid cells to the east of the previously proposed Southport windfarm were 'excluded' from the model. This was achieved by setting the initial resource abundances to be 0 in these cells. This resulted in a model with 99 patches available to the birds (Fig. 9.2). These still included all the *circa* 30 patches in which common scoter occur most frequently and some 60-70 cells in which common scoter seldom or never occur. Thus, even with only 99 patches in the model, the potentially exploitable habitat available to the common scoter population is far in excess of that which they currently exploit.

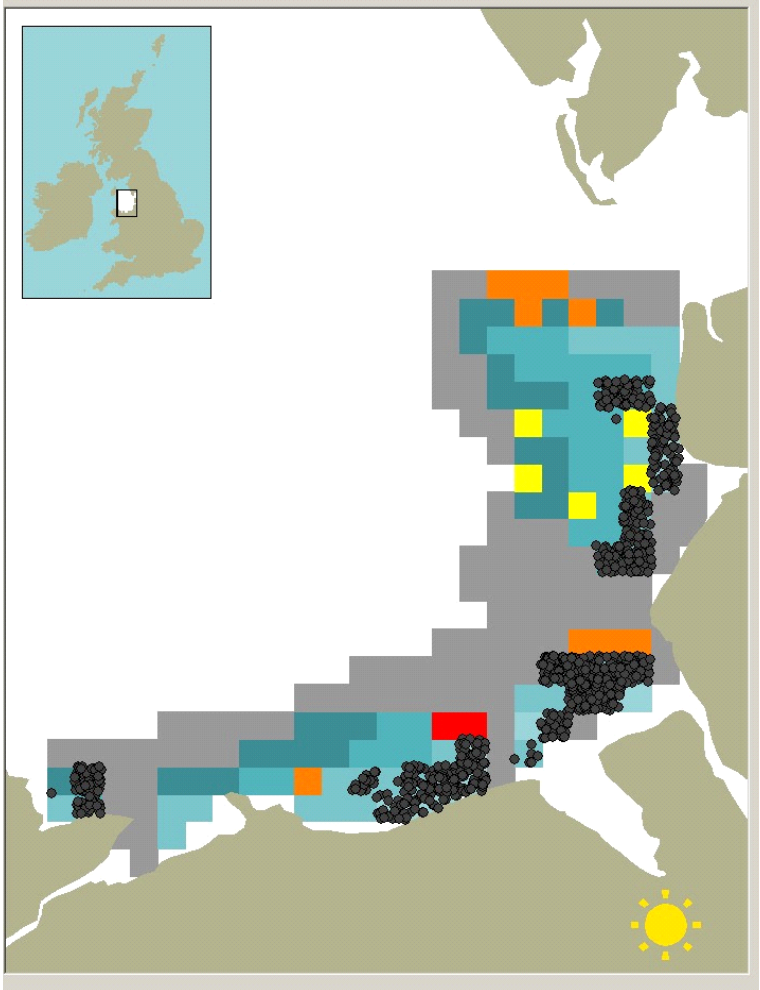

Figure 9.1. Screenshot of the model graphic display illustrating a typical 'snapshot' of the predicted distribution of common scoter at one particular point in time under the 'baseline' scenario in which 115 tidal grid cells within 2.5km of a benthic sampling station are included. The image shows the location of the study area within the UK and the coastline of north Wales, Cheshire, Lancashire and south Cumbria. Within the area of the Irish Sea, the 206 tidal grid cells considered for inclusion in the model are shaded. The initial biomass density of all resources was set to 0 in 91 grid cells which are further than 2.5km from any benthic sampling station. These cells, which are inaccessible to the birds in the model are shaded grey. The remaining 115 cells are coloured as follows. All cells are subject to variation in water depth with time. Greater water depth is indicated by the intensity of blue shading- which changes in each cell on an hour to hour basis. Cells in which a source of human disturbance is present during this particular hour are overlaid with a further colour: red denotes the permanent presence of a windfarm (at North Hoyle), orange denotes the temporary presence of a large ship passing through a cell at this point in time and yellow denotes the temporary presence of a helicopter passing over a cell at this point in time. Common scoter avoid a cell when one or more of these sources of disturbance occurs there but may visit it at other times in the absence of disturbing factors. Each black dot represents one super-individual each of which represents 30 common scoter. The image of the sun denotes that this 'snapshot' was taken during the hours of daylight.

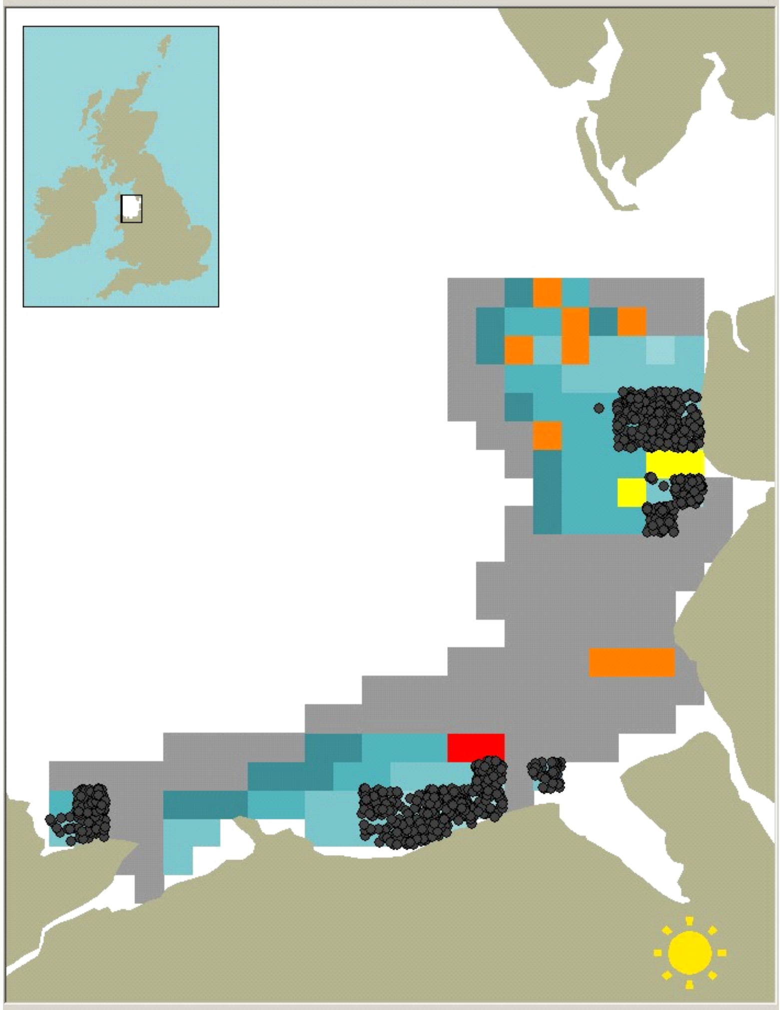

Figure 9.2. Screenshot of the model graphic display illustrating a typical 'snapshot' of the predicted distribution of common scoter under the 'baseline' scenario in which 11 cells on Burbo Bank and 5 cells near Southport are also excluded leaving 99 cells available to the birds in the model. The difference in the distribution and number of cells coloured with various shades of blue and with orange and yellow in this image from that shown in Fig 9.1 reflects the hour-to-hour variations in the water depth and the distribution of shipping and helicopter traffic. Other details of the image are as described in legend to Fig 9.1.

9.3 Model Validation

9.3.1 Proportion of daylight hours spent feeding

A key test of the model is whether it mimics the amount of time that common scoter devote to foraging each day in order to survive. It is essential to establish whether model birds have to 'work as hard' to survive as birds do in reality. If this were not the case, then predictions of the consequences of changes to the environment in simulations in which windfarms are present may be optimistic due to overly benign baseline conditions. Conversely, if model birds have to forage very much longer than birds do in reality, then predictions of the consequences of changes to the environment in simulations in which windfarms are present may be pessimistic due to overly harsh baseline conditions

The model predicted that under current conditions, the proportion of daylight hours that common scoter spend feeding i.e. engaged in dive bouts, increases from *circa* 0.4 in early autumn to a peak of *circa* 0.55 in mid-winter and then declines gradually thereafter to reach a minimum in late spring of *circa* 0.35 (Fig. 9.3). Thus, the values for the proportion of time spent feeding that are predicted by the model are consistent with the limited empirical data available (section 7.2.12). Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting that the birds spend wholly incorrect amounts of time foraging each day. It does not do so.

The fact that at all times of year the values did not exceed 0.6 means that the birds are not constrained by a lack of available feeding time. This has important implications in that birds appear to have the ability to buffer themselves against changes to environmental quality by increasing the proportion of daylight hours spent feeding (subject to constraints imposed by their physiology and gut capacity).

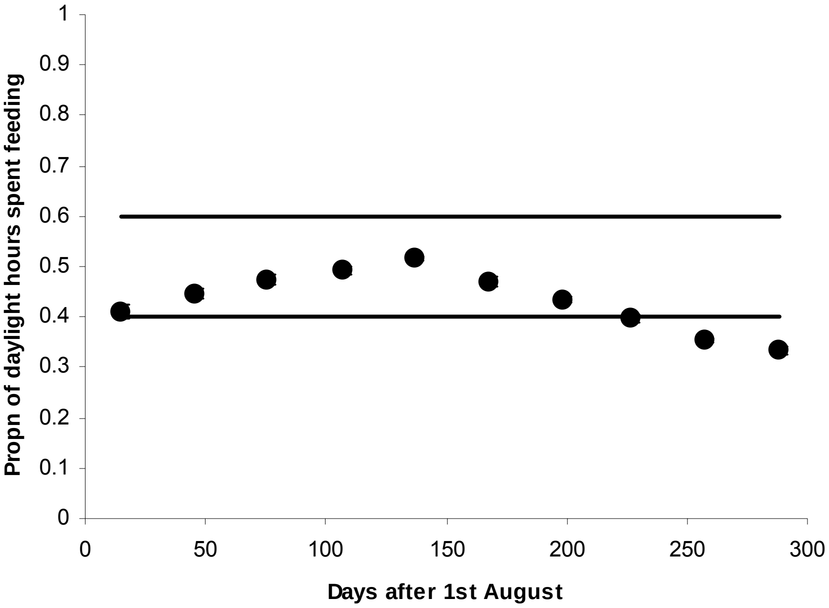

Figure 9.3 Seasonal variation in the predicted proportion of daylight hours spent actively feeding by common scoter in Liverpool Bay in comparison with empirical data. Each point represents the mean (across 5 replicate simulations) proportion of daylight hours spent feeding (+/- 2se) on the middle day of each month between August and May. The upper and lower horizontal bars depict values of 0.4 and 0.6 as the likely bounds throughout most of the modelled period, based on the literature review.

9.3.2 Daily consumption of food

The model predicted that under current conditions the daily consumption of food by common scoter in Liverpool Bay varies seasonally (Fig 9.4). Daily consumption declines from autumn and early winter to reach a minimum in mid-winter before increasing rapidly in late winter and especially in spring. To a large extent, this seasonal pattern simply reflects the assumption in the model that common scoter do not feed at night. Thus, in mid-winter when there is least daylight, the daily consumption of the birds is constrained more than either earlier or later in the season. The highest values in spring also reflect the assumption that the target body mass of common scoter is assumed to continue to increase (perhaps in preparation for spring migration). Although the seasonal pattern predicted by the model may be unrealistic, the range of values predicted is (with the exception of the low values in December and January) consistently between the likely upper and lower limits to their daily food consumption (see section 7.2.13). Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting that the birds consumed wholly incorrect quantities of food. It does not do so.

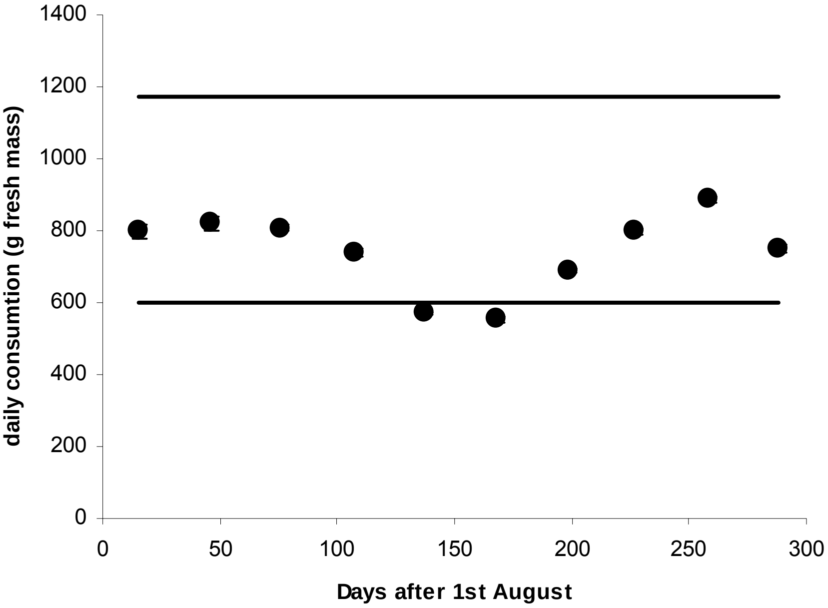

Figure 9.4 Seasonal variation in the predicted daily consumption of fresh mass of bivalve prey (shells included) by common scoter in Liverpool Bay in comparison with likely upper and lower limits derived from empirical data. Each point represents the mean (across 5 replicate simulations) daily food consumption (+/- 2se) on the middle day of each month between August and May. The upper and lower horizontal bars depict the likely bounds throughout most of the modelled period, based on the literature review.

9.3.3 Daily energy expenditure

The model predicted that under current conditions the daily energy expenditure of common scoter wintering in Liverpool Bay varied slightly through the season (Fig 9.5). To a large extent, this seasonal pattern simply reflects the assumption in the model that common scoter do not feed at night. Thus, in mid-winter when there is least daylight, the daily energy expenditure of the birds is reduced by the increased proportion of time that they spend resting at night (resting being less energetically expensive than foraging). The highest values in spring also reflect the assumption that the target body mass of common scoter is assumed to continue to increase (perhaps in preparation for spring migration) such that they ingest more food and consequently expend more energy (heating the food up from ambient to body temperature (section 7.2.10.6)). Although the seasonal pattern predicted by the model may be unrealistic, the range of values predicted is consistently above the predicted resting metabolic rate and, more importantly, below the likely upper limit to their daily energy expenditure (section 7.2.14), even in late spring when the birds' body masses are at their greatest. Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting that the birds expended wholly incorrect quantities of energy per day. It does not do so.

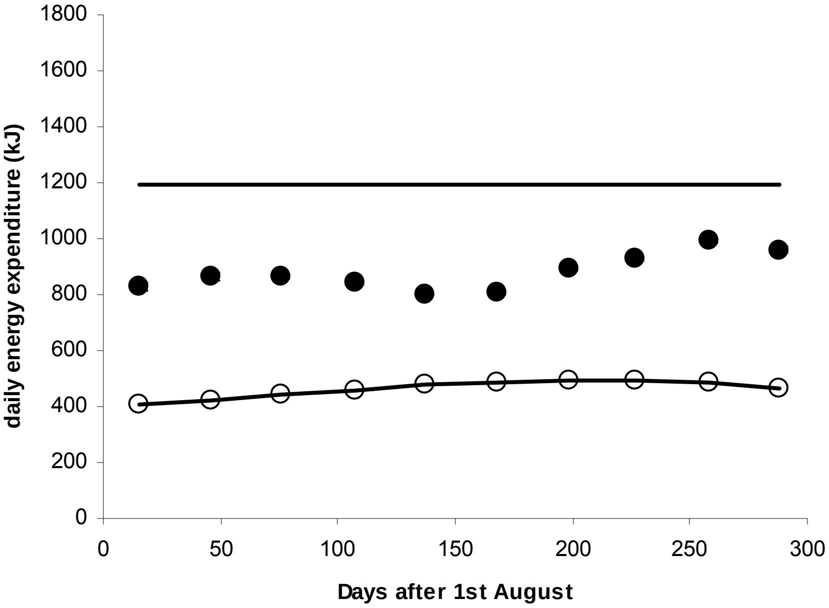

Figure 9.5 Seasonal variations in the predicted daily energy expenditure of common scoter in Liverpool Bay. Each point represents the mean (across 5 replicate simulations) daily energy expenditure (+/- 2se) on the middle day of each month between August and May. The upper horizontal line depicts a value of 1190kJ equivalent to 4.3*BMR, assumed to be the likely upper bound to common scoter DEE, based on the literature review. The lower solid line (with open circles) represents the predicted seasonal variation in the temperature-dependent resting metabolic rate.

9.3.4 Seasonal variation in body mass

The model predicted that under current conditions the body mass of common scoter wintering in Liverpool Bay varies through the season (Fig 9.6). Initially the model predicts that the birds are able to increase their body mass in line with their assumed increasing target mass. However, in the absence of night-time foraging, birds are not able to continue this mass increase through mid-winter and indeed are predicted to lose mass between November and February. Thereafter, as day length increases the birds are able to increase their mass once again and by the end of May are predicted to be able to attain the observed late spring body mass. As discussed in section 7.2.15, the assumed linear increase in target body mass is speculative. In fact, empirical data suggests that it is quite likely that diving ducks are often in negative energy balance during mid-winter and might indeed lose mass at this time of year (see section 7.2.15). The model output is, therefore, consistent with empirical data from other species of diving duck. Nonetheless, even in mid-winter the model predicts that under current circumstances the average body mass of those birds that do not starve is well in excess of the starvation mass. Under existing circumstances the majority of the population, although they are predicted to lose mass in mid-winter, are not in danger of starving. However, the mid-winter decline in mass of the bulk of the population suggests that the low over-winter mortality in the model (see section 9.3.6) does not reflect an overly benign model world, and accordingly that predictions of the consequences of environmental change (section 11) are not unduly optimistic.

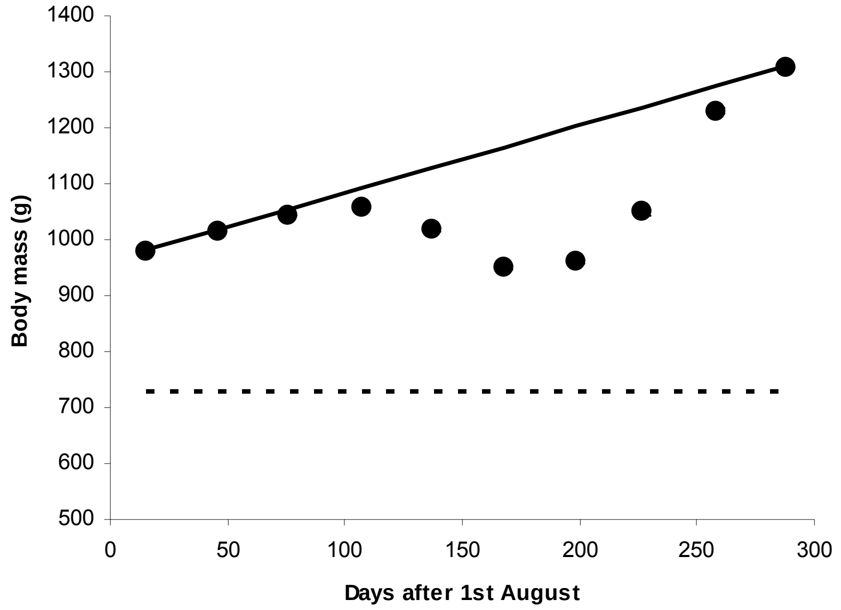

Figure 9.6 Seasonal variation in the predicted body mass of common scoter in Liverpool Bay in comparison with their assumed target body mass (solid line) and starvation mass (dashed line). Each point represents the mean (across 5 replicate simulations) body mass (+/- 2se) on the middle day of each month between August and May of those birds present in the model and alive on the day in question.

9.3.5 Distribution

The precise location of common scoter sighted in Liverpool Bay was recorded during 8 over flights made between August 2002 and March 2004. The results of each of the over flights were incorporated into the GIS of Liverpool Bay and the data interrogated to yield the total number of birds sighted within each of the tidal grid cells in the model. These data were further analysed to yield the proportion of the total number of ducks counted that were seen in each grid cell on each of the over flights. For each grid cell these 8 values were averaged to yield the mean proportion of the common scoter population seen within them. To generate an equivalent set of data from the model, the model was set to output the number of common scoter in each cell at midday on the middle day of each month between August and May. This yielded 10 ‘snapshots’ of the distribution of ducks in the model to compare with the 8 real-world ‘snapshots’. The model output data were also processed to generate the mean proportion of the population within each grid cell across the 10 ‘snapshots’ of the birds’ distribution.

Examination of the empirical data indicated that the highest overwinter average proportion of the population within a grid cell was 10% and that only 9 cells held on average in excess of 5% of the population. The common scoter population is very widely scattered. In order to analyse the match between the observed and model generated distribution of the ducks, both the empirical and the model output were split into two categories; cells containing on average less than 0.5% of the population and those containing more than this. These data were then analysed by means of Fisher’s exact test for 2 x 2 contingency tables. In each of the 5 replicates of the validation scenario, there was a highly significant association ($P < 0.01$) between the classifications of grid cells on the basis of common scoter usage predicted by the model and that generated on the basis of the over flight data. In general, the bulk of the cells which are seldom used by common scoter in reality were little used by model birds, and many of the cells used heavily by common scoter in reality were also much used in the model. Thus, when considering the distribution of common scoter across a large proportion of the area of Liverpool Bay which contains both heavily used and seldom used areas, the model, in broad terms, successfully matched the current distribution of common scoter within the bay. Errors in any of a large number of parameters and functions in the model, not least those resulting from the extensive but far from exhaustive benthic survey, could have resulted in the model predicting that the birds occurred in entirely the wrong places. It does not do so.

Although there was a highly significant association beteen the predicted and observed distribution of common scoter in all replicate simulations there was a tendency for birds in the model to be somewhat more aggregated than in reality – a few cells used heavily in reality were little used by model birds. This was most noticeable in the case of six tidal grid cells on Shell Flat (Fig. 9.7). In all of these cells the benthic bivalve community was dominated by small (0-12mm) thick bivalves. On the basis of analyses of samples of each of the resources in the model, these are the least nutritionally profitable; less than 10% of the dry mass being digestible flesh. This contrasts with thin-shelled and elongate bivalves in which the percentage of the dry mass that comprises flesh varies between 13% and 23% and between 23% and 35% respectively depending upon size (Fig. 8.4). Thus, the resources available over these areas of Shell Flat appear to be far less profitable than those available towards the south and east (areas which are heavily used by common scoter both in reality and in the model). The principal reason for the lack of a perfect fit between the distribution of foraging birds in the model and that suggested by the overflight data is that in the model the birds tended to concentrate on those patches where there are abundant bivalves belonging to the elongate prey type. In order to explore whether the removal of these resources would lead to an improved match between the predicted and observed duck distribution, the model was re-run without some of the elongate bivalve prey resources. This led to a reduction in the usage by model birds of the grid cell that in reality is the most heavily used of all, and did not lead to any noticeable increase in the usage of the Shell Flat cells that were previously little used by model birds. Instead, nearly 90% of the birds died. Clearly, these elongate bivalve resources are crucial to the birds' survival and must be included in the model in spite of the resultant lack of a perfect fit between the precise distribution of model birds and those in reality.

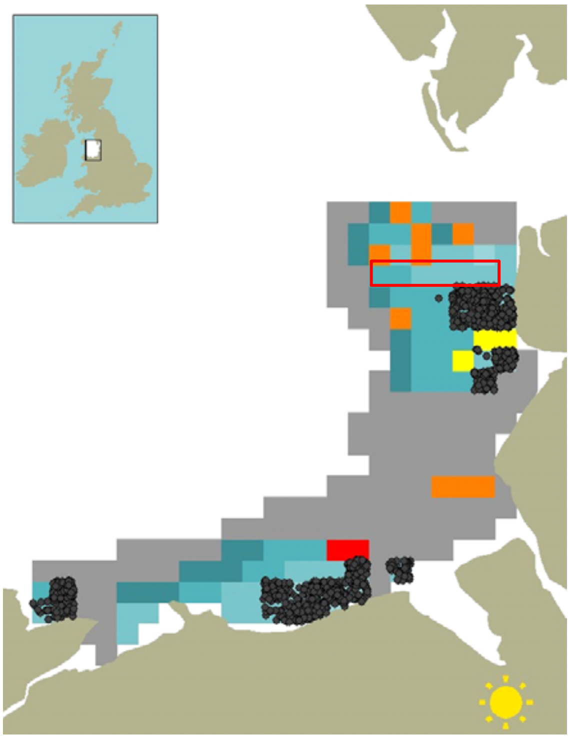

Figure 9.7. Screenshot of the model graphic display illustrating a typical 'snapshot' of the predicted distribution of common scoter under the 'baseline' scenario in which 99 cells were included. The group of 6 grid cells on Shell Flat which are heavily populated by common scoter in reality but in which model birds seldom forage are highlighted by the red rectangle. Other details of the image are as described in legend to Fig 9.1.

This lack of an absolutely perfect fit between the precise distribution of foraging common scoter predicted by the model and that of birds seen during over flights has a number of possible explanations. These explanations, and the implications that they may have for future research requirements, are discussed in more detail in sections 11.7 – 11.8. Given that at the scale of the bay as a whole, the distribution of birds predicted by the model was associated with that of the birds in reality and that in all other respects, especially the overwinter mortality (see below), the model output is consistent with expectations, the fine-scale mis-match between the model and reality concerning the extent of the reliance of the population on Shell Flat as a feeding ground is unlikely to lead to any significant errors in the predicted consequences for common scoter of any of the windfarms other than Shell Flat. It is, however, possible that the model will under-estimate the consequences for the common scoter population of the proposed Shell Flat windfarm. Indeed it is possible that, given the lack of predicted usage of much of the area in which the Shell Flat windfarm may be located, the model could wrongly predict no adverse effects of this windfarm at all. In fact, this is not the case (see section 11) and so this concern over the prediction of a 'false negative' does not in fact arise.

9.3.6 Over-winter mortality

Based on an analysis of: i) the known annual mortality rate of adult female common scoter, ii) an estimate of the proportion of this annual rate that occurs over-winter, iii) the bias in common scoter sex ratio and hence iv) an assumption that there is variation in the mortality rate between the sexes, the overall over-winter mortality of common scoter in Liverpool Bay was estimated to be in the region of 6.4% (see section 7.2.16). The model predicted that under current conditions the median over winter mortality of common scoter wintering in Liverpool Bay (across the 5 replicate simulations) is 7.3% (range 5.4% to 8.8%). Thus, there is very close agreement between the likely mortality in reality and that generated by the model. Errors in any of a large number of parameters and functions in the model could have resulted in the model predicting wholly incorrect over-winter mortality values. It does not do so.

9.4 Conclusions

In summary, 5 replicate simulations of the model MORPH were conducted in which the current environment, as experienced by common scoter was simulated (in terms of the extent of the geographic area that they exploit, the frequency and location of shipping and helicopter activity and the presence of the North Hoyle windfarm). The output of these simulations was compared with independent empirical data derived from the literature concerning the foraging behaviour, distribution and mortality of common scoter. In general, the model outputs were consistent with these independent data. This provides confidence that the birds in the model behave as do birds in reality and that the key features of the system have been incorporated in the model. On this basis, it is then possible to have some confidence in the predictions of the model when used to simulate novel environmental conditions in which additional windfarms are added to the Liverpool Bay system (sections 10 & 11).

10. Model scenarios

10.1 Introduction

The number of potential scenarios that the model could be used to simulate is limitless. During discussions with members of the COWRIE steering group in June 2005 a series of key scenarios was agreed. This deals explicitly with the existing/ consented and proposed windfarm sites. The key scenarios that were agreed upon and which have been explored, and the details of all the additional simulations that have been conducted, are discussed in this section.

10.2 Key Scenarios

The first priority scenario was to simulate the existing 'baseline' circumstances which common scoter currently face. In this scenario all the background shipping and helicopter traffic is included as is the North Hoyle windfarm. It was agreed that this should form the baseline because: i) the North Hoyle windfarm is already constructed, ii) some of the over flight data were gathered after it was built and iii) the benthic data were gathered while it was being built. This scenario is the one used to validate the model's outputs (see section 9) as well as being the baseline against which the results of the other 'novel scenario' simulations are compared (section 11).

The second priority scenario was to explore the consequences of adding the two Round 1 windfarm locations that have already been given consent i.e. Rhyl Flats and Burbo Bank in addition to the existing windfarm at North Hoyle.

The third and fourth priority scenarios were to explore the consequences of adding the proposed round 1 windfarm at Shell Flat or the proposed round 2 windfarm at Gwynt-y-Mor in addition to the existing windfarm at North Hoyle and the two consented locations at Rhyl Flats and Burbo Bank.

The final priority scenario was to explore the consequences for common scoter of the existence of all 5 windfarms within the study region.

10.3 Simulation options

For each of these five key scenarios, there are a number of potential factors over which there is a degree of uncertainty that could lead to uncertainty over the outcomes predicted by the model. These concern: i) the size of the common scoter population in Liverpool Bay, ii) the effects of windfarm maintenance traffic on the ducks, iii) the size of the buffer zones around windfarms, iv) the extent of the habitat exploited by the ducks, v) the accuracy of the measured resource abundances and vi) whether common scoter might feed by night as well as by day. These are discussed below.

10.3.1 Common scoter population size

It was agreed that the best estimate for the peak common scoter population within Liverpool Bay should be obtained from the Joint Nature Conservation Committee (JNCC) interpolated database. It was agreed that the priority should be to run the model only with this population size rather than to explore the consequences of variation in the size of the population.

Data held by JNCC indicates that the mean population of common scoter in Liverpool Bay in November – March 2001/2002 was 21,710 and in November – March 2002/2003 was 42,179 (A. Webb pers. comm.). This latter figure may, however, be somewhat elevated by an unusually high population estimate in February 2003. Although there is considerable uncertainty (and probably variability between years) around the long-term average peak population size of common scoter in Liverpool Bay,JNCC recommended that circa 30,000 ducks would be the best estimate of the average population of common scoter in Liverpool Bay in these years (A. Webb pers. comm.)

10.3.2 Windfarm maintenance traffic

It was agreed that the priority should be to conduct simulations including the windfarms and their associated maintenance traffic, rather than to explore simulations with and without the farms and the maintenance traffic. It was agreed that there was no point conducting simulations to explore the consequences of maintenance traffic using alternative routes to those currently proposed unless the priority set of simulations indicated that the windfarms and proposed traffic routes do significantly affect the ducks in some way. Subsequent to the meeting with the COWRIE steering group in June 2005, it proved impossible to obtain any information concerning the proposed routes or frequency of the maintenance traffic associated with each of the 5 windfarms within the study area. Thus, this factor has not been included in any of the model simulations.

10.3.3 Buffer zones

It was agreed that the key scenarios should be repeated assuming: i) a buffer zone of 0km around each windfarm structure (conservative approach) and ii) a buffer zone of 2km around each windfarm structure (precautionary approach based on existing Danish studies - section 7.2.11). In fact, the rule used in the model to define whether a cell was rendered unavailable to common scoter due to its proximity to a windfarm (i.e. that > 50% of a cell would have to overlap a given windfarm or the buffer zone surrounding it (section 8.6.2)) meant that in some instances there was no difference between simulations assuming 0km and 2km buffers. In this case, only one of the two buffer sizes was simulated. Thus, only 8 key scenarios were explored, as set out in Table 10.1. In particular, the scenarios in which the buffer zone around the North Hoyle windfarm extended over 0km (scenario 1) and 2km (scenario 2) did not differ in terms of the number of grid cells that were affected. Thus, it was not necessary to simulate scenario 2. The extent of the area of influence of the Gwynt-y-Mor windfarm, when a buffer of 0km was assumed, did not overlap the study area at all and so the scenario (scenario 7) intended to include North Hoyle, Rhyl Flats, Burbo Bank and Gwynt-y-Mor each with a 0km buffer zone did not differ from that in which only the first three of these farms were included (scenario 3). Thus, it was not necessary to simulate Scenario 7. The model grid cells affected by each of the windfarms under the assumptions of 0km and 2km buffer zones around them are illustrated in Figures 10.1 and 10.2.

Table 10.1 The details of the windfarms and the buffer zones incorporated in each of the 8 key scenarios explored. Scenario numbers correspond to those used in the following text and figures in this section.

Scenario number	Windfarms included	Assumed buffer zone radius
1	North Hoyle	0km
3	North Hoyle + Rhyl Flats + Burbo Bank	0km
4	North Hoyle + Rhyl Flats + Burbo Bank	2km
5	North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat	0km
6	North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat	2km
8	North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor	2km
9	North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat + Gwynt-y-Mor	0km
10	North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat + Gwynt-y-Mor	2km

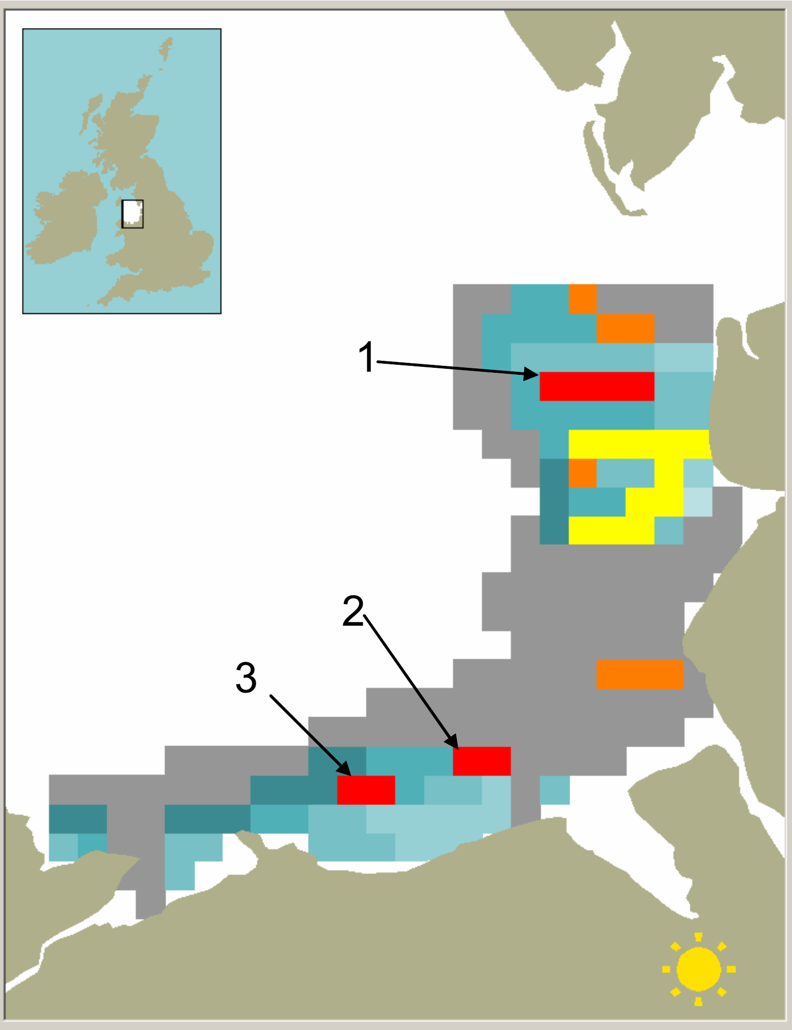

Figure 10.1 Screenshot of the model graphic display (without birds) illustrating the extent of the grid cells (coloured red) from which common scoter are excluded on the assumption of a 0km buffer zone around the existing (North Hoyle), consented (Rhyl Flats and Burbo Bank) and proposed (Gwynt-y-Mor and Shell Flat) windfarms within the Liverpool Bay study area. In this case a grid cell is rendered unavailable if over 50% of its area falls within the physical perimeter of the windfarm. The areas affected by the windfarms are numbered as follows: Shell Flat (1), North Hoyle (2) and Rhyl Flats (3). The extent of the area of influence of the Burbo Bank and Gwynt-y-Mor windfarms do not overlap with the 99 grid cells included in the model. The image shows the location of the study area within the UK and the coastline of north Wales, Cheshire, Lancashire and south Cumbria. Within the area of the Irish Sea, the 206 tidal grid cells considered for inclusion in the model are shaded. The initial biomass density of all resources was set to 0 in 91 grid cells which are further than 2.5km from any benthic sampling station and 16 further cells on Burbo Bank and off Southport (see section 9.2).These cells, which are inaccessible to the birds in the model, are shaded grey. The remaining 99 cells are coloured as follows. All cells are subject to variation in water depth with time. Greater water depth is indicated by the intensity of blue shading which varies on an hour-to-hour basis. Cells in which a source of human disturbance is present during this particular hour are overlaid with a further colour: red denotes the permanent presence of a windfarm (see above), orange denotes the temporary presence of a large ship passing through a cell at this point in time and yellow denotes the temporary presence of a helicopter passing over a cell at this point in time. Common scoter avoid a cell when one or more of these sources of disturbance occurs there but may visit it at other times in the absence of disturbing factors. The image of the sun denotes that this ‘snapshot’ was taken during the hours of daylight.

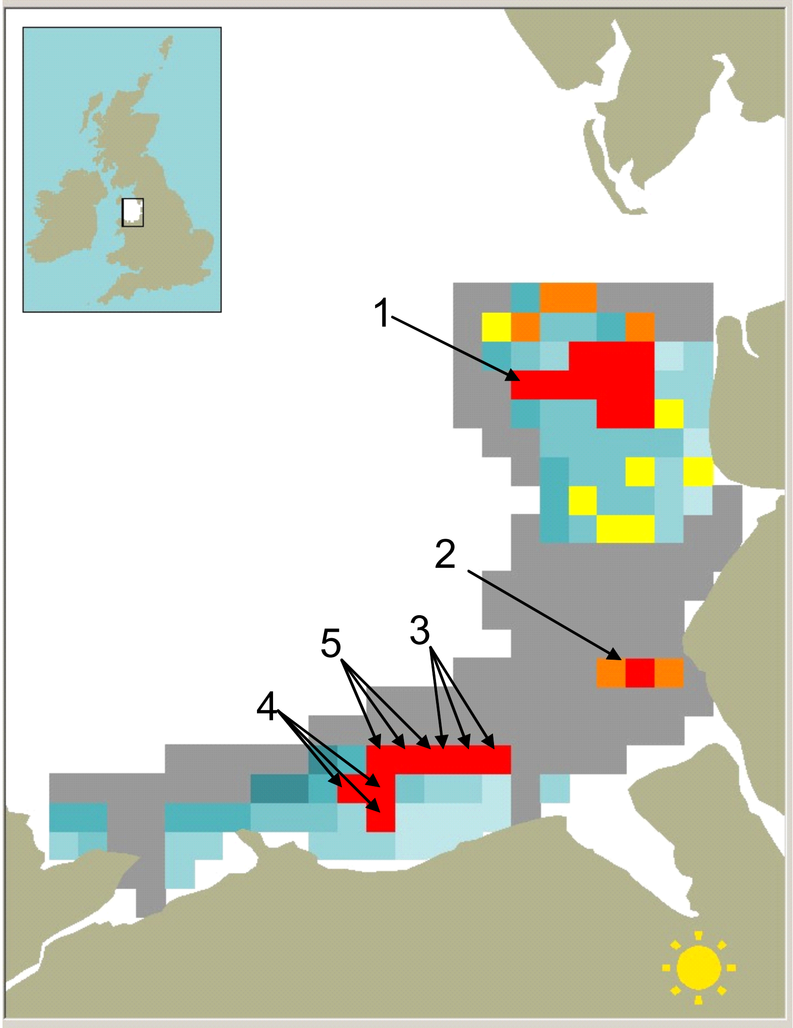

Figure 10.2 Screenshot of the model graphic display (without birds) illustrating the extent of the grid cells (coloured red) from which common scoter are excluded on the assumption of a 2km buffer zone around each windfarm within the Liverpool Bay study area. In this case a grid cell is rendered unavailable if over 50% of its area falls within the boundaries of the buffer zone around the perimeter of the windfarm. The areas affected by the windfarms are numbered as follows: Shell Flat (1), Burbo Bank (2), North Hoyle (3), Rhyl Flats (4) and Gwynt-y-Mor (5) Those cells affected by the windfarms at Burbo Bank and Gwynt-y-Mor which fall outside the 99 grid cells included in the model are not shown. Other details of the image are as described in the legend to Figure 10.1

For reasons outlined in section 9.2 the default version of the model included 99 cells and excluded 11 cells on Burbo Bank and 5 cells off Southport that appear to be highly attractive in terms of the food supplies present there but are little used by common scoter in reality. This was done so that the environment utilised by the model birds was similar to that utilised by ducks in reality. One consequence of this decision was that the cells which the Burbo Bank windfarm is likely to affect, assuming a 0km buffer zone, were in any case excluded from scenario 3 in which the consequences of the existence of this farm was to be explored (in conjunction with those at North Hoyle and Rhyl Flats) (Figure 10.1). Similarly, all but one of the grid cells that the Burbo Bank windfarm is likely to affect, assuming a 2km buffer zone, were also excluded from scenario 4 in which the consequences of the existence of this farm was to be explored (in conjunction with those at North Hoyle and Rhyl Flats) (Figure 10.2). The frequency of large ship traffic in this one cell meant that even in the absence of the Burbo Bank windfarm, it was already permanently unavailable to the ducks. Thus, in comparing the outputs of scenarios 3 and 4 with the baseline scenario (scenario 1) the model explicitly explores the consequences of the addition of the Rhyl Flats farm and not that of Burbo Bank. However, in both scenarios the model, by default, effectively assumes the worst case scenario concerning the effect of the Burbo Bank windfarm on the birds, i.e. that the birds are permanently excluded from all the grid cells in its vicinity. Even under this extreme assumption the model predicted that both the foraging behaviour (in terms of % daylight spent feeding) and the mortality of the birds were entirely consistent with independent empirical data. This result, in combination with the compete absence of common scoter from the Burbo Bank area in reality, can be taken as indicative that this particular windfarm is unlikely to have a noticeable impact on the common scoter population of Liverpool Bay.

10.3.4 Extent of habitat exploited

The benthic sampling programme conducted to quantify the spatial variation in the abundance of common scoter food supplies is one of the most extensive surveys of its kind ever undertaken in the coastal waters of the UK. Nonethless, given the financial, temporal and practical constraints within which the survey was conducted, the stratified survey design did not cover the entirety of Liverpool Bay in an even manner, the emphasis being on greater sampling effort in areas where common scoter are known to occur. As a result, the ability to interpolate the numerical abundance of each of the common scoter food resources across the entire study area on the basis of the point estimates of abundance made at each of the sampling stations was limited by the uneven distribution of the sampling stations. Interpolations could be made with reasonable confidence within a short distance of known sampling stations. However, interpolations to positions far from actual sampling stations are suspect. As described in section 8.6.3, such interpolation resulted in predictions of two extensive areas of abundant resources where no empirical sampling data from the survey exist to verify the predictions. Given the speculative nature of the interpolations in these areas, and the lack of common scoter in them, it was decided to constrain interpolations of benthic resource abundance to cells within 2.5km of a sampling station. This restriction resulted in 115 of the 206 grid cells being ‘included’ in the model. The other 91 cells were ‘excluded’ from the model by setting the initial numerical abundance of each resource to 0. Although this effectively removed a large area within which common scoter could in principle feed, the 115 usable patches within the model still encompass all of the areas which currently hold the vast majority of the common scoter population (*circa* 30 grid cells), and a further 80-90 grid cells that are little used by the birds at present. Thus, even with the restriction imposed by our precautionary approach to predicting the distribution of potential resources, the model still contains a far larger area of sea than that currently exploited by the Liverpool Bay common scoter population.

As explained in section 9.2, runs of the model during the calibration phase in which all 115 cells were included in the model, predicted that a substantial proportion of the population foraged consistently on the Burbo Bank area and inshore of the site originally proposed for the Southport windfarm. The over flight data indicates that these areas are virtually never used by ducks in reality. Possible reasons for this discrepancy between the observed and model predicted distribution are discussed in section 9.2. Whatever the reason for the discrepancy, it seems that although ducks do not currently occur in these areas, there are ample food supplies which they could exploit. These areas may represent currently underexploited areas to which feeding common scoter could redistribute in the face of alteration to the conditions within the areas that they currently do use – as for example may arise due to the avoidance of windfarms.

It was decided to run each of the 8 key scenarios while initially preventing the birds from feeding in the two areas that are in reality not exploited. As explained in section 9.2, 11 grid cells around the Burbo Bank area and 5 grid cells off Southport were ‘excluded’ from the model by setting the initial resource abundances to be 0 in these cells. This resulted in a model with 99 patches available to the birds. Even in this case the model still included all of the patches in which common scoter occur frequently (*circa* 30) and some 60-70 additional cells in which common scoter seldom or never occur. Thus, even with only 99 patches in the model, the potentially exploitable habitat available to the common scoter population is far in excess of that which they currently exploit.

If all simulations used this ‘restricted’ habitat, it is possible that predictions of adverse effects of windfarms on the common scoter population could be considered unduly pessimistic given the exclusion of two apparently suitable but currently little used areas of Liverpool Bay to which birds may redistribute. To address this issue it was decided that for any of the 8 key scenarios in which significant adverse effects were predicted the model should be re-run with the modification of allowing birds to have access to these two areas. The difference between the predictions under these two options reveals the extent to which predictions of adverse consequences of windfarm development might be offset by the ability of ducks to redistribute to parts of Liverpool Bay which they currently do not exploit.

10.3.5 Abundance of prey

Although the survey of the benthos conducted during this project was very extensive and costly in terms of man hours and ship time, the total area of the seabed sampled represents only a tiny fraction of the habitat available to common common scoter in Liverpool Bay. Given that the distribution of benthos was found to be extremely patchy on a very fine scale, the likelihood of sampling error in the estimation of resource abundance is high. Thus, predictions that windfarms would have no adverse effects on the common scoter population could arise if the abundance of food resources was over-estimated. Conversely, predictions that windfarms would have serious adverse effects on the common scoter population could arise if the abundance of food resources was under-estimated.

To address this possible source of uncertainty in the model, the benthic resource abundance dataset was analysed. Based on the mean and standard deviation of the total resource abundance and the number of sampling stations within each sampled grid cell, the likelihood that the survey under or overestimated the overall abundance of the resources was assessed, taking into account that, with random sampling error, density could be underestimated in one cell while being overestimated in another. Given the very large number of grid cells sampled, the average 95% confidence limit to total resource abundance within a given grid cell was only 1.4% of the mean numerical abundance. In other words a reduction in the abundance of resources within each and every one of 99 cells in the model by 1.4% of the mean value of abundance within that cell was all that was necessary to generate a simulation in which the total abundance of resources across the bay was reduced by the correct proportionate amount given the within cell sampling error and that density could be underestimated in one cell while being overestimated in another. In contrast had the abundance of resources within each and every one of 99 cells in the model been reduced by 5% of the mean value of abundance within that cell the reduction in resource abundance across the whole bay would be disproportionate as the probability of random sampling error consistently over-estimating resource abundance in every cell simultaneously is very unlikely.

To assess whether predictions of the effects of windfarms on the common scoter population might be unduly optimistic due to the food supply having been over-estimated, the model was re-run for all 8 key scenarios but applying the lower 95% limit to resource abundances in all grid cells. To assess whether predictions of significant adverse effects of windfarms on the common scoter population might be unduly pessimistic, due to the food supply having been under-estimated, the model was also re-run for those key scenarios in which such effects were predicted under the initial simulations, but applying the upper 95% limit to resource abundances in all grid cells. The differences between the predictions under these options reveal the extent to which the predictions of the consequences of windfarm development are influenced by the sampling error inherent in the benthic sampling programme.

10.3.6 Feeding activity window

On the basis of the literature review, it appears that sea ducks are essentially diurnal feeders. Thus, all of the initial simulations were conducted on the assumption that common scoter do not feed at night. However, there is some evidence that common scoter and other sea ducks do occasionally feed at night, especially under adverse circumstances, such as when daylight is restricted in mid-winter (section 7.2.3 Appendix 4). Thus, it is possible that any conclusions arising from the initial simulations regarding potentially adverse effects of windfarms on the common scoter population could be unduly pessimistic. In order to allow for the possibility that common scoter may respond to deteriorating environmental conditions by foraging at night, it was decided that simulations of any of the 8 key scenarios which predicted significant adverse effects on the common scoter population should be re-run but with the modification of allowing the birds to feed by night as well as by day. The differences between the predictions under these options reveal the extent to which any predicted adverse consequences of windfarm development on diurnally feeding common scoter may be offset if their behavioural response to environmental change is to feed at night as well as during the day.

10.3.7 The suite of simulations

Exploration of all of the various options described above for each of the 8 key windfarm scenarios could have given rise to a total of 40 scenarios. In fact, the results of the simulation of the initial 8 key scenarios, in which default parameter values and assumptions were used, necessitated the exploration of only a further 14 scenarios to address each of the points raised in sections 10.3.4 – 10.3.6. Each of the 8 key scenarios was re-run assuming a reduced food supply (section 10.3.5), and two were also repeated assuming: i) an increased food supply (section 10.3.5), ii) an increased exploitable area (section 10.3.4) and iii) night time feeding (section 10.3.6).

10.3.8 Additional simulations

The simulations conducted to validate the model (section 9) each generated a predicted distribution of common scoter which was compared with the observed distribution of birds as described in section 9.3.5.. The model output was used to identify those cells which were the most heavily used over the course of the winter. It was decided to conduct additional model runs in which the construction of windfarms in each of the highly preferred areas was simulated. The results of these simulations reveal the potential consequences for the common scoter population of the construction of windfarms on their most favoured foraging grounds (if these areas can be identified in reality).

10.4 Sensitivity analyses

In addition to the uncertainty in the areas outlined above, there is of course a varying degree of uncertainty in all of the model’s parameter values. In an ideal world, the first phase of a modeling project like this would involve collation of the best available estimates of all parameter values. The second phase would be to conduct a full sensitivity analysis of the key model outputs to likely variation in the value of each and every parameter in order to quantify the extent to which the model’s predictions are sensitive to this uncertainty. This information could then be used to highlight those parameters whose values must be more precisely estimated by further research during a third phase of the project. Then one could conduct the final phase of the project in which predictive modeling is conducted with the confidence that all parameter values, especially those to which model output is most sensitive, are as well estimated as necessary/possible. The version of MORPH used in this project has many parameters not least because of the large number of patches, resources and components that have been included to deal with the spatial scale of the study and the dietary resources of the birds. It was, therefore, not practical, within the constraints of this project, to conduct the process described above. Instead we have proceeded with the predictive modeling phase of the project on the basis of the first phase only i.e. collation of the best available estimates of all the parameter values. However, in a retrospective attempt to highlight those key areas of the model’s parametrisation to which its output is most sensitive we have conducted a ’broad-scale’ sensitivity analysis of model output to groups of key variables. This was carried out in the same way as the sensitivity analysis of a precursor of the model MORPH that was published by Stillman et al (2000).

Model parameters can be grouped into categories in terms of the key parameter which they most directly influence. These five key parameters are:

1) The rate of energy expenditure
2) The rate of food consumption
3) Physiological constraints on the rate of food consumption
4) The efficiency with which energy is assimilated from food consumed
5) The rate of seasonal changes in prey abundance

The rate at which birds in the model expend energy is calculated from equations with several coefficients. This is true of several of the 5 key parameters. To explore the sensitivity of the model's predictions to the value of each coefficient in each category in turn would be extremely time consuming. Thus, to explore the extent to which the model's output is sensitive to uncertainty over the values of all the parameters in these groups a simplified approach based on that described by Stillman et al (2000) was adopted.

Sensitivity simulations were conducted for the baseline scenario (i.e. scenario 1 in which North Hoyle only is included), using only default values/assumptions for all other parameters. In these runs, a simple multiplication factor of either 0.75 or 1.25 was applied to the final calculated values of each of the 5 key parameters listed above. These multiplication factors were applied to each of the 5 key parameters separately. The results of these simulations, in comparison with the equivalent simulation in which no such multiplication factors were used (i.e. a value of 1 was assumed), indicate the sensitivity of the model's predictions to a +/- 25% variation in the value of each of the key parameters listed above.

The principal purpose of this sensitivity analysis is to identify the extent to which the mortality rate predicted by the model is sensitive to variation in its key parameters. The purpose of this is to suggest the priorities for future research aimed at improving the precision with which the key model parameters are estimated. The purpose is not to determine the 'likely' bounds to the possible outcomes under any given windfarm scenario because: i) the chosen variation of +/- 25% of the default values is purely arbitrary, ii) the true magnitude of the uncertainty around each of the key parameters and its component coefficients is largely unknown and hence iii) no more meaningful range of values can be easily derived. The variation in predicted mortality under each of the windfarm scenarios is more properly explored by the simulations described in section 10.3 in which the effects of uncertainty concerning: i) the radius of buffer zones around windfarms, ii) the accuracy of the survey of the benthic food resources, iii) the ability of the ducks to redistribute to unexploited areas of Liverpool Bay, and iv) the ability of ducks to forage at night, are explored.

10.5 Replicate simulations

The foraging efficiency of each super-individual within the model is drawn at random from a normal distribution with specified mean and standard deviation (see section 7.2.6). Even with 1000 super individuals there is a degree of variation between runs in the average and range of foraging efficiency values within the modelled population. This, along with other stochastic elements in the model, means that there is scope for variation in the output between replicate simulations of a given environmental scenario. Accordingly, for each scenario explored, 5 replicate simulations were conducted and comparisons between the scenarios were based on non-parametric statistical analyses of the median values of the model outputs.

11. Model results

11.1 Introduction

In total, one hundred and eighty runs of the model MORPH, exploring 36 different 'scenarios', were conducted in the course of producing the results which are presented here. Principally, these address the consequences for the common scoter population of Liverpool Bay of a number of different windfarm scenarios and whether these consequences might vary depending upon various uncertainties in model parameterisation. Additional simulations explore the consequences of removing what appear in the model to be the most profitable feeding areas within Liverpool Bay and also the sensitivity of model outputs to variation in its key parameters. These results are discussed in turn in the following sub-sections and form the basis of the conclusions of this study.

11.2 Simulations using default parameter values and assumptions

11.2.1 Proportion of daylight hours spent feeding

Under the 'baseline' simulation of existing circumstances (scenario 1 Table 10.1), the average proportion of daylight hours spent feeding by common scoter (weighted to take account of the seasonal variation in the proportion of time feeding and the population size) was 0.436. There was statistically significant variation in this parameter between the 8 principal scenarios (Kruskall-Wallis test H = 29.70 d.f. =7, P < 0.001) (Fig. 11.1). The significance of this test was much reduced if the results of the two scenarios in which mortality was markedly elevated (see below) were excluded from the analyses. Most of the pair wise comparisons between scenario 1 and each of the other scenarios (by means of Wilcoxon's Rank Sum tests) yielded statistically significant differences. However, in no case was the proportion of daylight hours spent feeding predicted to exceed that under the 'baseline' scenario. This was unexpected. However, the magnitude of the difference between the mean value across the 40 simulations and the lowest and highest predicted values amounted to only -3.7% and +2.6% of the mean value. Thus, although many comparisons between simulations were statistically significant (due to the very small variation between replicate simulations) the proportion of daylight hours that common scoter spent feeding was effectively constant between scenarios (Fig. 11.1).

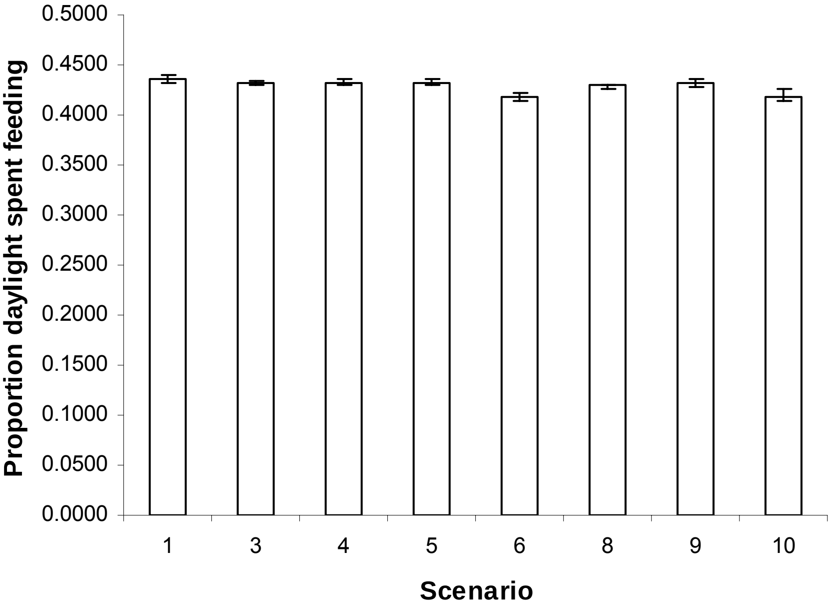

Figure 11.1 The median (and range) of the weighted mean proportion of daylight hours spent actively feeding by common scoter under the baseline scenario (1) and each of the other windfarm scenarios, assuming default values for all parameters.

11.2.2 Body mass

Under the 'baseline' simulation of existing circumstances (scenario 1), the average deviation of common scoter body mass from their seasonally varying target mass (weighted to take account of the seasonal variation in the magnitude of the deviation and the population size) was 132g. There was statistically significant variation in this parameter between the 8 principal scenarios (Kruskall-Wallis test H = 19.20 d.f. =7, P < 0.01) (Fig 11.2). This was not the case if the outputs of scenarios 6 and 10, under both of which the body mass deviation was more pronounced than under the baseline scenario, were excluded from the analyses (Kruskall-Wallis test H = 3.14 d.f. =5, NS). Pair wise comparisons between scenario 1 and each of the other scenarios (by means of Wilcoxon's Rank Sum tests) were not statistically significant except that for scenario 10 (Wilcoxon's W = 40, P = 0.012). The comparison between scenarios 1 and 6 was not quite statistically significant (Wilcoxon's W = 36, P = 0.095).

Thus, under scenarios 3,4,5,8 and 9 there is no suggestion that the exclusion of common scoter from the buffer zones around windfarms will have any detrimental effect on their ability to accumulate body mass over the winter. Only in the cases of scenarios 6 and 10 is there evidence that the combined effects of windfarms will adversely influence the average over-winter body condition of common scoter in Liverpool Bay (Fig. 11.2).

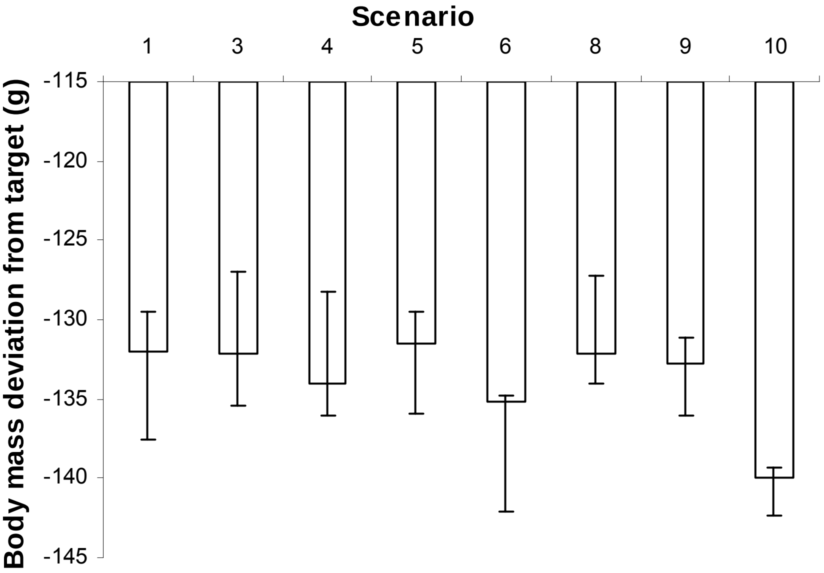

Figure 11.2 The median (and range) of the weighted mean deviation of common scoter body masses from the target mass under the baseline scenario (1) and each of the other windfarm scenarios, assuming default values for all parameters.

11.2.3 Over winter mortality

Under the 'baseline' simulation of existing circumstances (scenario 1), the median over winter mortality of common scoter was predicted to be 7.3% (range 5.4% - 8.8%). There was statistically significant variation in this parameter between the 8 principal scenarios (Kruskall-Wallis test H = 29.36 d.f. =7, P < 0.001) (Fig. 11.3). This variation was less pronounced if the outputs of scenarios 6 and 10, the two scenarios under which the predicted over-winter mortality was markedly higher than under the baseline scenario, were excluded from the analyses (Kruskall-Wallis test H = 12.62 d.f. =5, P < 0.05). Only the pair wise comparisons between the predicted overwinter mortality under scenario 1 and that under scenarios 6 and 10 yielded evidence of statistically significantly elevated mortality (Wilcoxon's W = 15, P = 0.012 in both comparisons) (Fig. 11.3).

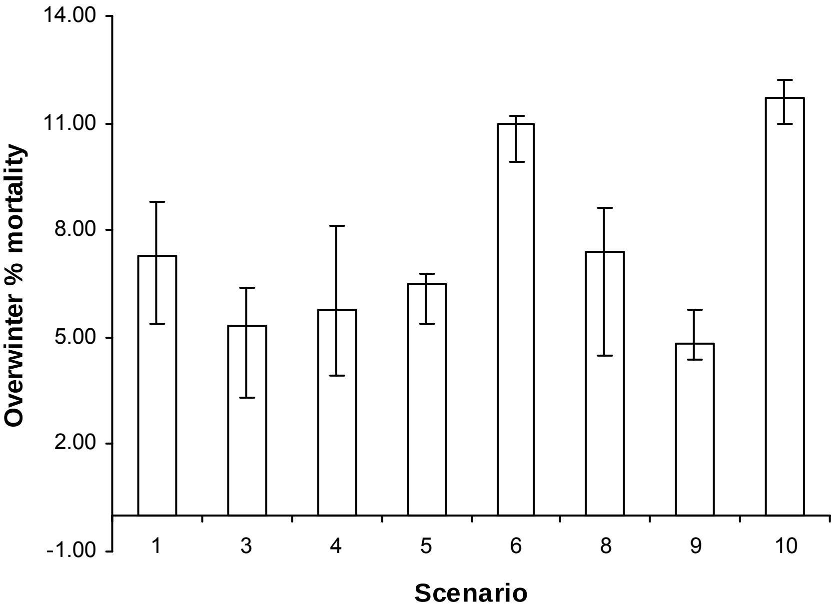

Figure 11.3 The median (and range) of predicted % overwinter mortality of common scoter under the baseline scenario (1) and each of the other windfarm scenarios assuming default values for all parameters.

11.3 Simulations to explore consequences of windfarms assuming a reduced food supply

11.3.1 Proportion of daylight hours spent feeding

There was statistically significant variation in the proportion of daylight hours spent feeding between the 8 principal scenarios (Kruskall-Wallis test H = 28.02 d.f. =7, P < 0.001). This was not the case, when the two scenarios in which overwinter mortality was predicted to be elevated (6 and 10) were removed from the analyses (Kruskall-Wallis test H = 10.70 d.f. =5, NS). In pair wise comparisons between the values predicted under the default scenarios (assuming estimated mean resource abundances) and those predicted here, only in two out of eight cases was the proportion of daylight hours spent foraging significantly higher in the face of reduced food supplies (scenario 5 Wilcoxon’s W = 17 P < 0.05, scenario 8 Wilcoxon’s W = 15 P = 0.01) (Fig. 11.4). However, in both these cases, the proportion of daylight spent foraging was no higher than that under the ‘baseline’ conditions predicted under scenario 1. Thus, even given a reduction in the abundance of benthic resources that is consistent with the error within the benthic database, there is no evidence that common scoter would feed for markedly longer than they are predicted to under current circumstances. Thus, there is no evidence that in this regard the predicted consequences of any of the proposed windfarms are overly optimistic simply because our benthic survey may have over-estimated the abundance of the food resources, .

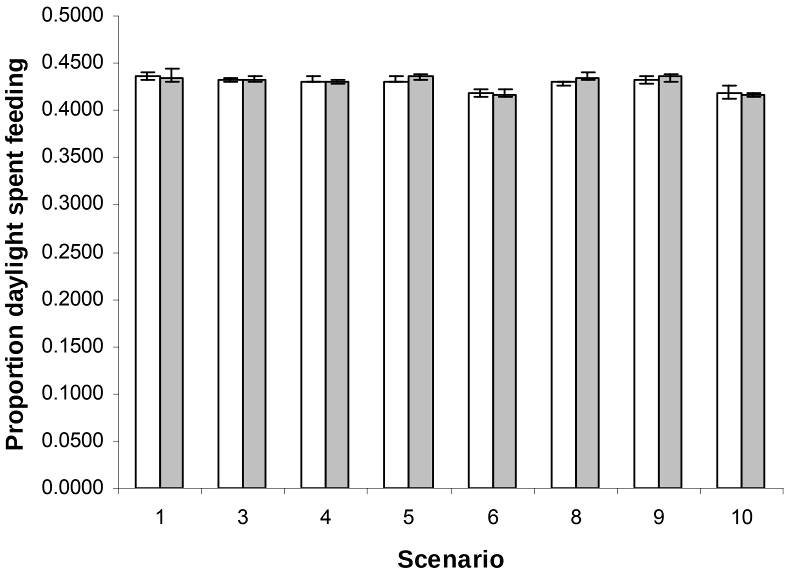

Figure 11.4 The median (and range) of the weighted mean proportion of daylight hours spent actively feeding by common scoter under the baseline scenario (1) and each of the other windfarm scenarios, assuming either: i) default values for all parameters (open bars) or ii) a reduced abundance of all resources (shaded bars).

11.3.2 Body Mass

The variation in the weighted mean deviation of common scoter body masses from their target masses between the 8 principal scenarios was not statistically significant (Kruskall-Wallis test H = 10.67 d.f. =7, NS). In seven out of eight pairwise comparisons between the predicted values under the default scenarios and those examined here, there was no significant difference between the weighted mean body mass deviations (Fig 11.5). In the one case in which there was a significant difference, the body mass deviation was marginally less pronounced under the assumptions of reduced food supplies (Wilcoxon's W = 17 P < 0.05). Thus, in no case was there any evidence that the predicted consequences of any of the proposed windfarms might be markedly more severe were the food supply to be reduced to its lower likely limit. Thus, there is no evidence that the predicted consequences of any of the proposed windfarms are overly optimistic, in terms of the consequences for the ability of common scoter to maintain a certain level of body mass throughout the year, simply because our benthic survey may have over-estimated the abundance of the food resources

11.3.3 Over winter mortality

There was statistically significant variation in this parameter between the 8 principal scenarios (Kruskall-Wallis test H = 25.12 d.f. =7, P < 0.001) (Fig. 11.6). This was not the case when the results of the two scenarios in which mortality was elevated under default conditions (6 and 10) were excluded from the analysis (Kruskall-Wallis test H = 5.67 d.f. = 5, NS). In pair wise comparisons between the values predicted under the default scenarios (assuming estimated mean resource abundances) and those predicted here, only in two out of eight cases was the % overwinter mortality significantly higher in the face of reduced food supplies (scenario 3 Wilcoxon's W = 15.5 P < 0.05, scenario 9 Wilcoxon's W = 16 P < 0.05) (Fig. 11.6). However, in both these cases, the % overwinter mortality was still no higher than that predicted under 'baseline' i.e. current conditions (scenario 1). The predicted % overwinter mortality generated by the two worst scenarios under default assumptions (scenarios 6 and 10) did not get any worse under the conditions of reduced food supply. Thus, there is no evidence that in this regard the predicted consequences of any of the proposed windfarms are overly optimistic, simply because our benthic survey may have over-estimated the abundance of the food resources.

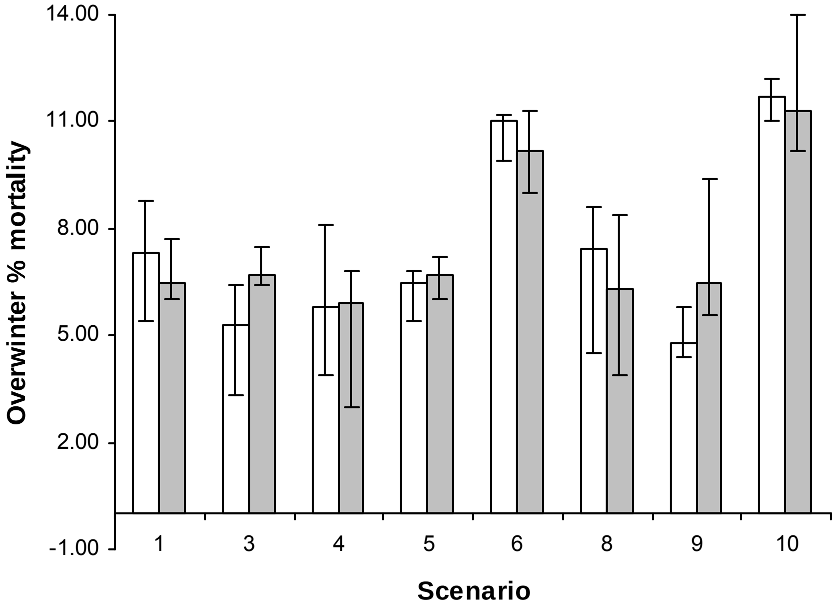

Figure 11.5 The median (and range) of the weighted mean deviation of common scoter body masses from the target mass under the baseline scenario (1) and each of the other windfarm scenarios, assuming either: i) default values for all parameters (open bars) or ii) a reduced abundance of all resources (shaded bars).

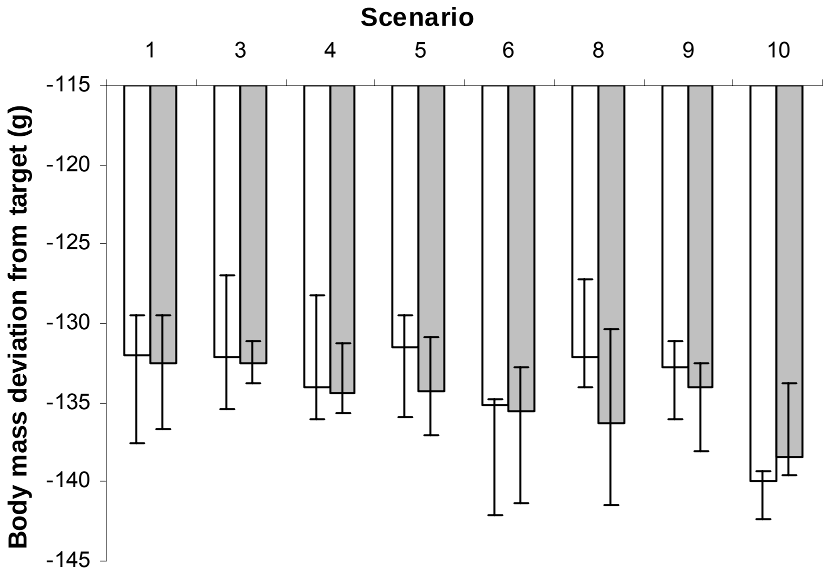

Figure 11.6 The median (and range) of predicted % overwinter mortality of common scoter under the baseline scenario (1) and each of the other windfarm scenarios, assuming either: i) default values for all parameters (open bars) or ii) a reduced abundance of all resources (shaded bars).

11.4 Simulations assuming a more favourable environment

For each of the two scenarios (6 and 10) which generated evidence of adverse effects of windfarm developments on the common scoter population (significantly reduced overwinter body mass and elevated overwinter mortality), simulations were conducted to explore whether these predictions might be unduly pessimistic for a number of reasons.

11.4.1 Proportion of daylight hours spent feeding

For both scenarios, the proportion of daylight hours spent feeding by common scoter was significantly reduced below that under the default conditions (i.e. 99 cells, mean resource abundance and daytime only feeding) if either: i) they were allowed access to additional alternative habitat (the 11 cells on Burbo Bank and the 5 cells off Southport or ii) they were allowed to feed at night as well as by day (in all 4 tests Wilcoxon's W = 40.0 P = 0.01) (Fig. 11.7). Increasing the abundance of the food resources (to the upper 95% confidence limit) had no such effect. Thus, the adverse effects of the windfarm developments predicted under scenarios 6 and 10 may be overly pessimistic if common scoter either: i) redistribute in space to apparently suitable but currently unused areas within Liverpool Bay or ii) feed at night as well as by day within the areas of the bay that they currently exploit.

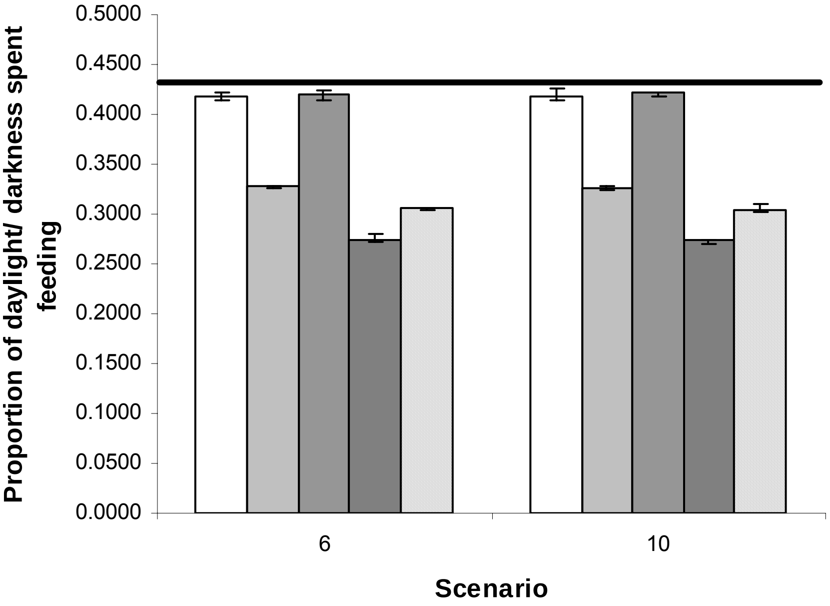

Figure 11.7 The median (and range) of the weighted mean proportion of daylight hours spent actively feeding by common scoter for each of the two windfarm scenarios which resulted in significantly elevated mortality under the assumption of default values. Open bars: default values for all parameters, lightest shaded bars: area of habitat available increased, darker shaded bars: abundance of all resources increased, darkest shaded bars: common scoter allowed to feed by night as well as by day. For comparison, the cross-hatched bars show the weighted median proportion of the hours of darkness spent actively feeding by common scoter when allowed to feed at night as well as by day. The horizontal line indicates the median weighted mean proportion of daylight hours spent actively feeding by common scoter predicted under current conditions (scenario 1) and assuming default parameter values (scenario 1).

11.4.2 Body Mass

For both scenarios, the median weighted mean deviation of common scoter body masses from their target mass was significantly reduced below that under the default conditions (i.e. 99 cells, mean resource abundance and daytime only feeding) if either: i) they were allowed access to additional alternative habitat (the 11 cells on Burbo Bank and the 5 cells off Southport or ii) they were allowed to feed at night as well as by day (in all 4 tests Wilcoxon's W = 40.0 P = 0.01) (Fig. 11.8). Increasing the abundance of the food resources (to the upper 95% confidence limit) had no such effect in the case of scenario 6 and only a marginal effect in the case of scenario 10 (Wilcoxon's W = 17.0 P < 0.05). Thus, the adverse effects of the windfarm developments predicted under scenarios 6 and 10 may be overly pessimistic if common scoter either: i) redistribute in space to apparently suitable but currently unused areas within Liverpool Bay or ii) feed at night as well as by day within the areas of the bay that they currently exploit.

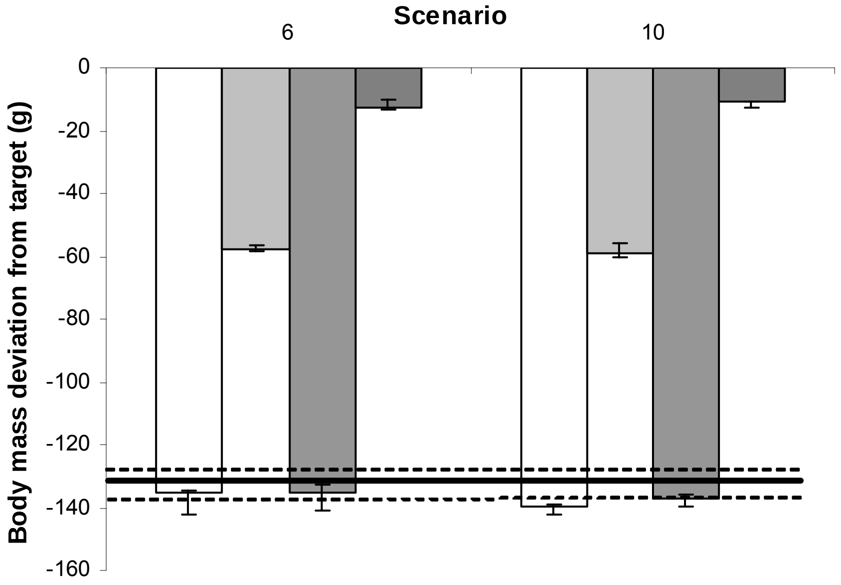

Figure 11.8 The median (and range) of the weighted mean deviation of common scoter body masses from the target mass for each of the two windfarm scenarios which resulted in significantly elevated mortality under the assumption of default values. Open bars: default values for all parameters, lightest shaded bars: area of habitat available increased, darker shaded bars: abundance of all resources increased, darkest shaded bars: common scoter allowed to feed by night as well as by day. The solid (and dashed) horizontal line(s) indicates the median (and range of the) weighted mean deviation of common scoter body masses from the target mass predicted under current conditions (scenario 1) and assuming default parameter values (scenario 1).

11.4.3 Over winter mortality

For both scenarios, the median % overwinter mortality was significantly reduced below that predicted under the default conditions (i.e. 99 cells, mean resource abundance and daytime only feeding) if common scoter were allowed either to: i) have access to additional alternative habitat (the 11 cells on Burbo Bank and the 5 cells off Southport (mortality predicted to be reduced to 0% in both cases)) or ii) feed at night as well as by day (in both cases Wilcoxon's W = 40.0 P = 0.01) (Fig. 11.9). Increasing the abundance of the food resources (to the upper 95% confidence limit) had no such effect in the case of scenario 6. However, increasing the resource abundances did lead to a significant reduction in the predicted overwinter mortality under scenario 10 (Wilcoxon's W = 40 P = 0.01). Thus, the adverse effects of the windfarm developments simulated by scenarios 6 and 10 may be pessimistic if common scoter either: i) redistribute in space to apparently suitable but currently unused areas within Liverpool Bay or ii) feed at night as well as by day within the areas of the bay that they currently exploit. The adverse effects of the windfarm developments simulated by scenario 10 may also be overly pessimistic given the uncertainty within the benthic sampling database. However, even under the assumption of increased resource abundance the predicted overwinter mortality under scenario 10 (median 9.4%, range 9.2% - 9.7%) was still in excess of that under current conditions (scenario 1: median 7.3%, range 5.4% - 8.8%). Thus, although the uncertainty concerning the precise values of resource abundance means that the magnitude of the predicted elevation of overwinter mortality under scenario 10 may be uncertain, it is unlikely that the prediction of elevated mortality is incorrect if common scoter do not feed at night and cannot redistribute to apparently suitable but currently unused areas of the bay.

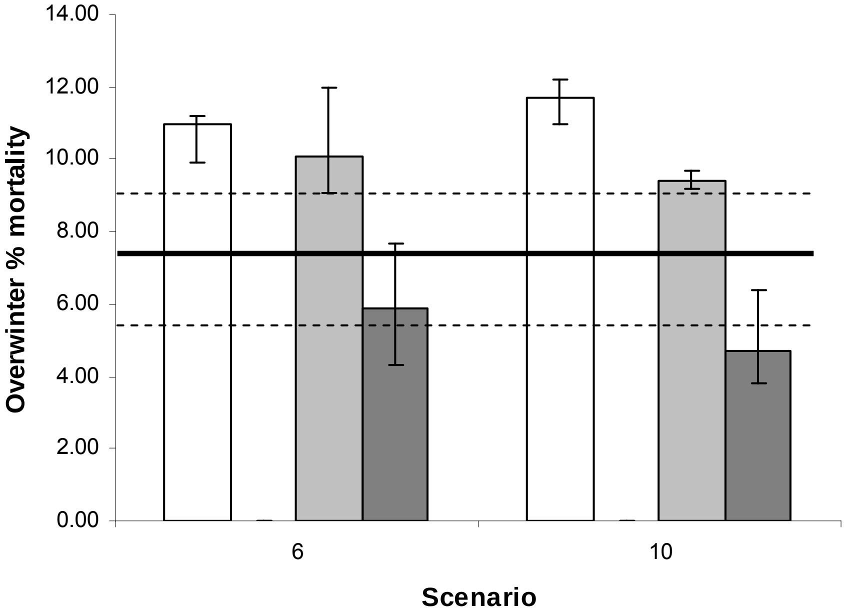

Figure 11.9 The median (and range) of predicted % overwinter mortality of common scoter for each of the two windfarm scenarios which resulted in significantly elevated mortality under the assumption of default values. Open bars: default values for all parameters, lightest shaded bars (both 0%): area of habitat available increased, darker shaded bars: abundance of all resources increased, darkest shaded bars: common scoter allowed to feed by night as well as by day. The solid horizontal line indicates the median % mortality predicted under current conditions (scenario 1) and assuming default parameter values. The upper and lower dashed horizontal lines indicate the maximum and minimum predicted % mortality under current conditions (scenario 1) and assuming default parameter values.

11.5 Scenarios in which key foraging areas removed

In each of the 5 replicates of the baseline scenario (scenario 1) the model generated a predicted distribution pattern of foraging ducks. These outputs were used to calculate for each run, the average overwinter proportion of the population within each cell. These figures were then averaged across the 5 replicate simulations and the top 10 cells identified. These fell into four discrete locations (Fig. 11.10). Simulations were conducted in which common scoter were excluded from each of these areas in turn (as well as from the North Hoyle windfarm area) to explore the relative consequences of the loss of each of the areas in comparison with the consequences of the windfarm developments simulated under scenario 10 (see Table 10.1) i.e. the worst of the key scenarios explored. In each case, the predicted overwinter mortality was predicted to be significantly greater than under scenario 10 (Fig. 11.11) (Wilcoxon's W = 15 P = 0.01 in all cases). The most pronounced effect was caused by the removal of four neighbouring cells off Blackpool (largely to the south and east of the proposed location of the Shell Flat windfarm) (Figs. 11.10 & 11.11). These results suggest that (in the absence of access to apparently suitable but unused areas on Burbo Bank and off Southport, and in the absence of night-time feeding) the loss of key foraging areas to windfarm developments is likely to lead to significantly increased overwinter common scoter mortality.

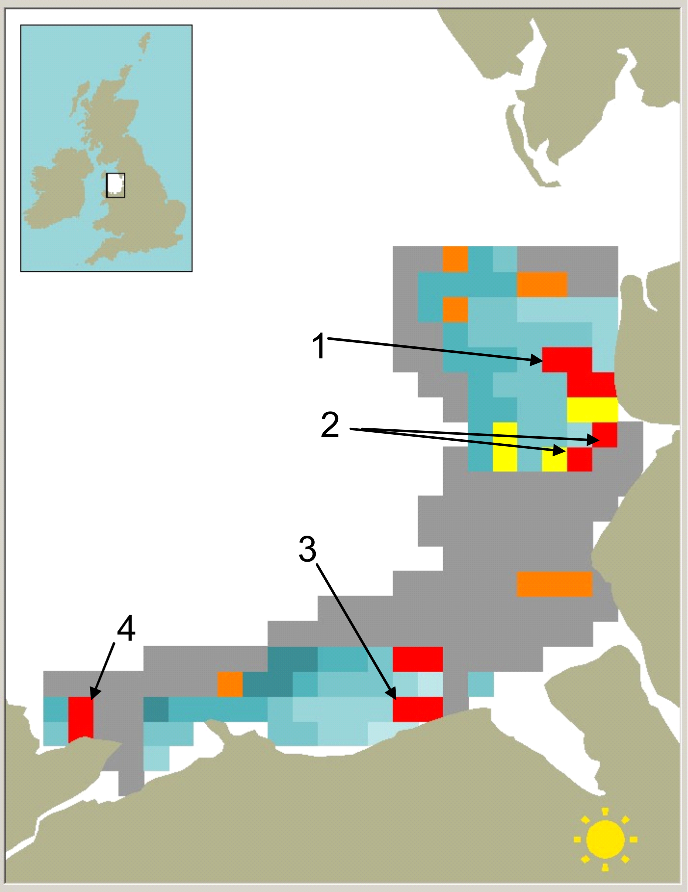

Figure 11.10 Model graphic display illustrating the four groups of cells (coloured red) removed under each of the additional scenarios to explore the consequences of the removal of cells identified by the model as favoured feeding areas. The number of each area corresponds to the scenario number in Figure 11.11. North Hoyle, which was also included in these simulations, is also shown in red (un-numbered). The image shows the location of the study area within the UK and the coastline of north Wales, Cheshire, Lancashire and south Cumbria. Within the area of the Irish Sea, the 206 tidal grid cells considered for inclusion in the model are shaded. The initial biomass density of all resources was set to 0 in 91 grid cells which are further than 2.5km from any benthic sampling station and 16 further cells on Burbo Bank and off Southport (see section 9.2).These cells, which are inaccessible to the birds in the model, are shaded grey. The remaining 99 cells are coloured as follows. All cells are subject to variation in water depth with time. Greater water depth is indicated by the intensity of blue shading which varies on a hour-to-hour basis. Cells in which a source of human disturbance is present during this particular hour are overlaid with a further colour: red denotes either the extent of the area of favoured feeding areas from which common scoter are excluded in the additional scenarios (see above) or the permanent presence of a windfarm at North Hoyle, orange denotes the temporary presence of a large ship passing through a cell at this point in time and yellow denotes the temporary presence of a helicopter passing over a cell at this point in time. Common scoter avoid a cell when one or more of these sources of disturbance occurs there but may visit it at other times in the absence of disturbing factors. The image of the sun denotes that this ‘snapshot’ was taken during the hours of daylight.

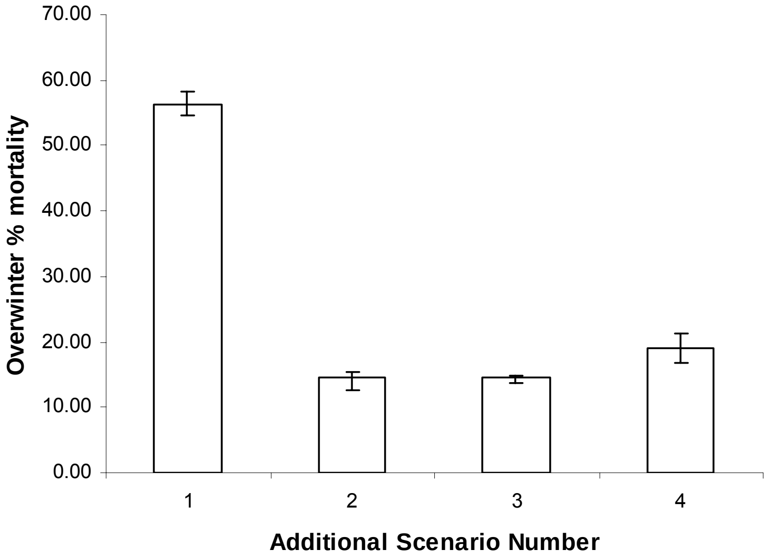

Figure 11.11 The median (and range) of predicted % overwinter mortality of common scoter under four additional scenarios in which groups of cells identified during baseline model simulations (scenario 1) as favoured feeding areas of common scoter in the model are removed. In these additional scenarios the cells removed were: inshore of Shell Flat (1), off the mouth of the Ribble (2), immediately offshore at Rhyl (3) and in Red Wharf Bay (4) (see Figure 11.10).

11.6 Sensitivity Analyses

Increasing or decreasing the values of each of the 5 key parameters by +/- 25% resulted in statistically significant decreases or increases in the predicted overwinter mortality (Wilcoxon's W = 40 P = 0.01 in all cases) (Fig. 11.12). Decreasing the rate of energy expenditure and increasing: i) the rate of food consumption, ii) the maximum rate of food consumption and iii) the assimilation efficiency, all reduced mortality to near 0%. Increasing the daily proportionate change in resource abundance also reduced mortality, but to a lesser extent. Increasing the rate of energy expenditure or decreasing the assimilation efficiency produced the most marked increases in mortality (Fig. 11.12). Decreasing either the rate of food consumption or the maximum rate of food consumption also produced marked increases in mortality. The increase in mortality that resulted from a decrease in the daily proportionate change in resource abundance was the least pronounced of all. The mortality rate predicted by the model is clearly highly sensitive to all of the key parameters explored here.

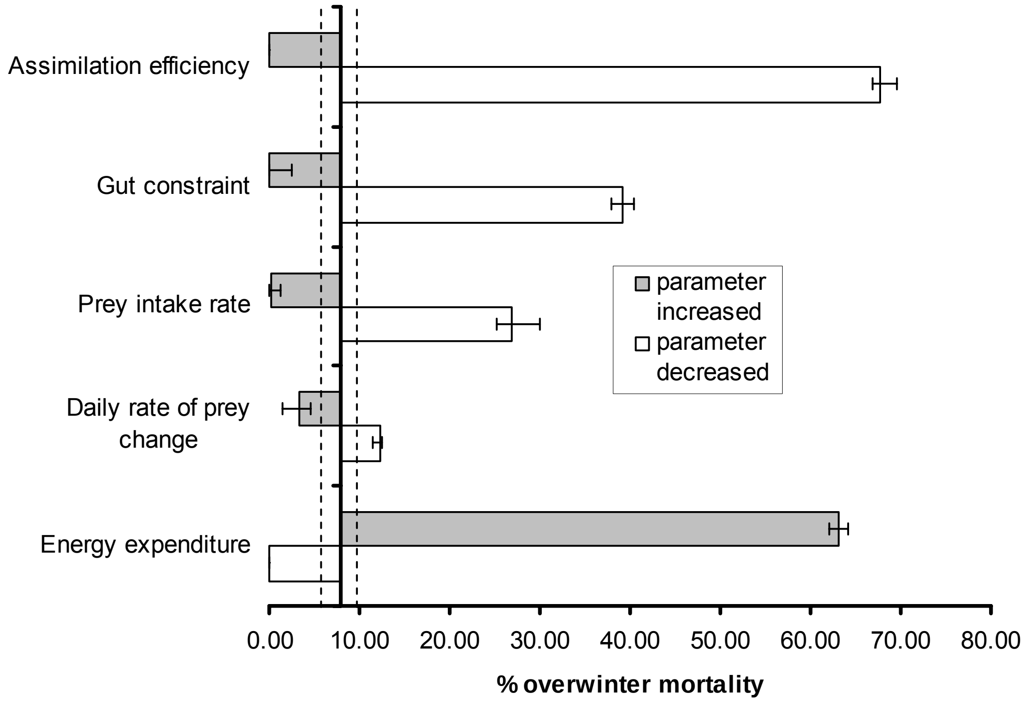

Figure 11.12 Sensitivity of predicted overwinter mortality to changes in five key parameters. The thick vertical line shows the median mortality predicted by 5 replicate simulations using the standard parameter values. The dashed vertical lines denote the minimum and maximum mortality predicted under these conditions. Bars show the median mortality (error bars denote the minimum and maximum) predicted by 5 replicate simulations when each key parameter was decreased or increased by 25% of their standard value.

11.7 Discussion

11.7.1 Observed and predicted distribution of common scoter

The initial runs of the model during the calibration phase (section 9.2) predicted that a substantial proportion of the common scoter population should feed on Burbo Bank and in the vicinity of the site originally proposed for the Southport windfarm. The overflight data clearly indicate that both areas are virtually unused by common scoter in reality. There are a number of possible explanations for this discrepancy which are discussed in section 9.2. Having excluded these areas from the model, the distribution of ducks across the remaining 99 tidal grid cells that was predicted by the model was significantly associated with that generated by the overflight data. Thus, across the whole of Liverpool Bay, the model is generally correct in its discrimination between those tidal cells that are heavily used by common scoter and those which are not. Given that errors in any of a large number of parameters and functions in the model, not least those resulting from the extensive but far from exhaustive benthic survey, could have resulted in the model predicting that the birds occurred in entirely the wrong places, this is a very impressive result.However, closer investigation of the results revealed a few grid cells that are heavily used by ducks in reality but were seldom or never visited by model birds. This was most noticeable in the case of six tidal grid cells on Shell Flat (Fig.9.7). The principal reason behind this lack of a perfect fit i.e. that birds in the model avoided areas of Shell Flat because of the dominance of the bivalve community by the least profitable size classes of the least profitable prey type, was discussed in section 9.3.5. However, this discrepancy between the output of what is in essence a ‘foraging distribution’ model and the overflight data may also be caused by the fact that the two are in fact not directly comparable.

The output of the model indicated that common scoter in Liverpool Bay are likely to be engaged in foraging bouts for just under half of daylight hours. This is in line with limited empirical data on other benthic-feeding seaducks (section 9.3.1). It follows that for approximately half of daylight hours common scoter are resting. During this time they may maintain their position over their feeding grounds by actively swimming against the prevailing currents and winds. In this case, the distribution of ducks recorded during overflights will give a clear picture of their distribution while foraging. However, ducks may allow themselves to be drifted by the tide and wind between periods of foraging activity (the timing of which may be dictated by tidally driven variation in water depth and current speed) before returning (perhaps by flying) to their feeding grounds. In this case, the distribution of ducks recorded by overflights will not necessarily provide an accurate picture of the distribution of birds while feeding. Modelling work by HR Wallingford (Anon 2003) indicates that common scoter which feed to the southern edge of Shell Flat could be drifted passively north by tide and wind.This may explain the discrepancy between model output and overflight data. Thus, the lack of a perfect match between the distribution predicted by the model and that observed in reality is not fatal to the application of this model to the issue of predicting the consequences of windfarms on the common scoter population of Liverpool Bay. Indeed, given the practical constraints on the benthic sampling programme, it is encouraging that the model does in fact generally identify heavily and little used areas correctly. The lack of an absolutely perfect fit may be viewed as a valuable model insight that the distribution of ducks as recorded by overflights is not necessarily as good an indicator of the key foraging areas of common scoter as might have been assumed. Future studies of common scoter in Liverpool Bay should examine spatial and temporal variation in their foraging activity rather than simply recording their distribution (see section 11.8.3).

Regardless of the precise cause of the lack of a perfect fit between the observed distribution of common scoter and the distribution generated by the model, the relatively low usage of parts of Shell Flat under baseline conditions has implications for how the results of model simulations should be interpreted. First, the lack of usage of six tidal cells on Shell Flat in all simulations means that the simulations which predict the consequences of the development of windfarm(s) at all the other locations effectively predict the cumulative effect of each of those windfarm(s) in combination with the exclusion of birds from that part of Shell Flat. They are, therefore, ‘precautionary’. In contrast, however, it is possible that the lack of usage of parts of Shell Flat that is predicted under baseline conditions means that the magnitude of any increase in overwinter mortality predicted in the scenarios in which the construction of the Shell Flat wind farm is simulated will be underestimated.

11.7.2 Simulations using default values

Three indicators of the consequences of environmental change that have been utilised in previous applications of the model MORPH are: i) the proportion of time spent feeding by birds, ii) the body mass of the birds and iii) the overwinter mortality. The logic underlying the use of these three indicators is as follows. Faced with deterioration to feeding conditions, birds will respond behaviourally by increasing their feeding effort to compensate for the reduced rewards available. This may be sufficient to offset the environmental change such that birds’ body masses and mortality remain unchanged. If, however, an increase in foraging effort is insufficient to offset the deterioration of the foraging conditions, the birds may fail to maintain their body mass. Even so, birds may not die. Thus, under many circumstances environmental change may lead to changes to bird’s behaviour and body condition without leading to elevated mortality. Mortality may only increase under severe changes to the environment. Examining a range of indicators provides the scope to detect significant sub-lethal effects on birds as well as quantifying the most important consequence at the level of the population i.e. mortality.

In the current model, the proportion of time spent foraging, weighted across the overwinter period to take into account the seasonal variation in the feeding effort and the size of the common scoter population, proved to be virtually constant between all of the scenarios. Thus, even in the case of scenarios in which average overwinter body mass fell and mortality increased, the proportion of time that birds spent feeding did not increase noticeably. This is almost certainly a reflection of the limits imposed on the birds’ foraging schedules by digestive constraints (see Appendix 12). Bustnes (1998) noted that the general problem for these birds is not to find food (fast enough) but to locate prey with sufficient energy density to fulfil the daily energy requirement. Guillemette *et al* (1992) suggested that resting after a meal provides time to process a part of the food ingested and to lose mass by defecation and excretion and consequently that resting bouts can be considered as an obligatory part of the foraging behaviour of benthic feeding ducks. In such systems, the proportion of time that birds spend actively feeding may not be a good indicator of sub-lethal detrimental effects of environmental change on foraging birds.

Only two scenarios resulted in significant increases in the difficulty that birds experienced in accumulating body mass. These two scenarios (6 and 10) were also the only two that resulted in a significant increase in predicted over winter mortality. Scenario 6 simulated the existence of 2km buffer zones around windfarms at North Hoyle, Rhyl Flats, Burbo Bank (although not modelled explicitly (see section 10.3.3)) and Shell Flat. In Scenario 10, an additional exclusion zone of 2km around the proposed Gwnt-y-Mor windfarm site was also incorporated. By comparison with other scenarios it is possible to deduce that the principal cause of the adverse effects apparent under these scenarios was the assumed 2km exclusion zone around the proposed Shell Flat windfarm. Scenario 6 differed from scenario 4 (which had no adverse effects on the birds) only in the presence of the Shell Flat windfarm with a 2km buffer zone. Furthermore, scenario 10 only differed from scenario 8 (which had no adverse effects on the birds) for the same reason. Thus, in the absence of the Shell Flat windfarm, the over winter body condition and mortality of common scoter are predicted to be unaffected by the existence of windfarms at any of the other existing, consented or proposed locations explored here. This is also predicted to be the case if the common scoter do not show any tendency to avoid the area around the Shell Flat windfarm (i.e. a 0km buffer zone is assumed (scenarios 5 and 9)). Simulations using default model parameters and assumptions indicate that only if common scoter avoid the area within 2km of the Shell Flat windfarm is the presence of a windfarm on this site, in conjunction with farms at the other 4 sites, predicted to lead to significant detrimental effects on the common scoter population of Liverpool Bay. The magnitude of this effect may, as discussed in section 11.7.1 be somewhat under-estimated. Nonetheless, under the precautionary assumption of a 2km buffer zone, an effect is predicted.

11.7.3 Simulations to explore consequences of windfarms assuming a reduced food supply

These simulations were conducted in order to establish whether the magnitude of the effects predicted by the model (section 11.7.2) was significantly affected by the variation inherent in the sampling of the benthic food resources. Thus, all of the scenarios were repeated while reducing the abundance of all resources across the whole of the bay by an amount based upon the degree of sampling error within grid cells and upon the number of grid cells over which the resource abundances were predicted (i.e. 99 grid cells). Comparison of the results of these simulations with the corresponding simulations conducted assuming mean resource abundances revealed no significant increases in the proportion of daylight hours spent feeding to reach a value in excess of that predicted under current conditions (scenario 1), and no significant increases in the body mass deviation from target mass. Furthermore, although there were two instances of increased mortality in comparison to the default runs, in neither case was the predicted mortality in excess of that predicted under current conditions (scenario 1). Mortality under the two worst scenarios (6 and 10) did not increase any further when the food supply was reduced. Thus, the conclusions outlined above (section 11.7.2) are unaltered even assuming that the abundance of common scoter food resources was reduced in line with the sampling error in the empirical data. Only if common scoter avoid the area within 2km of the Shell Flat windfarm is the presence of a windfarm on this site, in conjunction with farms at the other 4 sites, predicted to lead to significant detrimental effects on the common scoter population of Liverpool Bay. The magnitude of this effect may, as discussed in section 11.7.1 be somewhat under-estimated. Nonetheless, under the precautionary assumption of a 2km buffer zone, an effect is predicted.

11.7.4 Simulations assuming a more favourable environment

These simulations were conducted in order to explore whether the predicted adverse effects on common scoter apparent under scenarios 6 and 10 (sections 11.7.2 and 11.7.3) might be unduly pessimistic given that: i) common scoter may relocate to currently little used areas of Liverpool Bay where there are ample food sources, ii) common scoter may feed by night as well as by day and iii) the mean resource abundance values used in the default simulations may be too low. The results of these simulations indicate whether the adverse effects under scenarios 6 and 10 may not occur given the possibility of behavioural responses by the ducks and given the uncertainty over the quantity of food available in the system.

The results of these simulations clearly indicate that if common scoter respond to the presence of windfarms by: i) redistributing to currently little used (but apparently highly profitable) areas of Liverpool Bay or ii) by feeding during the hours of darkness as well as during daylight, the predicted adverse cumulative effects of a 2km buffer zone around the Shell Flat windfarm, in combination with that around the other windfarms, will be avoided.

Behavioural responses of this kind, whereby birds redistribute their foraging effort in space and time, are precisely the sort of responses which might be expected in the face of environmental change (Stillman et al 2000). The key question in all attempts to understand and predict the consequences of environmental change is whether feeding in alternative places and at other times is sufficient to prevent any decrease in birds' body condition and any increase in mortality. In the current system it would appear that the possibility of feeding at night (at an efficiency assumed to be the same as that achieved during daylight) or the possibility of exploiting other parts of Liverpool Bay, which are currently little used yet hold considerable benthic resources, would be sufficient.

Given that one study has observed that scoter dive to the seabed at night (Durinck et al. 1993), that other benthic bivalve feeding ducks feed at night, and that all such birds probably feed by touch rather than by sight it would seem quite likely that common scoter could respond to habitat loss by increasing night-time feeding activity- perhaps even in places that are not used at all during daylight. Indeed, exclusion of common scoter from their current foraging locations may precipitate exploratory behaviour whereby currently underexploited areas of Liverpool Bay that are rich in food are 'discovered'. There seems little reason to believe that common scoter would not be physically capable of locating such areas. However, their exploitation of such areas may be constrained then, as perhaps it is now, by unfavourable environmental conditions. If the key factor constraining common scoter usage of such areas is human activity e.g. recreational boating then action could perhaps be taken to regulate such activity to compensate for the effects of the habitat loss in other areas due to the avoidance of wind farms.

11.7.5 Scenarios in which key foraging areas are removed

The purpose of these simulations was to explore the consequences for the common scoter population of the removal of precisely those locations which are identified in the model to be the most profitable feeding areas within Liverpool Bay.

The result of each of the four scenarios explored was an increase in predicted overwinter mortality significantly in excess of that under the most detrimental of the key scenarios (scenario 10). These results indicate that the construction of windfarms in those places where common scoter concentrate their feeding effort is likely to result in significantly increased mortality. Given the lack of knowledge concerning the distribution of common scoter while actively foraging (see section 11.7.1) future research must identify those parts of the ducks' current distribution which are most heavily used while the birds are foraging (see section 11.8.3).

11.7.6 Sensitivity analyses

The principal purpose of these simulations was to identify the extent to which the mortality rate predicted by the model is sensitive to variation in its key parameters. The purpose of this was to suggest the priorities for future research aimed at improving the precision with which the key model parameters are estimated. The purpose was not to determine the 'likely' bounds to the possible mortality rates under any given windfarm scenario because: i) the chosen variation of +/- 25% of the default values is purely arbitrary, ii) the true magnitude of the uncertainty around each of the key parameters and its component coefficients is largely unknown and hence iii) no more meaningful range of values can be easily derived.

The results presented in Figure 11.12 should not be interpreted as indicating the potential range of the overwinter mortality of common scoter under current circumstances. What the results in

Figure 11.12 do indicate is that the principal model prediction i.e. overwinter mortality is highly sensitive to each of the five key parameters. Given that the model is an energy balance model it is not surprising that it is most sensitive to the rate at which birds metabolise energy and the efficiency with which they assimilate the food that they ingest. These findings are very similar to those of the sensitivity analyses conducted on a precursor of the model MORPH by Stillman et al. (2000).

This sensitivity increased the chances that the model produced, for the wrong reasons, accurate forecasts of the winter starvation rate under the various windfarm scenarios. A wide variety of combinations of parameter values could, in principle, produce the same outcome. The only way to ensure that the model accurately captures the most important elements of the system is to explore its properties continually by testing its component predictions in order to detect a quantitative mismatch between prediction and observation. In the present model, the component predictions concerning the birds' behaviour, energetics and mortality were quantitatively consistent with independent empirical data (see section 9). There was also a highly significant association between the observed distribution of birds between the 99 core grid cells and that predicted by the model. In general, the bulk of these cells which are seldom used by common scoter in reality were little used by model birds, and many of these cells used heavily by common scoter in reality were also much used in the model. Together, these results suggest that the model captures the main features of the system. The only, mismatch of concern was that the model failed to generate a perfect fit to the distribution of birds as discussed above. But with so many of the other component predictions supported by observation, we regard this as a stimulus for further investigation of common scoter distribution rather than as being fatal to the value of this study.

The results of the sensitivity analyses also suggest that although much effort was involved in deriving the current best estimates of all the various parameters and functions within the model, there is merit in further review work, and indeed further empirical and experimental research on the energetics of foraging diving ducks. This will serve to refine parameter estimates and to define realistic confidence intervals around them. These can be the subject of further sensitivity analyses of the outcomes of future models.

11.8 Conclusions

11.8.1 Effects of existing/ consented and proposed windfarms

11.8.1.1 North Hoyle (Scenario 1):

Under current conditions the proportion of daylight hours spent feeding, the daily consumption of food, the daily energy expenditure and overwinter mortality of common scoter were all in good agreement with independent empirical data. This suggests that the presence of this windfarm has not had any significant adverse effects on common scoter. This conclusion holds regardless of the assumed radius of the buffer zone around the physical perimeter of the windfarm (up to a limit of 2km) and regardless of the sampling error inherent in the benthic resource database.

11.8.1.2 North Hoyle + Rhyl Flats + Burbo Bank (Scenarios 3 and 4):

The presence of windfarms at Rhyl Flats and Burbo Bank (assuming by default complete avoidance of the area around the latter) in addition to that at North Hoyle is not predicted to have any significant adverse effects on common scoter mortality. This conclusion holds regardless of the assumed radius of the buffer zone around the physical perimeter of the windfarms (up to a limit of 2km) and regardless of the sampling error inherent in the benthic resource database.

11.8.1.3 North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat (Scenarios 5 and 6):

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter) and at Shell Flat, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality if there is no buffer zone around the physical perimeter of the windfarms. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter) and at Shell Flat, in addition to that at North Hoyle, is predicted to have a significant adverse effect on common scoter mortality if the buffer zone around the physical perimeter of the windfarms is assumed to extend to a radius of 2km. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

The adverse effects on common scoter mortality of the presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter) and at Shell Flat, in addition to that at North Hoyle, assuming that the buffer zone around the physical perimeter of the windfarms extends to a radius of 2km may be negated if common scoter either: i) redistribute to currently unused but apparently profitable feeding areas within Liverpool Bay such as Burbo Bank or ii) feed during the hours of darkness as well as during daylight.

11.8.1.4 North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor (Scenario 8) (i.e. all windfarms except Shell Flat):

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter) and at Gwynt-y-Mor, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality. This conclusion holds regardless of the assumed radius of the buffer zone around the physical perimeter of the windfarms (up to a limit of 2km) and regardless of the sampling error inherent in the benthic resource database.

11.8.1.5 North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat + Gwynt-y-Mor (Scenarios 9 and 10):

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter), Gwynt-y-Mor and Shell Flat, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality if there is no buffer zone around the physical perimeter of the windfarms. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter), Gwynt-y-Mor and at Shell Flat, in addition to that at North Hoyle, is predicted to have a significant adverse effect on common scoter mortality if the buffer zone around the physical perimeter of the windfarms is assumed to extend to a radius of 2km. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

The adverse effects on common scoter mortality of the presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter), Gwynt-y-Mor and at Shell Flat, in addition to that at North Hoyle, assuming that the buffer zone around the physical perimeter of the windfarms extends to a radius of 2km may be negated if common scoter either: i) redistribute to currently unused but apparently profitable feeding areas within Liverpool Bay such as Burbo Bank or ii) feed during the hours of darkness as well as during daylight.

11.8.1.6 The effect of Shell Flat:

Comparison of the results of scenarios 4 and 6 and of scenarios 8 and 10 indicate that it is the cumulative effect of the presence of a windfarm on Shell Flat which, in conjunction with the others and on the assumption that the radius of the buffer zone around them all extends to 2km, leads to increased common scoter mortality. The magnitude of this effect may be underestimated by the model, but nonetheless, a significant effect is predicted. However, this cumulative adverse effect may be negated if: i) the radius of the buffer zone is smaller than 2km, ii) common scoter redistribute to currently unused but apparently profitable feeding areas within Liverpool Bay such as Burbo Bank or iii) common scoter feed during the hours of darkness as well as during daylight.

11.8.1.7 Confidence in predicted effects of existing/ consented and proposed windfarms

The model MORPH that has been used to make the predictions outlined above is a parameter rich, complex model. Many of the values for the parameters and functions in the model are empirical estimates that are subject to measurement error and uncertainty. The model also has numerous assumptions within it, many relating to the seldom studied foraging ecology of common scoter. All of this, coupled with the sensitivity of the key model output i.e. mortality to the values of each of its key parameter values (section 11.6) may lead to the conclsion that the model's key predictions cannot be deemed reliable. However, given all the uncertainty it is encouraging that the model, when set up to simulate the current circumstances within Liverpool Bay, in terms of areas of habitat exploited, food abundance and location and frequency of disturbance, predicts an over-winter mortality rate that is very similar to the likely real-world value. However, it is of course possible that the model gets this prediction right for the wrong reasons, A wide variety of combinations of parameter values could, in principle, produce the same outcome. As discussed above, it is only by testing the model's component predictions in order to detect a quantitative mismatch between prediction and observation that one can ensure that the model accurately captures the most important elements of the system. In every validation test discussed in section 9.3, the model successfully matched independent empirical data. Although such comparisons are always open to interpretation, we are confident that they indicate that the model does indeed capture the most important elements of the system. This provides some confidence that the model's predictions concerning the consequences of further windfarm developments in Liverpool Bay are, within the limits of the issues addressed (section 8.3), reliable.

The model predicted that the presence of windfarms at Rhyl Flats, Burbo Bank and Gwynt-y-Mor will not result in an increase in the over-winter mortality of common scoter irrespective of two keys areas of uncertainty i.e. i) the size of the radius of the exclusion zone around offshore windfarms and ii) the sampling error within the benthic food resource database. This prediicted lack of an effect was also not dependent upon making any untested assumptions that common scoter can feed at night as well as by day or that they will be able to locate and exploit currently unused resources within the bay.Thus, subject only to the caveats concerning the possible effects that the mechanisms of disturbance that the model has not included may have (section 11.8.3), we are confident that the predictions concerning these windfarm locations are reliable.

Only in the case of the proposed wind farm at Shell Flat has this project indicated uncertainty concerning the possible impact on common scoter. This is not a failure of the model or of the project but reflects the current lack of knowledge concerning: i) the radius of exclusion zones around offshore windfarms, ii) the nocturnal foraging activity of seaducks in general and common scoter in particular and the fact that there is a large number of unknown potential environmental factors that may override the simple reltionship between the distribution of any bird population and that of their food resources – especially in the case of a species that has been so little studied as the common scoter. The fact that the model predicts differing impacts of the Shell Flat windfarm subject to these uncertainties simply indicates that further work is required (see section 11.8.2).

11.8.2 Future research needs

11.8.2.1 Interpretation of overflight distribution data

There is a need to determine whether the distribution of ducks derived from overflight data is a true reflection of the distribution of their feeding grounds and the extent to which this is confused by the movements of non-feeding birds. Future work should seek to quantify the influence of factors such as water depth and current speed on the feeding activity of common scoter and whether any such tidal influences on common scoter behaviour result in birds feeding in certain places at certain stages of the tide and resting in other places at other stages of the tidal cycle. In particular it would be valuable to examine the behaviour and movements of ducks in detail over the course of a tidal cycle to determine whether they remain over their foraging grounds at all times or whether they drift to other areas between periods of tidally driven feeding activity. Increased precision in identifying where and when common scoter forage will be invaluable in identifying the key foraging areas within Liverpool Bay as distinct from areas to which birds may drift while resting. It is clear from the simulations conducted in this study that the presence of windfarms on common scoter preferred feeding areas is (subject to certain assumptions) likely to have adverse effects on their mortality.

11.8.2.2 Diurnal/ nocturnal feeding by common scoter

Most of the limited empirical data concerning the feeding behaviour of benthic feeding sea ducks suggests that they are primarily diurnal feeders. This was the default assumption in most of the model simulations. However, in simulations in which the ducks were allowed to feed during the hours of darkness with the same efficiency as during daylight, it was clear that this would markedly increase the ease with which birds could survive the winter. Indeed night time feeding was predicted to be sufficiently profitable to offset the adverse effects on mortality that were predicted to occur under the assumption of daylight only foraging. Given that benthic feeding ducks feeding in freshwater habitats do feed during darkness and the likelihood that these birds feed by touch rather than visually, it is difficult to see why seaducks should not feed at night as efficiently as during the day. Future research should seek to quantify the extent to which common scoter in Liverpool Bay feed during darkness and during daylight and whether the locations in which they feed at such times differ and whether there is seasonal variation in any night feeding activity. This has important implications for: i) identifying the key foraging areas within Liverpool Bay, ii) determining whether common scoter are capable of feeding at night, and iii) determining whether the extent to which they do so varies in line with varying seasonal energy demands i.e. with the difficulty that they have in meeting their requirements. The latter may indicate whether increased night time feeding might be a likely response to a reduction in feeding opportunities caused by the avoidance of areas around windfarms.

11.8.2.3 Limited usage of Burbo Bank and the mouth of the Ribble estuary

The original model simulations during the calibration phase in which 115 cells within 2.5km of a benthic sampling station were included in the model resulted in a large proportion of the population foraging off the coast at Southport (inshore of the site originally proposed for a windfarm) and an even larger proportion feeding over Burbo Bank (Fig. 9.1). The overflight data indicate that common scoter are very seldom seen in either of these areas (Fig 8.1). There are a number of possible explanations for this discrepancy between the model and the empirical data (see section 9.2). The survey of the benthos of Liverpool Bay indicates that both of these areas contain abundant benthic bivalves that common scoter could consume. Further research should therefore seek to identify those non-food related environmental factors that may conspire to render these areas unsuitable for common scoter. If such factors can be identified, the lack of common scoter from these apparently suitable feeding grounds might be explicable. It might then be possible to assess the likelihood that common scoter would be able to redistribute to such areas in the light of windfarm developments elsewhere within the bay. The results of the current study indicate that the ability of birds to redistribute to these areas has important implications for the likely consequences of some windfarm developments in Liverpool Bay.

11.8.2.4 Exclusion zones around offshore wind farms

In this study we explored the effect of common scoter being excluded either from within the physical boundary of an array of wind turbines (radius = 0 km) or from an area with a larger radius (2 km) around this core area. These radii were chosen on the basis of the recent Danish studies which found no common scoter within the boundaries of either of two offshore windfarms and found none within 1.5km of one of these (see section 7.2.11). These Danish studies also indicated significant changes in the distribution of seaducks before and after windfarm construction at distances of several kilometers. However, these changes could not be attributed unequivocally to the presence of the windfarms. These studies are the most detailed investigations to date of the behavioural response of seabirds to offshore windfarms. Nonetheless, they are very preliminary. The results of the current study indicate that in the case of some proposed sites for windfarms, the precise scale of such displacement is likely to have a significant influence on the magnitude of the population-level effect. Thus, further research must be conducted at all existing windfarms to quantify the avoidance distance of sea ducks to such structures, to identify any environmental factors that might cause this distance to vary between locations and to determine whether birds habituate to such static structures over time.

11.8.3 Limitations to existing model

The construction and presence of offshore windfarms in shallow coastal waters have the potential to affect over-wintering common scoter populations in a number of different ways. These were discussed in section 8.3. In this report we have been concerned solely with one of these - the consequences of habitat loss due to the avoidance of man made structures i.e. the windfarms themselves. Thus, the model has not incorporated the possibility of an increased mortality due to the collision of ducks with the turbines. The model has also not incorporated the consequences of the fact that birds seem to alter their flight paths to avoid windfarms and so may incur increased flight costs due to the need to take circuitous routes around windfarms. It proved impossible to gather data on the frequency and routes of maintenance traffic associated with each windfarm and so the possible adverse effects of this source of disturbance on birds' feeding opportunities and daily energy expenditure have not been addressed. Finally, the model has not addressed the issue of the consequences of the construction of the windfarms and associated underwater cabling on the seabed and benthic communities. Thus, there are a number of possible mechanisms by which the construction, presence and servicing of offshore windfarms could have adverse effects on common scoter that have not been included in the predictions made here. All the predictions of the model might, therefore, be considered to be somewhat conservative. However, it is our view that by dealing with the consequences of habitat loss due to the avoidance of the windfarms themselves we have addressed the principal means by which offshore windfarms are likely to affect over-wintering populations of benthic-feeding sea ducks. As discussed in section 8.3 the most important of these various mechanisms that have not been considered is probably the disturbance caused by windfarm maintenance traffic. However, given the large areas of the sea that are not heavily used by common scoter and the possibility of routing windfarm maintenance traffic through such areas eg by approaching the proposed Shell Flat wind farm from the north, it should be possible to minimise the impact of such traffic on the birds. Ideally, such options would have been explored in the current project but this proved impossible. All possible mechanisms by which the construction of offshore windfarms could affect common scoter should ideally be included in any future modelling work. In principle there is no reason why these factors could not be incorporated in future versions of the model MORPH.

11.8.4 Project Achievements

Hitherto. one of the principal techniques employed in assessing the potential impact of offshore windfarms on bird populations due to avoidance displacement has been the use of 'proportional distribution maps' of aerial survey results (see for example RPS 2005) In essence, bird distribution data from overflights is analysed on the basis of a grid of cells and the proportion of the bird population within each grid cell is calculated. The sum of the proportion of the population accounted for by those cells that fall within the boundaries of a proposed windfarm (or within some buffer zone around it) is then calculated to derive the interaction between the windfarm and the birds. However, this technique, being virtually bereft of biological understanding, leaves the key question of the ecological consequences of such displacement still outstanding (RPS 2005). The population impact can only be determined by assigning an associated mortality rate with the displacement. This cannot be done with such a mapping approach. This project provides all of those concerned with predicting the ecological consequences of offshore windfarms in Liverpool Bay with precisely such quantitative predictions. This is the principal achievement of this project.

This project has provided the first quantitative predictions of the change in overwinter mortality rate of the common scoter population of Liverpool Bay under various alternative windfarm scenarios. It is predicted that the presence of wind farms at Rhyl Flats, Burbo Bank and Gwynt-y-Mor, in addition to that at North Hoyle, will not cause any increase in over-winter mortality. These predictions hold irrespective of the assumed radius of the exclusion zone, the sampling error inherent in the benthic database and regardless of whether common scoter feed at night or not or whether they can or cannot relocate to currently unused areas of Liverpool Bay. Thus, this project has provided unequivocal quantitative predictions concerning the effect of four of the five existing/ consented/ proposed windfarm locations within Liverpool Bay. Only in the case of the proposed wind farm at Shell Flat is the predicted change in common scoter mortality subject to uncertainty dependent upon the radius of the exclusion zone and whether common scoter will respond by feeding at night or by redistributing to apparently suitable but currently unused parts of Liverpool Bay. The uncertainty concerning these issues is not a failing of this study. Rather, the uncertainty reflects the current lack of knowledge in the wider scientific community concerning: i) the nocturnal behaviour of seaducks in general and common scoter in particular, ii) the avoidance of offshore windfarms exhibited by seaducks in general and common scoter in particular and iii) the total number and relative importance of environmental factors (other than food abundance/ availability/ quality) that influence the distribution of foraging birds. Even so, the ability to make quantitative predictions of mortality under alternative scenarios has allowed us to explore the significance of these areas of uncertainty and highlight the key issues that must be the focus of future research in order to increase certainty in the predicted effects of a wind farm on Shell Flat (see section 11.8.2).

All approaches to predicting how populations of animals will respond to environmental change depend upon making assumptions. Simple ‘models’ such as ‘proportional distribution map’ models (RPS 2005) make assumptions about the mortality rate of displaced birds. However, as this is the parameter of most importance in determining the true population-level effect of displacement this is far from ideal. Indeed, the apparent simplicity of simple models often hides a very complex suite of unstated assumptions. The individuals-based modelling approach upon which this project is founded is relatively complex and relies upon detailed information about the biology of the species concerned and its environment. The presentation in this report of all the information gathered during this project allows the reader to identify the uncertainties and assumptions. This transparancy does not mean that the approach is any less credible than any other. Indeed, it makes clear where further research should be focussed in order to continually improve the predictive power of such ecological models.

In conclusion, this study has resulted in the development of a new tool which enables the quantitative prediction of the population-level impacts of offshore windfarm development on over-wintering common scoter populations. This is a major advance on any previous approach applied in this field of research. It has indicated that the displacement of common scoter from the areas around four out of five existing/ consented/ proposed windfarms within Liverpool Bay will have no adverse effect on the over-winter mortality of the population. In contrast, it has indicated that the presence of a wind-farm on Shell Flat, given the current best estimates of how these birds behave, will have an adverse effect on the over-winter mortality of the population. However, uncertainty concerning various aspects of the biology of this elusive species means that this prediction may not hold. This highlights the further research that is needed in order to improve the predictive power of future model applications.

12. Summary

12.1 Physical habitat

The first component of the project involved a description of the physical attributes of the habitat over which common scoter were seen most frequently in order to reveal key habitat parameters that might act as proxies of potentially important feeding grounds. This was undertaken by using hindcasting from tidal models for Liverpool Bay related to the geographical position of each bird recorded. These tidal models permitted the following key parameters to be ascertained for each bird observations: depth of water, surface current speed, seabed shear stress. In addition we were able to describe other key physical parameters that may influence the distribution of the birds' prey such as wave erosion at the seabed.

A tidal model of the Irish and Celtic Seas was developed with a grid resolution of approximately 3.7 x 3.35 km to simulate the tidal elevations and currents at the locations and times when common scoter were observed during aerial and land-based surveys. The tidal model was then combined with a 1 km resolution database of water depths in order to derive the actual water depth (mean depth plus tidal elevation) and the speed of the tidal current for each of the observations. We were then able to calculate the depth of water beneath each bird at the time of observation and the speed of drift at the sea surface.

The model was used to assess the fraction of the sea bed that lay within specified depth limits, and the variation of that fraction was assessed during the spring/neap cycle. With respect to mean sea level, c 22% of the region contained water depths of less than 20 m; however the value decreased to c 17% at the time of high water spring tides, and increased to c 27% during low water at spring tides. Thus the area of available habitat was reduced by approximately a third when comparing low water and high water spring tide conditions.

Estimates of the sea bed stress were obtained via the tidal model and also through the application of a regional wave model using wind data from the years 1997-2001. The sea bed stress due to waves was estimated to be an order of magnitude larger than that associated with the tidal motion in the relatively shallow region along the Lancashire coastline; a result that has implications for the spatial distribution of the sea bed bivalve molluscs on which the ducks feed (see section 3). Erosion at the seabed is a major source of mortality for seabed biota (benthos). Wave erosion was less severe along the relatively sheltered North Wales coastline. The implications of the difference in wave erosion are reflected in the depth at which peak bivalve biomass occurred. Off the sheltered North Wales coastline the peak in biomass occurred at a shallow depth of 8 m whereas off the Lancashire coastline the peak occurred in deeper water at 14 m. Thus birds that remain to feed off the Lancashire coastline have to dive deeper and expend more energy to acquire their food.

A histogram of duck numbers as a function of the mean water depth showed an approximately domed distribution with most of the birds concentrated around depths of 10-12m with a range of from 2-22m. When the depths were tidally corrected, however, the histogram became more ramp-like with a relatively rapid decline in numbers where the depth was greater than 18 m. Again, this relationship reflects the need to minimise energy expenditure on diving and a decline in bivalve biomass in water deeper than 14 m.

A histogram of duck numbers as a function of the current speed showed a similar distribution with a threshold at 0.6 ms^{-1}. Areas with surface tidal currents above this value may move birds too rapidly away from profitable patches of prey and hence may be avoided by common scoter. To illustrate this point, the tidal excursion for an object drifting freely with the surface water was computed to have a value of around 10 km along the Lancashire coastline. This parameter is relevant to the energy that would be expended by the ducks if they wished to maintain their positions above a selected portion of the sea bed.

12.2 Distribution and variation in prey

The distribution of feeding common scoter is expected to be influenced to a large extent by the spatial distribution of suitable prey. In addition to quantifying the distribution, quantity and identity of suitable prey species it was also necessary to quantify the relative abundance and distribution of prey of different sizes within these species as size affects the profitability of a prey item and may influence birds' distribution. In addition, the prey resource will diminish over the winter period as common scoter and other bivalve predators graze down prey populations. Hence the survival rate of prey was also ascertained. Length-mass relationships for each bivalve type were also ascertained for parameterisation of the behavioural ecology model.

The highest numbers of common scoter coincided with sites that had a high abundance and biomass of bivalve prey species, and bivalve biomass was among the strongest predictors of common scoter numbers observed during overflight surveys. The maximum observed biomass of bivalves occurred at a mean depth of c 14m off the Lancashire coast and at c 8m off the north Wales coast. The biological explanation for the peak in biomass is linked to the physical parameters that act at these sites. The peak arises from a trade-off between the transport of organic matter (bivalve food) by seabed currents (stronger closer to the shore) and the negative effects of wave erosion at the seabed (causing direct mortality) which decreases with increasing water depth and wave height. The distribution of bivalve biomass from shallow to deeper water coincided well with the distribution of common scoter off Lancashire, but less well with the distribution of birds off North Wales. The weaker relationship off North Wales is probably explained by the greater spatial heterogeneity of depth of the seabed at this site due to offshore sand bank systems. However there is a strong suggestion that high resolution wave models would enable us to improve the fit of the relationship at this site.

Water depth and median phi (a measure of sediment particle composition) were the strongest predictors of bivalve biomass and consequently can also be used to predict common scoter distribution. Median phi also represents the combination of physical forcing factors that act on the seabed sediments (wave erosion and currents).

The distribution of prey species was extremely patchy even when these were grouped into 'prey-types'. Prey-types were categorised according to morphological features of the prey i.e. brittle-shelled oval prey, hard-shelled oval prey, elongate prey. The large number of bivalve prey species in Liverpool Bay varies considerably in their distribution and this reduces the spatial variability of overall prey available to common scoter. It is likely that common scoter select their prey according to the morphological features described and according to actual size. One important implication for future EIAs related to windfarms is that it will not be possible to use an 'indicator species' to represent bivalve prey as the distribution of one species on its own has little or no resemblance to the distribution of the entire bivalve assemblage.

Interannual variation in bivalve abundance was much lower than spatial variation in their abundance for a four year period between 2001 and 2004. Thus, while the abundance of individual species may vary from one year to the next the number of species of bivalve in Liverpool Bay means that there is usually likely to be a sufficient abundance of some species to meet the energetic requirements of the common scoter.

12.3 Behaviour and sources of disturbance

Little is known of the behaviour of common scoter other than on their breeding grounds. This is primarily because common scoter spend their overwinter season off-shore and are extremely sensitive to any form of disturbance. Thus the results reported in the current study are a unique addition to our knowledge of this species.

Immature birds and moulting birds occur in Liverpool Bay during the summer months. Migrants begin to arrive in September/October. The vast majority of these birds are male. Females arrive much later and the sex ratio approaches parity in December. Females are also the first to depart Liverpool Bay and most have left by the end of February. Thus activities in Liverpool Bay will affect different components of the population at different times of the year. Population level impacts are likely to be most serious during those months that affect female birds most. This is because in many high latitude 'capital breeding' species clutch size and the quality and hence survivorship of the ensuing progeny in the breeding season are directly related to the body condition in which the female starts the breeding season. Thus, reduced body condition of females at the end of winter may feed through to reduced population–level reproductive output. In addition, increased winter-mortality of the rarer sex, in a species with a monogamous pairbond, is also more likely to lead to a reduction in population-level reproductive output than is an increase in mortality that effects both sexes equally.

Common scoter tend to face into the current or the wind depending upon which has the greatest influence on their position at any particular time. Birds appear to move in a primarily east/west direction off the North Wales coastline which suggests periodic relocation to reposition over main feeding grounds. Severe weather does not appear to change the utilisation of particular areas, and sheltered areas such as Conwy Bay were not used to any greater degree during severe weather conditions.

Common scoter often dive to the seabed in groups and remain submerged for periods of c. 30 – 50 seconds. They spend more time submerged in deeper water and it appears that they have to spend a longer time feeding at the seabed at shallower sites along the North Wales coastline (food may be less abundant).

Common scoter are sensitive to disturbance by a moving vessel. Observations from a 390 t (35 m long) vessel indicated that large flocks of common scoter were put to flight at a distance of 2 km from the vessel, while smaller flocks were less sensitive and only put to flight at a distance of 1 km. Vessels larger than that used in the study would be expected to have a larger flushing distance. The study did not have a remit to determine disturbance from other boat users (recreational fishing, yachting, jet-skiis) or disturbance generated by low flying aircraft.

Commercial shipping activities are considered one of the major forms of disturbance that may affect common scoter distributions. Analysis of a database of commercial shipping activity revealed that there is little seasonal fluctuation in this activity. The great majority of birds observed in Liverpool Bay do not coincide with the areas of heaviest commercial shipping traffic (vessels > 300 t). Thus common scoter would appear to be excluded from areas of the seabed that coincide with these activities at present. It is possible that if forced to utilise such areas the birds may be able to habituate or tolerate these activities. This is however entirely subjective. Direct observations of fishing activities indicate that these are concentrated in areas deeper than 20 m depth and they do not interfere with common scoter in Liverpool Bay other than on the outbound and inbound journey. Helicopter maintenance flights to oil and gas installations in Liverpool Bay occur directly across the main aggregations of common scoter, but are relatively infrequent and hence to not appear to have an influence on the distribution of the birds.

12.4 Behavioural modelling

The purpose of the behavioural modelling was to determine the consequences for common scoter of removing access to feeding habitat by the construction of windfarms on the assumption that common scoter will show an avoidance response to windfarms. In simple terms, this means that if the total available feeding area measured 10 000 km² and the total area occupied by windfarms was 1 000 km², the remaining available feeding habitat would be 9 000 km². The model predicts how each individual bird would redistribute its foraging effort in space and time under the novel circumstances and whether these behavioural responses would enable them to survive the winter or not. Changes in the body condition and perhaps the survival of each bird may occur if its energy expenditure is increased and/or its energy intake rate is decreased under the new circumstances due to intensified competition for access to a reduced area of foraging habitat of potentially lower suitability. It is the combination of the survival outcomes of each of the individuals within the population that determines the population-level mortality rate predicted by the model under any given scenario.

In total, one hundred and eighty runs of the behavioural model (called MORPH), exploring 36 different ‘scenarios’, were conducted in the course of producing the results presented in this report. Principally, these address the consequences for the common scoter population of Liverpool Bay of a number of different windfarm scenarios (Table 1) and whether these consequences might vary depending upon various uncertainties in model parameterisation. Additional simulations explore the consequences of removing what appear in the model to be the most profitable feeding areas within Liverpool Bay and also the sensitivity of model outputs to variation in its key parameters.

Table 12.1 The details of the windfarms and the buffer zones incorporated in each of the 8 key scenarios explored. Scenario numbers correspond to those used in the following text and figures in this section. A 'snapshot' of the model graphic display while running scenario 1 is shown in Figure 12.1.

Scenario number	Windfarms included	Assumed buffer zone radius
1	North Hoyle	0km
3	North Hoyle + Rhyl Flats + Burbo Bank	0km
4	North Hoyle + Rhyl Flats + Burbo Bank	2km
5	North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat	0km
6	North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat	2km
8	North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor	2km
9	North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat + Gwynt-y-Mor	0km
10	North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat + Gwynt-y-Mor	2km

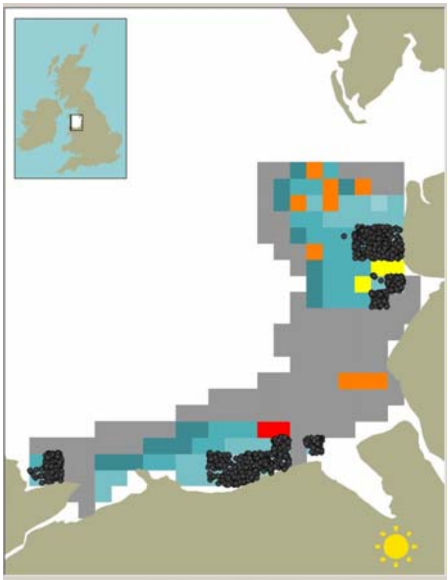

Figure 12.1 Screenshot of the model graphic display illustrating a typical 'snapshot' of the predicted distribution of common scoter under the 'baseline' scenario (scenario 1) in which 99 tidal grid cells are available to the birds in the model and the North Hoyle windfarm is present. The image shows the location of the study area within the UK and the coastline of north Wales, Cheshire, Merseyside, Lancashire and south Cumbria. Within the area of the Irish Sea, the 206 tidal grid cells considered for inclusion in the model are shaded. The initial biomass density of all resources was set to 0 in grid cells which are further than 2.5km from any benthic sampling station. These cells, which are inaccessible to the birds in the model are shaded grey. The remaining cells are coloured as follows. All cells are subject to variation in water depth with time. Greater water depth is indicated by the intensity of blue shading. As the tide ebbs and flows the shade of blue in each cell changes accordingly. Cells in which a source of human disturbance is present during this particular hour are overlaid with a further colour: red denotes the permanent presence of a windfarm (at North Hoyle), orange denotes the temporary presence of a large ship passing through a cell at this point in time and yellow denotes the temporary presence of a helicopter passing over a cell at this point in time. Common scoter avoid a cell when one or more of these sources of disturbance occurs there but may visit it at other times in the absence of disturbing factors. Each black dot represents one super-individual each of which represents 30 common scoter. The image of the sun denotes that this 'snapshot' was taken during the hours of daylight.

12.4.1 Scenarios using default parameter values

Examination of the proportion of time common scoter spend feeding during daylight under the 8 different scenarios showed statistically significant differences. However, in terms of their absolute magnitude these changes were so minor that they are considered to be of negligible biological significance (mean proportion of time spent feeding 0.436 with a range of -3.7% - 2.6% of this value). The body mass achieved by common scoter was only significantly reduced under the scenario (scenario 10) in which all windfarms were present and the buffer zones around them were assumed to have a radius of 2km. The baseline median overwinter mortality for common scoter is estimated to be 7.3% of the birds in Liverpool Bay (range 5.4% - 8.8%). **Only in the cases of scenarios 6 and 10 did the model predict a significant increase in**

mortality for common scoter (scenario 6 median 11.0% (range 9.9% - 11.2%), scenario 10 median 11.7% (range 11.0% - 12.2%) (Fig. 12.2).

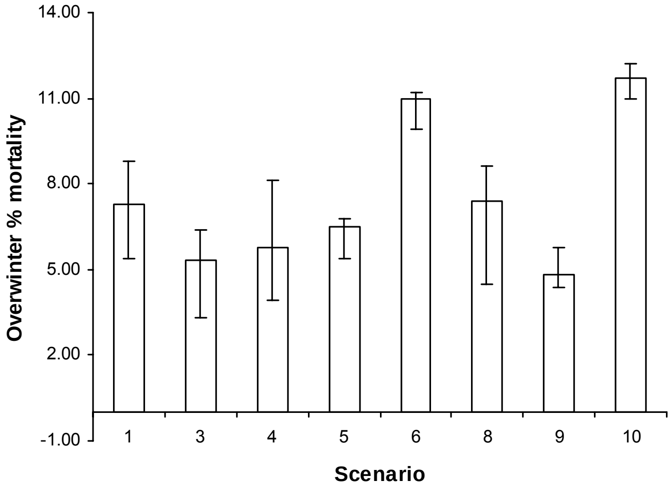

Figure 12.2 The median (and range) of predicted percentage overwinter mortality of common scoter under the baseline scenario (1) and each of the other windfarm scenarios assuming default values for all parameters.

12.4.2 Worst-case scenarios

A set of scenarios were run assuming that our default estimates of food supply were overly-optimistic (i.e. the mean values obtained from the seabed survey of bivalves). In these simulations the lower 95% confidence interval for benthic prey was used as the value of the resource abundance. Even under this reduced prey resource scenario, the model predicted that birds did not significantly alter the proportion of time spent feeding. Similarly the body mass achieved by common scoter was not significantly worse than that achieved with higher values of food availability **(Fig. 12.3)**. For overwinter mortality, only in two out of eight cases was the percentage overwinter mortality significantly higher in the face of reduced food supplies (scenario 3 and scenario 9). However, in both these cases, the **percentage overwinter mortality was still no higher than that predicted under 'baseline'** i.e. current conditions (scenario 1). The predicted % overwinter mortality generated by the two worst scenarios under default assumptions (scenarios 6 and 10) **did not get any worse under the conditions of reduced food supply.**

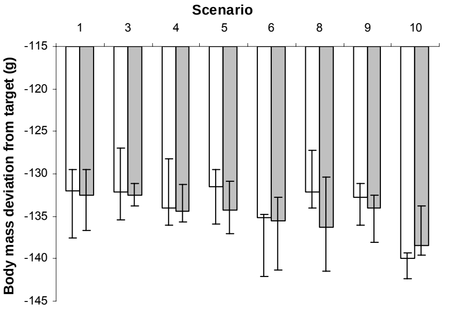

Figure 12.3 The median (and range) of the weighted mean deviation of common scoter body masses from the target mass under the baseline scenario (1) and each of the other windfarm scenarios, assuming either: i) default values for all parameters (open bars) or ii) a reduced abundance of all resources (shaded bars).

12.4.3 Best-case scenarios

For each of the two scenarios (6 and 10) which generated evidence of adverse effects of windfarm developments on the common scoter population (significantly reduced overwinter body mass and elevated overwinter mortality), simulations were conducted to explore whether these predictions might be unduly pessimistic.

For both scenarios, the proportion of daylight hours spent feeding by common scoter was significantly reduced below that under the default conditions and body mass achieved was significantly higher (default conditions = 99 cells, mean resource abundance and daytime only feeding) if either: i) they were allowed access to additional alternative habitat (the 11 cells on

Burbo Bank and the 5 cells off Southport or ii) they were allowed to feed at night as well as by day. Increasing the abundance of the food resources (to the upper 95% confidence limit) had no such effect. Thus, the adverse effects of the windfarm developments predicted under scenarios 6 and 10 may be overly pessimistic if common scoter either: i) redistribute in space to apparently suitable but currently unused areas within Liverpool Bay or ii) feed at night as well as by day within the areas of the bay that they currently exploit.

For both scenarios, the median percentage overwinter mortality was significantly reduced below that predicted under the default conditions (i.e. 99 cells, mean resource abundance and daytime only feeding) if common scoter were allowed either to: i) have access to additional alternative habitat (the 11 cells on Burbo Bank and the 5 cells off Southport or ii) feed at night as well as by day. Increasing the abundance of the food resources (to the upper 95% confidence limit) had no such effect in the case of scenario 6. However, increasing the resource abundances did lead to a significant reduction in the predicted overwinter mortality under scenario 10. Thus, the adverse effects of the windfarm developments simulated by scenarios 6 and 10 may be pessimistic if common scoter either: i) redistribute in space to apparently suitable but currently unused areas within Liverpool Bay or ii) feed at night as well as by day within the areas of the bay that they currently exploit. The adverse effects of the windfarm developments simulated by scenario 10 may also be overly pessimistic given the uncertainty within the benthic sampling database. However, even under the assumption of increased resource abundance the predicted overwinter mortality under scenario 10 (median 9.4%, range 9.2% - 9.7%) was still in excess of that under current conditions (scenario 1: median 7.3%, range 5.4% - 8.8%). Thus, although the uncertainty concerning the precise values of resource abundance means that the magnitude of the predicted elevation of overwinter mortality under scenario 10 may be pessimistic, it is unlikely that the prediction of elevated mortality is incorrect if common scoter do not feed at night and cannot redistribute to apparently suitable but currently unused areas of the bay.

12.4.4 Scenarios in which key foraging areas removed

An additional set of scenarios were run to remove the best quality feeding habitats (with respect to prey resources) within the model, in order to understand the importance of such areas for common scoter. Any significant effects on common scoter would indicate that these areas might require high priority status for protection from human-related sources of disturbance.

In each of the 5 replicates of the baseline scenario (scenario 1) the model generated a predicted distribution pattern of foraging ducks. These outputs were used to calculate for each run, the average overwinter proportion of the population within each cell. These figures were then averaged across the 5 replicate simulations and the top 10 cells identified. These fell into four discrete locations (Fig. 12.4). Simulations were conducted in which common scoter were excluded from each of these areas in turn (as well as from the North Hoyle windfarm area) to explore the relative consequences of the loss of each of the areas in comparison with the consequences of the windfarm developments simulated under scenario 10 i.e. the worst of the key scenarios explored. In each case, the overwinter mortality was predicted to be significantly greater than under scenario 10 (Fig. 12.5). The most pronounced effect was caused by the removal of four neighbouring cells off Blackpool (largely to the south and east of the proposed location of the Shell Flat windfarm). These results suggest that (in the absence of access to apparently suitable but unused areas on Burbo Bank and off Southport, and in the absence of night-time feeding) the loss of key common scoter foraging areas to windfarm developments is likely to lead to significantly increased overwinter common scoter mortality.

12.4.5 Sensitivity analysis

A sensitivity analysis of the model indicated that the principal model prediction i.e. overwinter mortality is highly sensitive to each of its five key parameters. Given that the model is an energy balance model it is not surprising that it is most sensitive to the rate at which birds metabolise energy and the efficiency with which they assimilate the food that they ingest. These findings are very similar to those of the sensitivity analyses conducted on a precursor of the model MORPH.

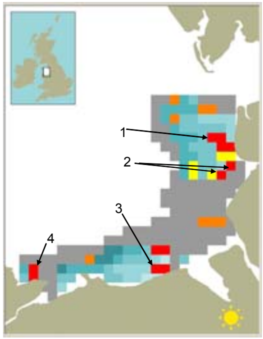

Figure 12.4 Model graphic display illustrating the four groups of cells (coloured red) removed under each of the additional scenarios to explore the consequences of the removal of cells identified by the model as favoured common scoter feeding areas. The number of each area corresponds to the scenario number in Figure 12.5. North Hoyle, which was also included in these simulations, is also shown (un-numbered). Grid cells coloured grey are not available to the birds. Increasing water depth is denoted by darker shades of blue. Grid cells in which there is a windfarm, large ship traffic or helicopter traffic in this particular time step are coloured red, orange and yellow respectively.

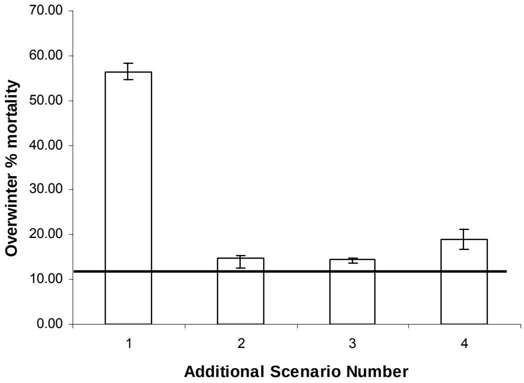

Figure 12.5 The median (and range) of predicted % overwinter mortality of common scoter under four additional scenarios in which groups of cells identified during baseline model simulations (scenario 1) as favoured feeding areas of common scoter in the model are removed. In these additional scenarios the cells removed were: inshore of Shell Flat (1), off the mouth of the Ribble (2), immediately offshore at Rhyl (3) and in Red Wharf Bay (4) (see Figure 12.4). The solid horizontal line denotes the median predicted overwinter mortality under scenario 10.

This sensitivity increased the chances that the model produced, for the wrong reasons, accurate forecasts of the winter starvation rate under the various windfarm scenarios. A wide variety of combinations of parameter values could, in principle, produce the same outcome. The only way to ensure that the model accurately captures the most important elements of the system is to explore its properties continually by testing its component predictions in order to detect a quantitative mismatch between prediction and observation. In the present model, the component predictions concerning the birds' behaviour, energetics and mortality were quantitatively consistent with independent empirical data. There was also a highly significant association between the observed distribution of birds between the 99 core grid cells and that predicted by the model. In general, the bulk of the cells which are seldom used by common scoter in reality were little used by model birds, and many of the cells used heavily by common scoter in reality were also much used in the model. Together, these results suggest that the model captures the main features of the system.

The only, mismatch of concern was that the model failed to generate an absolutely perfect fit to the distribution of birds. A perfect fit is, however, a very exacting standard, particularly given the spatial scale of the study, the practical constraints on the benthic sampling programme and especially in a case where it is unknown how well the observed distribution of birds actually reflects the distribution of their foraging grounds. With so many of the other component predictions supported by observation, we regard this issue as a stimulus for further investigation of common scoter' distribution rather than as being fatal to the value of this study.

The results of the sensitivity analyses also suggest that although much effort was involved in deriving the current best estimates of all the various parameters and functions within the model, there is merit in further review work, and indeed further empirical and experimental research on the energetics of foraging diving ducks. This will serve to refine parameter estimates and to define realistic confidence intervals around them. These can be the subject of further sensitivity analyses of the outcomes of future models.

12.4.6 Summary of the predicted effects of existing/ consented and proposed windfarms

North Hoyle (Scenario 1):

Under current conditions the proportion of daylight hours spent feeding, the daily consumption of food, the daily energy expenditure and overwinter mortality of common scoter were all in good agreement with independent empirical data. This suggests that the presence of this windfarm has not had any significant adverse effects on common scoter. This conclusion holds regardless of the assumed radius of the buffer zone around the physical perimeter of the windfarm (up to a limit of 2km) and regardless of the sampling error inherent in the benthic resource database.

North Hoyle + Rhyl Flats + Burbo Bank (Scenarios 3 and 4):

The presence of windfarms at Rhyl Flats and Burbo Bank (assuming by default complete avoidance of the area around the latter) in addition to that at North Hoyle is not predicted to have any significant adverse effects on common scoter mortality. This conclusion holds regardless of the assumed radius of the buffer zone around the physical perimeter of the windfarms (up to a limit of 2km) and regardless of the sampling error inherent in the benthic resource database.

North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat (Scenarios 5 and 6):

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter) and at Shell Flat, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality if there is no buffer zone around the physical perimeter of the windfarms. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter) and at Shell Flat, in addition to that at North Hoyle, is predicted to have a significant adverse effect on common scoter mortality if the buffer zone around the physical perimeter of the windfarms is assumed to extend to a radius of 2km. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

The adverse effects on common scoter mortality of the presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter) and at Shell Flat, in addition to that at North Hoyle, assuming that the buffer zone around the physical perimeter of the windfarms extends to a radius of 2km may be negated if common scoter either: i) redistribute to currently unused but apparently profitable feeding areas within Liverpool Bay such as Burbo Bank or ii) feed during the hours of darkness as well as during daylight.

North Hoyle + Rhyl Flats + Burbo Bank + Gwynt-y-Mor (Scenario 8) (i.e. all windfarms except Shell Flat):

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter) and at Gwynt-y-Mor, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality. This conclusion holds regardless of the assumed radius of the buffer zone around the physical perimeter of the windfarms (up to a limit of 2km) and regardless of the sampling error inherent in the benthic resource database.

North Hoyle + Rhyl Flats + Burbo Bank + Shell Flat + Gwynt-y-Mor (Scenarios 9 and 10):

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter), Gwynt-y-Mor and Shell Flat, in addition to that at North Hoyle, is not predicted to have any significant adverse effects on common scoter mortality if there is no buffer zone around the physical perimeter of the windfarms. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

The presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter), Gwynt-y-Mor and at Shell Flat, in addition to that at North Hoyle, is predicted to have a significant adverse effect on common scoter mortality if the buffer zone around the physical perimeter of the windfarms is assumed to extend to a radius of 2km. This conclusion holds regardless of the sampling error inherent in the benthic resource database.

The adverse effects on common scoter mortality of the presence of windfarms at Rhyl Flats, Burbo Bank (assuming by default complete avoidance of the area around the latter), Gwynt-y-Mor and at Shell Flat, in addition to that at North Hoyle, assuming that the buffer zone around the physical perimeter of the windfarms extends to a radius of 2km may be negated if common scoter either: i) redistribute to currently unused but apparently profitable feeding areas within Liverpool Bay such as Burbo Bank or ii) feed during the hours of darkness as well as during daylight.

12.4.7 The effects of Shell Flat

Comparison of the results of scenarios 4 and 6 and of scenarios 8 and 10 indicate that it is the cumulative effect of the presence of a windfarm on Shell Flat which, in conjunction with the others, and on the assumption that the radius of the buffer zone around them all extends to 2km, leads to an increase in predicted common scoter mortality. This reflects that the fact that only in the scenarios in which a 2km buffer zone around Shell Flat was included did the model predict that common scoter would be excluded from a number of grid cells in which the model predicted that they would otherwise feed heavily. The magnitude of this effect may be underestimated by the model, but nonetheless, a significant effect is predicted. However, this cumulative adverse effect may be negated if: i) the radius of the buffer zone is smaller than 2km, ii) common scoter redistribute to currently unused but apparently profitable feeding areas within Liverpool Bay such as Burbo Bank or iii) common scoter feed during the hours of darkness as well as during daylight.

13. Conclusions

13.1 Project Achievements

Hitherto, one of the principal techniques employed in assessing the potential impact of offshore windfarms on bird populations due to avoidance displacement has been the use of 'proportional distribution maps' of aerial survey results (see for example RPS 2005) In essence, bird distribution data from overflights is analysed on the basis of a grid of cells and the proportion of the bird population within each grid cell is calculated. The sum of the proportion of the population accounted for by those cells that fall within the boundaries of a proposed windfarm (or within some buffer zone around it) is then calculated to derive the interaction between the windfarm and the birds. However, this technique, being virtually bereft of any understanding of underlying biological mechanisms, leaves the key question of the ecological consequences of such displacement still outstanding. As stated in a recent Environmental Statement employing this approach (RPS 2005) "the corresponding population impact *(of a displacement)* can only be determined by **assigning** an associated mortality rate". In contrast, this project **provides** all of those concerned with predicting the ecological consequences of offshore windfarms in Liverpool Bay with **precisely such quantitative predictions of mortality**. This is the principal achievement of this project. The behavioural model is generic and hence provided that empirical data are available for other areas it is applicable to those situations.

This project has provided the **first quantitative predictions of the change in overwinter mortality rate of the common scoter population of Liverpool Bay** under various alternative windfarm scenarios. It is predicted that the presence of wind farms at Rhyl Flats, Burbo Bank and Gwynt-y-Mor, in addition to that at North Hoyle, will not cause any increase in over-winter mortality. These predictions hold irrespective of the assumed radius of the exclusion zone, the sampling error inherent in the benthic database and regardless of whether common scoter feed at night or not or whether they can or cannot relocate to currently unused areas of Liverpool Bay.

The project has provided unequivocal quantitative predictions concerning the effect of four of the five existing/ consented/ proposed windfarm locations within Liverpool Bay. Only in the case of the proposed wind farm at Shell Flat is the predicted change in common scoter mortality subject to uncertainty dependent upon the radius of the exclusion zone and whether common scoter will respond by feeding at night or by redistributing to apparently suitable but currently unused parts of Liverpool Bay. The uncertainty concerning these issues is not a failing of this study. Rather, the uncertainty reflects the current lack of knowledge in the wider scientific community concerning: i) the nocturnal behaviour of seaducks in general and common scoter in particular, ii) the avoidance of offshore windfarms exhibited by seaducks in general and common scoter in particular and iii) the total number and relative importance of environmental factors (other than food abundance/ availability/ quality) that influence the distribution of foraging birds. Even so, the ability to make quantitative predictions of mortality under alternative scenarios has allowed us to explore the significance of these areas of uncertainty and highlight the key issues that must be the focus of future research in order to increase certainty in the predicted effects of a wind farm on Shell Flat (see section 11.8.2).

All approaches to predicting how populations of animals will respond to environmental change depend upon making assumptions. Indeed, the apparent simplicity of simple models often hides a very complex suite of un-stated assumptions. The individuals-based modelling approach upon which this project is founded is relatively complex and relies upon detailed information about the biology of the species concerned and its environment. The presentation in this report of all the information gathered during this project allows the reader to identify the uncertainties and assumptions. This transparency does not mean that the approach is any less credible than any other. Indeed, it has the advantage of making clear where further research should be focussed in order to continually improve the predictive power of such ecological models.

In conclusion, this study has resulted in the development of a new tool which enables the quantitative prediction of the population-level impacts of offshore windfarm development on over-wintering common scoter populations. This is a major advance on any previous approach applied in this field of research. It has indicated that the displacement of common scoter from the areas around four out of five existing/ consented/ proposed windfarms within Liverpool Bay will have no adverse effect on the over-winter mortality of the population. In contrast, it has indicated that the displacement of common scoter from an area around a wind-farm on Shell Flat, given the current best estimates of how these birds behave, will have an adverse effect on the over-winter mortality of the population. However, uncertainty concerning various aspects of the biology of this elusive species means that this prediction may not hold. This highlights the further research that is needed in order to improve the predictive power of future model applications.

13.2 Confidence in predictions of model MORPH

The model MORPH that has been used to make the predictions outlined above is a parameter rich, complex model. Many of the values for the parameters and functions in the model are empirical estimates that are subject to measurement error and uncertainty. The model also has numerous assumptions within it, many relating to the seldom studied foraging ecology of common scoter. All of this, coupled with the sensitivity of the key model output i.e. mortality to the values of each of its key parameter values (section 11.6) may lead to the conclusion that the model's key predictions cannot be deemed reliable. Such an assessment is of course largely subjective and each reader must come to their own view. However, given all the uncertainty we are encouraged that the model, when set up to simulate the current circumstances within Liverpool Bay, in terms of areas of habitat exploited, food abundance and location and frequency of disturbance, predicts an over-winter mortality rate that is very similar to the likely real-world value. However, it is of course possible that the model gets this prediction right for the wrong reasons, A wide variety of combinations of parameter values could, in principle, produce the same outcome. It is only by testing the model's component predictions in order to detect a quantitative mismatch between prediction and observation that one can ensure that the model accurately captures the most important elements of the system. In every validation test discussed in section 9.3, the model successfully matched independent empirical data. Although such comparisons are always open to interpretation, we are confident that they indicate that the model does indeed capture the most important elements of the system. This provides some confidence that the model's predictions concerning the consequences of further windfarm developments in Liverpool Bay are, subject to the limits of the issues addressed (section 8.3), reliable.

The model predicted that the displacement of common scoter from areas of sea around windfarms at Rhyl Flats, Burbo Bank and Gwynt-y-Mor will not result in an increase in their over-winter mortality irrespective of two keys areas of uncertainty in the model i.e. i) the size of the radius of the exclusion zone around offshore windfarms and ii) the sampling error within the benthic food resource database. This predicted lack of an effect was also not dependent upon making any untested assumptions that common scoter can feed at night as well as by day or that they will be able to locate and exploit currently unused resources within the bay. Thus, subject only to the caveat that our model does not consider the possible effects that the mechanisms of disturbance which we excluded might have (section 11.8.3), we are confident that the predictions concerning these windfarm locations are reliable.

Only in the case of the proposed wind farm at Shell Flat has this project indicated uncertainty concerning the possible impact on common scoter. This is not a failure of the model or of the project but reflects the current lack of knowledge concerning: i) the radius of exclusion zones around offshore windfarms, ii) the nocturnal foraging activity of seaducks in general and common scoter in particular and the fact that there is a large number of unknown potential environmental factors that may override the simple relationship between the distribution of any bird population and that of their food resources – especially in the case of a species that has been so little studied as the common scoter. The fact that because of these uncertainties the model predicts differing potential impacts of the displacement of common scoter from an area of sea around a windfarm on Shell Flat simply indicates that further work is required (see section 11.8.2).

13.3 General applicability of the model MORPH

The model MORPH described in section 6 is coded in such a way that it has no system-specific features. It is entirely generic and has the flexibility to be applied to a very wide range of consumer-resource systems, subject to appropriate parameters being available. It is the contents of the parameter file which must be specified in order to determine the particular application to which the model MORPH is to be put.

The development during this project of the basic ‘scoter parameter file’, variations of which have been used to explore all of the scenarios described in section 10, has involved a combination of tidal modelling, benthic survey work, observations of free-living common scoter, an extensive literature review and considerable thought as to how the key elements of the foraging ecology of common scoter should be incorporated in such a model. The result is a model which, like all of its predecessors, is based on sound ecological principles and is parameterised with the best available estimates of all the necessary parameters and functions. As we anticipated at the outset of the project, the application of the individuals-based modelling approach to predicting the consequences of environmental change on benthic feeding sea ducks has proved possible. The model has been successfully applied to predict the impact of the displacement of common scoter from areas of sea around windfarms in Liverpool Bay on their overwinter mortality. Having established this model there is no reason why it cannot be used in the future to explore other cases of potential interactions between common scoter and offshore windfarms either within Liverpool Bay or elsewhere.

With the existing parameter file(s) it would be very easy to conduct additional simulations of the presence of windfarms, and subject to the necessary data being made available, the presence of associated maintenance traffic, at any other location within the boundaries of the Liverpool Bay study area addressed in this report. Thus, should data become available concerning the proposed routes and frequencies of maintenance traffic associated with each of the 5 windfarms discussed here, the additional effect of this source of disturbance could be explored with no further data collection. The efficacy of possible mitigation measures to re-route maintenance traffic in space and time could also be explored. Furthermore, any new proposed location for an offshore windfarm within this area under any new round of licence applications e.g. Round 3, could be explored with the existing model and with minor modifications to the parameter file to simulate the proposed new windfarm locations.

In order to apply the model to predict the consequences of offshore windfarm development for common scoter populations at any other area around the coast of the UK (or indeed any other country) it will be necessary to collect data concerning the population of birds in question, its food supplies at that locality and the characteristics of the study area. The detailed data requirements in order to do this are set out in section 12.

Because of the basic ecological principles on which the model is based, and our ability to develop over a two year period a model of benthic feeding sea ducks from a model which hitherto had only been applied to intertidal feeding shorebirds and terrestrial feeding geese, we are confident that the model could, with appropriate parameterisation, be applied to a wide range of other potential interactions between bird populations and offshore windfarms. For example, it should be relatively straightforward to model other species of benthic-feeding sea duck such as common eiders. It should also be able to model pursuit feeding diving birds such as divers (Gaviidae), grebes (Podicipedidae) and cormorants (Phalacrocacidae). Furthermore, the same approach could, again subject to appropriate parameterisation, be applied to examine the interactions between all of these types of birds and other types of renewable energy generation developments that may take place in the coastal zone e.g. tidal barrages.

13.4 Recommendations for future common scoter work

As indicated earlier there are number of assumptions and uncertainties that are inevitable with this type of study, but these provide direction for improving modelling approaches in the future, here we provide a brief list of areas where our understanding could be improved and our recommendations for action.

1) An underpinning element of this project is the data relating to the distribution of common scoter. This was obtained using overflights with small aircraft during the daylight. At present we still do not know if there are large-scale movements of birds at night or whether the birds feed at

night. Overflights cannot tell us anything about the behaviour of the birds at the time of observation. At present we still have no direct observations of birds feeding at Shell Flat. Such observations may be obtained by the use of a coastal network of radar to track bird movements along the coastline, the use of an observation platform (anchored vessel) and night vision binoculars to assess feeding and other behaviours during night at different localities.

**Recommendations: i) conduct direct observations of common scoter foraging/resting activity throughout the tidal cycle, ii) investigate night time movements and feeding activity, iii)
confirm that birds feed at sites off Lancashire.**

2) The physical modelling and quantified distribution of bivalve prey gave good predictions of the distribution of common scoter off the coast of Lancashire. However the complex nature of the seabed at a spatial scale less than the resolution of the physical models introduced a higher degree of variation for the relationships off the North Wales coastline. This could be easily rectified using a higher resolution wave model such as the WAM (wave amplitude model) developed by Proudman Oceanographic Laboratory, Liverpool. As wave erosion appears to be a key forcing factor, this could also change with climate change (increasing strength and amplitude) and possibly drive the biomass peak further offshore into deeper water. However, such effects of increasing wave erosion may also be mitigated by the 'barrier effect' of wind-farm arrays and therefore help to minimise such effects.

Recommendations: run WAM model for higher resolution calculations of physical forcing on the seabed. Run wave climate change model to predict changes in wave erosion in the future. Model the effects of windfarm arrays on dissipation of wave energy.

3) While spatial variation in prey abundance would at present seem to exceed inter-annual variation in prey abundance, important changes to prey resources could occur in the future, and these may occur independent of the presence of windfarms. Climate change and fishing activities both have the potential to affect prey resources. Warming of coastal seas in the future will increase the basal metabolic rate of bivalves during the overwinter period when food is scarce or absent and could potentially lead to mass mortalities of bivalves due to starvation. With ever dwindling fish stocks the fishing industry is keen to diversify into new species' markets. Consequently, the Liverpool Bay area could be subject to requests for licenses to harvest shellfish (bivalves). Such activities may represent direct competition with birds for their food resource.

Recommendations: fund desk based study to ascertain future risk of prey resource collapse with changes in sea temperature and possible extractive fishing activities.

4) The population of common scoter in Liverpool Bay is male-biased. However, female common scoter do occur in Liverpool Bay, primarily in the months of December to February. Little is known of the extent to which the sexes (and indeed age classes) segregate spatially within the bay. Any such segregation (which may be driven by social status) may have implications for the extent to which adverse effects of windfarms are distributed within the population This in turn may have implications for the long-term dynamics of the wider common scoter population of which the Liverpool Bay birds form a part.

Recommendation: investigate the spatial distribution of different age and sex classes within the common scoter population.

5) Common scoter appear to avoid areas of heavy shipping activity. However quantitative data concerning the frequency and location of small ship traffic, recreational fishing activity, yachting and jet-ski usage does not exist at present. Any possible effects of these activities on common scoter cannot yet be estimated. Nevertheless most of these activities are likely to occur primarily in the summer when impacts on common scoter will be negligible.

Recommendation: undertake observations of common scoter responses to small ship traffic (e.g. fishing vessels) and recreational boat user activities. Quantify the spatial and temporal variation in these activities across the bay.

6) At present the best quality information for possible sources of disturbance from boat and ship related activities relate to commercial vessels > 300 tonnes and fishing activities on commercial fishing grounds. Data on all sources of vessel related activities would inform management to minimise the potential negative effects of disturbance by creating ‘no go’ areas, particularly with respect to chronic disturbance by maintenance traffic.

Recommendation: implement more detailed study of disturbance effects of smaller vessels.

7) Prior to submission of the current research project the investigators had intended to include a controlled tank study to measure the energetics of common scoter feeding on prey buried in sediments at the base of a dive tank. This study would have quantified the energetic cost of diving for common scoter at given water temperatures and would have revealed the precise mechanism of foraging. However, such a study was beyond the budget outlined. Although such a study might have provided the actual measurements required to input into the model, respiration rate is closely related to body mass and hence the approach utilised in the current project is entirely valid in the absence of directly measured values. Tank studies are also open to the criticism that they do not replicate natural conditions and that the birds utilised are often those from sanctuaries whose body condition and behaviour may not represent those of healthy, free-living birds. Thus, to minimise any concerns regarding the validity of a model based largely on investigations of the foraging ecology, diving behaviour and energetics of species other than the study species, the best approach would be a combination of tank studies using common scoter and field measurements of wild birds carrying tags that measure dive depth, time and respiration rate (among other parameters). This is likely to be a very labour intensive and time consuming research programme. It may, however, be the only way to ensure that any future model of common scoter behaviour is free from any misgivings concerning the validity of the information that lies at its core.

Recommendation: Encourage studies of the foraging ecology of captive and wild common scoter

14. General applicability and Guidance Notes

The model MORPH described in section 6 is coded in such a way that it has no system-specific features. It is entirely generic and has the flexibility to be applied to a very wide range of consumer-resource systems, subject to appropriate parameters being available. It is the contents of the parameter file which must be specified in order to determine the particular application to which the model MORPH is to be put. The basic parameter file that has been developed during this project has been used to generate a number of variations in order to explore all of the scenarios described in section 10. On this basis it would be very easy to conduct additional simulations of the presence of windfarms, and subject to the necessary data being made available, the presence of associated maintenance traffic, at any location within the boundaries of the Liverpool Bay study area addressed in this report. Thus, should data become available concerning the proposed routes and frequencies of maintenance traffic associated with each of the 5 windfarms discussed here, the additional effect of this source of disturbance could be expored with no further data collection. The efficacy of possible mitigation measures to re-route maintenance traffic in space and time could also be explored. Furthermore, any new proposed location for an offshore windfarm within this area under any new round of licence applications eg Round 3, could be explored with the existing model and with minor modifications to the parameter file to simulate the proposed new windfarm locations.

In order to apply the model to predict the consequences of offshore windfarm development for common scoter populations at any other area around the coast of the UK (or indeed any other country) it will be necessary to collect data concerning the population of birds in question, its food supplies at that locality and the characteristics of the study area. In the following sections we present guidance notes detailing the parameters and functions that must be estimated in any such future application of the model MORPH to predict the consequences of other potential offshore windfarm development locations for over-wintering populations of common scoter.

We have restricted these notes to deal only with those parameters and functions that characterise the environment in the study area in question and the common scoter population that inhabits the area. In other words we deal here only with those parameters and functions whose values or coefficients might be site-specific. We have also restricted these notes to deal only with those parameters and functions that are already included in the existing version of the model MORPH. However, we also discuss two further site-specific factors, notably current speeds and windfarm maintenance traffic, that have not been included in the current version of the model MORPH but should be included in future applications of the model. All other parameters and functions in the model that have been derived from the literature are not considered here. Future studies should seek to utilise the most up to date information concerning these parameters and functions. This should be achieved by a continual review of new research.

14.1 Existing Global variables

14.1.1 Day length

The annual maximum and minimum day length (sunrise to sunset) at the latitude of any future study site should be derived. In the current study this information was obtained from data held on the website http://aa.usno.navy.mil/cgi-bin/aa_rstablew.pl. Using a simple cosine function, these maximum and minimum values can be used to calculate the duration of daylight on each day. Assuming, for simplicity, symmetry of sunrise and sunset around noon, predicted day length can be used to ascribe each time step to occur either in darkness or daylight.

14.1.2 Water temperature

Data should be collected concerning the water temperature within the study area. In the current model, daily average water temperature values for Liverpool Bay were assumed to apply across the whole study area. Yet, variation in water temperature (especially that between locations) may influence the energy costs associated with feeding (and resting) in different places and may influence the birds' distribution. Ideally, water temperature data should be collected within each of the areas that are to be considered as distinct patches within the study area (see below). As a minimum, water temperature data should be recorded during the day and night.

14.2 Existing Patch variables

14.2.1 Number of patches

The extent of the study area should be defined at the outset of any future studies and a decision taken as to the appropriate spatial resolution to be considered. The latter may depend upon the former and will have major implications for amongst other things: i) the amount of benthic sampling, ii) the accuracy with which the model can predict bird distribution and iii) the model running time.

14.2.2 Size of each patch

The area of seabed (i.e. foraging habitat) within each patch needs to be defined. This may differ between patches if (as in the current model) a grid based approach to defining patch boundaries is used and some cells adjoin the land.

14.2.3 Central coordinates of each patch

In order to calculate the energetic cost associated with moving between patches, the central location of each patch needs to be determined. In the current version of the model, patch coordinates were expressed in terms of decimal degrees of latitude and longitude.

14.2.4 Water Depth

In the present study the tidal model of the Irish and Celtic Seas developed by Alan Elliot (see section 2) was used to calculate the temporal variation in water depth on an hourly basis in each patch within the model. The same tidal model could be re-applied in any future applications of the model MORPH to proposed windfarm developments within the Irish and Celtic Seas. A similar tidal model might need to be developed in order to apply the model MORPH to other locations around the UK coast.

14.2.5 Presence of a windfarm

The location of any proposed windfarm(s) within the study area need to be defined. With the use of a GIS, the proportion of each patch within the study area that overlaps the physical perimeter of each windfarm, or any assumed buffer zone around it, should be calculated. If the resolution of the patches can be made sufficiently fine, each patch could be defined as falling entirely within or outside the area assumed to be affected by a windfarm. This was not possible in the current study because of the resolution of the tidal model and the large geographical area with which the study was concerned.

14.2.6 Shipping activity

In the current study, empirical data on commercial shipping (ships > 300 t) activity was analysed to yield values for the number of ships passing though each patch per annum. These values were converted to a frequency of ships per hour per patch on the assumption of no diurnal, tidal or seasonal variation in shipping activity. A patch was rendered unavailable to common scoter for the entirety of those time steps (i.e. for 1 hour) in which a ship was deemed, on a probabilistic basis, to pass through it. Ideally future studies should obtain more precise data on the temporal variation in shipping activity within each patch to be modelled within the study area. In addition, more detailed information on the avoidance distances of common scoter to large ships (i.e. the flushing distance) and the time taken by common scoter to return to an area of sea once a large ship has passed would be valuable. It may be that common scoter take 2 or more hours to return to an area once a large ship has passed through it. In this case the behaviour of birds in the model would need to be adjusted accordingly.

In the current study it was not possible to gather information of the spatial and temporal variation in the passage of small shipping traffic and indeed of recreational craft such as jet-skis. Ideally, data on the frequency of all such potentially disturbing activity should be recorded for each patch within the area to be modelled. This should be combined with data concerning the avoidance distances of common scoter to these smaller vessels and the return times to areas disturbed by these craft.

14.2.7 Helicopters

In the current study, empirical data on the routes and frequency of helicopter traffic to and from oil and gas installations was incorporated into the GIS of Liverpool Bay. The GIS was used to calculate the proportion of the area of each patch that overlapped the presumed 3km wide flight patch of helicopters on each known route. If the percentage of a patch that overlapped the flight path exceeded 50%, that patch was rendered unavailable to common scoter for the entirety of those time steps (i.e. for 1 hour) in which a helicopter was deemed, on a probabilistic basis, to pass through it. Ideally future studies should obtain more precise data on the temporal variation in helicopter activity within each patch to be modelled within the study area. This should be combined with more precise data concerning the avoidance distances of common scoter to helicopters (i.e. the flushing distance). If the resolution of the patches can be made sufficiently fine, each patch could be defined as falling entirely within or outside the area assumed to be affected by a helicopter. This was not possible in the current study because of the resolution of the tidal model and the large geographical area with which the study was concerned.

In addition, more detailed information on the time taken by common scoter to return to an area of sea once a helicopter has passed over it would be valuable. It may be that common scoter take 2 or more hours to return to an area once a helicopter has passed over. In this case the behaviour of birds in the model would need to be adjusted accordingly.

14.2.8 Number of resources

In the current study, the only resources considered were benthic bivalves. This reflects the overwhelming importance of bivalves in all quantitative studies of common scoter diet. It also reflects the fact that within Liverpool Bay there are enormous benthic bivalve resources which, on the basis of the model results, would appear to be sufficient on their own to support the common scoter population (i.e. for the over-winter mortality to be in line with expectations). It may be that in other locations around the coasts of the UK, benthic bivalves will be much scarcer than in Liverpool Bay and that the common scoter that inhabit such areas must, to a certain degree, feed on other resources. Thus, in future studies elsewhere around the UK (and indeed in any future studies within Liverpool Bay) it would be useful to obtain common scoter corpses for analyses of their diet within the study area in question. Whether, this is possible or not, the prey items included within the common scoters' diet need to be identified/ decided upon.

Having identified the prey species to be made available to common scoter in the model, it is necessary to decide upon how these should be categorised as distinct resources in the model. The energetic profitability of a given prey item is influenced by a number of factors including the energy density of its dry flesh and the proportion of the total mass that comprises: i) dry flesh, ii) indigestible inorganic matter and iii) water. All of these have the potential to vary between prey species and between individuals of different sizes within species. In the current study, benthic bivalves of 21 different species were categorised as belonging to one of only three principal prey types: i) elongate bivalves, ii) thin and brittle shelled bivalves and iii) thick and solid shelled bivalves. This categorisation was made for a number of reasons. First, analyses of bivalves from Liverpool Bay showed that the ratio of dry flesh to indigestible shell varied widely between these three prey types. Thus, they differ widely in their profitability to common scoter. Second, for pragmatic reasons it was desirable to minimise the number of separate resources to be used in the model. Third, the distribution of each individual species was very patchy, yet common scoter tend to eat whatever bivalve species is locally abundant. Analyses of bivalves from Liverpool Bay also showed that the ratio of dry flesh to indigestible shell varied widely with size among each of the three prey types. Thus, prey of different sizes differ widely in their profitability to common scoter. Thus, it was necessary in the current study to categorise each prey type into different size classes (6 classes of elongate bivalves and 4 each of thin and thick-shelled bivalves). Thus, in the model there were 14 different resources each of which had a different profitability to common scoter. In any future study, this should probably form the minimum number of categories of bivalve resources. It is therefore necessary to ensure that the numerical density of each size class of each prey type can be derived (see section 14.2.9).

14.2.9 Initial density of each resource on each patch

For each resource that is to be included in the model, a value must be derived for the starting density that is to apply in each patch within the model. In the case of studies dealing with over-wintering populations of birds, surveys should be conducted in August-September in order to estimate the initial resource abundance present at the end of the summer growth period and prior to the arrival of and depletion by large numbers of birds in the autumn.

In the current project resource density was expressed as the numerical density of each bivalve size class and type (n m^{-2}) in each patch. In most previous applications of the model MORPH, resource densities have been expressed in units of biomass density (grams ash-free dry mass or grams of dry mass m^{-2}). The reason for this difference in approach is that the best available functional response for common scoter, which determines their rate of intake as a function of the density of the resources, expressed the density of resources in terms of numerical rather then biomass density. Thus, in future applications of the model MORPH to common scoter it is likely that resource densities will need to continue to be expressed in numerical terms. Nonetheless, information should be gathered (see below) in order to convert numerical to biomass densities.

In the current study an extensive stratified survey of the benthos was conducted that sampled areas of the sea where common scoter had been observed and also areas where common scoter were not observed. For the purposes of the present study, Liverpool Bay was divided into two main areas; the Lancashire coast that extended from just north of Shell Flat to the centre of the entrance to the River Mersey, and the North Wales coast that extended from Red Wharf Bay across to the centre of the entrance of the River Mersey. These two areas held distinct high density aggregations of common scoter. The outer limits of the survey area were set by the reported maximum dive depth for common scoter which is commonly believed to be 20 m. As depth directly affects energy expended on travelling to and from the seabed and while foraging on it, depth bathymetries were calculated at 5 m intervals for both spring and neap tides. When possible, selection of the sample sites coincided with the intersection between these depth bathymetries and the aerial survey flight paths in order to enable a direct analysis of the relationship between common scoter abundance and prey abundance at these sites. Additional survey sites were selected to ensure that the full gradient of depth zones was sampled across Liverpool Bay. Three surveys were undertaken in August (initial survey) and in December 2003 and April 2004 to span a full over-wintering season of common scoter in Liverpool Bay (see below).

This protocol resulted, as intended, in good coverage of the resource densities in each of the principal areas frequented by common scoter within Liverpool Bay. However, it had the drawback that a large number of patches within the study area that are currently little used by birds were not sampled directly at all. Such areas may, however, be of great importance. They represent alternative areas to which common scoter may redistribute if displaced from their current feeding grounds by windfarm developments. It is, therefore, desirable to include all such areas in a model. In order for these patches to be included in the model, the original intention was to use interpolation techniques to estimate resource abundance across the whole study area. However, this proved problematic due the uncertainty generated by an uneven coverage of samples. In future, it would be advisable to employ one of the following two options. First, the number of patches to be modelled within the study area should be decided upon in advance and their boundaries defined. Benthic surveys should then be conducted in order to ensure equal sampling effort in all patches, regardless of common scoter usage patterns. Alternatively, a grid based survey should be designed within the boundaries of the study area in order to ensure an even sampling effort across the whole of the study area, again regardless of common scoter usage patterns. Analysis of this data, perhaps in combination with other environmental variables, might suggest the number and location of patches that differ from one another in terms of the resource base or other environmental characteristics. Each sampling location can then be ascribed to a particular patch. Both of these methods will ensure that empirical data on the birds' food resources are gathered from every patch within the study area. This will avoid the need for interpolation over long distances from the nearest sampling station.

At each sampling station several 0.1 m^2 Day grab samples should be taken (at least two) and the contents sieved using seawater over a 1 mm mesh aboard ship. The contents of the sieve should be fixed in 4% formalin and, after a number of days, washed in freshwater and preserved in IMS.

All macro-invertebrates in each sample should be counted and identified to the lowest necessary level of taxonomic detail (i.e. species level for all except those such as small worms). The maximum length of all individuals of the key species should be measured to the nearest 0.1mm using Vernier callipers. Maximum length of bivalves should be measured along the anterior-posterior margin axis. Maximum width (of bivalves) should be measured by placing the callipers on the umbo and sliding them along the ventral margin until the maximum width is reached. These data yield the numerical density of each mm size class of each of the principal macrozoobenthic species at each sampling station. This finely structured dataset provides the flexibility to combine mm size classes into larger size class categories and to combine species into prey types at a later stage of data processing

For each of the key species a small number of individuals spanning the range of sizes present should also be collected at each sampling station for the purposes of establishing size-mass relationships and the conversion of numerical to biomass densities. Ideally, these specimens should be gathered from an additional grab sample taken at each sampling station specifically for the purpose of obtaining these particular individuals, rather than from the samples taken to measure resource densities. If this is not possible, then these individuals can be removed from the other samples, but clear notes must be made of which individuals came from which sample. Each live specimen should be blotted dry, placed in an individual plastic bag and frozen.

For each of the key species, a total of 50 or more of the frozen individuals should be randomly selected from all the samples in order to establish size-mass relationships. Each individual should be weighed while still frozen to obtain the fresh mass. Each individual should then be thawed in a pre-weighed crucible. Where possible the flesh should be separated from the hard indigestible parts of each animal and the hard parts put in a separate pre-weighed crucible. Both components should be dried to a constant mass at 90°C to yield the dry mass of flesh and indigestible material. Crucibles should then be placed in a muffle furnace set at 550°C for 2 h to determine, by subtraction of the resulting mass of ash, the ash free dry mass content (AFDM) of the flesh and 'shell'. Elongate bivalves (particularly *Pharus*) are quite commonly broken during sampling and only the anterior part may be collected in the samples. For these species, Length-Width relationships should be established from intact individuals using regression analysis in order to calculate the length of broken individuals.

For each species the data relating the dry mass (or ash-free dry mass) of both the flesh and the indigestible 'shell' of an individual to its length should be transformed ($\log_e$) and a regression model fitted to the data. Species-specific regression equations should be derived to predict the dry mass (or ash-free dry mass) of an individual within each size class across the full size range for that species. These values can be used either: i) to provide the values for the density of each component (flesh and 'shell') within each individual belonging to each prey species or ii) to multiply the numerical density of individuals within each size class of each species at each sampling station to yield the biomass density (of flesh and 'shell') of that size class of that species at that station.

The data layout and calculations for these parameters can be found in the spreadsheets provided with the report.

14.2.10 Expression to update each resource density on each patch

Sensitivity analyses of the model output in the current study indicated that predicted mortality of common scoter is sensitive to the values ascribed to the rate at which the abundance of resources changes on a day to day basis due to factors other than predation by common scoter. Thus, a programme of repeat sampling must be undertaken to quantify the seasonal changes in the abundance of each resource. Ideally, the sampling stations at which this regular monitoring is conducted should be located in areas where common scoter do not occur. Although spatial variation in the population processes of prey species may mean that values derived from such locations differ from those where common scoter do occur, data gathered from the latter locations are likely to be heavily influenced by the depletion by the ducks themselves. This duck-driven depletion factor must be excluded from the values derived here as depletion by the birds occurs within the model in any case. Thus, sampling stations at which common scoter seldom or never occur should be identified. Samples should be taken from each of these stations at least three times over the winter (early autumn, mid-winter and spring). On each occasion, several 0.1 m^2 Day grab samples (at least two) should be taken and processed as described above to determine the numerical density of each of the size classes of each prey species. These data should be used to calculate the daily survival rate of each size class of each prey type between each sampling occasion. By collecting data on different size classes of each prey type it is possible to incorporate any growth of animals from lower size classes to higher size classes over the winter (daily survival rates of some size classes may exceed 1). Given the improved flesh:'shell' ratio that accompanies growth in length (at least in the case of bivalves) this growth may be of importance to changes in the overall profitability of the resource base over the course of the winter.

14.2.11 Number of resource components

In the current study, two components within each resource were identified i.e. dry flesh and dry shell. This recognises that common scoter ingest their prey whole. In the case of prey such as bivalves this means that a large fraction of what they ingest is indigestible. The ratio of flesh to shell varies between prey types and between size classes within prey types. Given the patchiness of the distribution of prey species, and indeed of size classes, this has important implications for variation in the nutritional profitability of the resource base available in different patches and hence common scoter distribution. Thus, future applications of the model should also distinguish between the digestible and indigestible components of their diet.

The number of prey items that a bird can consume in a given period of time, if not limited by its ability to find prey, is limited by the capacity of its gut. How many prey items it takes for a bird's gut capacity to be reached depends upon the rate at which its gut processes food, its overall volume and upon the fresh mass of each animal that it consumes. Thus, the water content of a prey item is important in this context rather than the simply the mass of its dried flesh and 'shell'. This is particularly true of soft-bodied prey items. Thus, it would be useful in future applications of the model MORPH to incorporate water as a third resource component.

14.2.12 Density of each component in each resource on each patch

Values for the mass of dry flesh and of dry indigestible material within each individual belonging to each size class of each prey type should be derived as described above (section 14.2.9). An equivalent value for the mass of water contained within each individual should be obtained by subtracting the sum of the dry masses of flesh and 'shell' of each individual (i.e. those processed for the purposes of biomass determination as described under section 14.2.9) from their fresh mass. These values can then be transformed and regressed against length (as described in section 14.2.9) to yield water content – length relationships for each prey type. These relationships can then be used to predict the water content of individuals belonging to each size class of each prey type.

It is possible that the make up of the various components within individuals belonging to different size classes of different prey types changes seasonally. Thus, samples from repeat monitoring stations (section 14.2.10) should be processed to yield data on any seasonal changes in the predicted dry flesh, dry 'shell'; and water content of each size class of each prey type.

In studies of the interaction between diving ducks and their prey *Dreissena polymorpha* in Lake Ijsselmeer, de Leeuw (1997g) noted that mussels from deeper water tended to have lower flesh contents (up to 40%) than those in shallower water. This was a major factor influencing the profitability of feeding in deeper water in this system and hence the distribution of the ducks. Thus, in future studies it would be useful if data concerning the seasonal variation in the dry flesh, dry 'shell' and water content of each resource could be obtained from monitoring stations that lie in different depths of water within the study area.

14.3 Existing Forager parameters

14.3.1 Number of forager types

In the current study only one type of forager was modelled. The only source of variation between individuals lay in their dominance (and hence the order in which they were processed in the model) and in their feeding efficiency. In reality, these characteristics are likely to differ systematically between birds of different ages and sexes. This has the consequence that sub dominance and poor foraging ability may be typical of one particular subset of birds within the population e.g. juvenile females. If so, any adverse effects of environmental change that either reduces the extent or the quality of habitat available to the birds may fall predominantly on one sex/ cohort. This may have more serious implications for population dynamics than an elevated mortality that affects all types of birds equally. However, until quantitative empirical data concerning the magnitude of the differences in the dominance or feeding efficiency of different types of common scoter becomes available there is no possibility of considering more than one type of forager within the common scoter population.

14.3.2 Number of foragers in each forager type

The seasonal variation in the number of common scoter within the study area needs to be defined in the model. Thus, regular counts of the number of common scoter within the study area should be made. These data should be analysed to yield the peak population size and the seasonal variation in population size. The latter can be used to control the arrival and departure days of each bird in the model in order to generate the observed seasonal pattern in population size within the study area.

14.3.3 Maximum common scoter density

Many studies of benthic-feeding diving ducks suggest that interference competition may occur in these systems (appendix 8). However, there is as yet very little quantitative data on the strength of this interference or of the extent to which susceptibility to interference differs between individuals of differing social status. Given that the effects of interference (a reduction in instantaneous intake rate with increasing competitor density) typically only become manifest once the density of competitors exceeds some threshold value (see section 7.2.7) a maximum density of common scoter was used in the current study to limit the number of birds that could occupy a given patch, and to exclude socially sub-dominant individuals from such favoured places. Until such time as empirical work is conducted to find direct evidence of interference amongst foraging common scoter and to quantify its magnitude, the current approach, which is based on the observed distribution of common scoter in the field, is the simplest way of ensuring that common scoter do not all aggregate in the best patches in the model. Thus, when common scoter are counted in the study area, the distribution of each bird or flock should be recorded precisely. This distribution data should then be combined, within a GIS framework, with the boundaries of the patches to be included in the model in order to calculate the maximum recorded density of common scoter in any patch on any survey date. This value can then be used as an upper limit to the density of common scoter in the model. Accurate data on the variation in the number of ducks between patches within the study area can also be used to validate the model's predictions of duck distribution under current conditions.

14.3.4 Number of diets

In the current study, all bivalve resources were combined into a single diet. Birds were assumed not to choose between feeding on different size classes of different prey types but to ingest each in proportion to its availability in a given patch. Patches differed in their suitability as foraging habitat due to variation in the relative proportions of the bivalve community that comprised the different resources. The assumption that common scoter are non-selective was based on uncertainty in the literature as to whether common scoter select for different size classes of bivalves. Furthermore, if each of the 14 resources was treated as a separate diet, the numerical densities for many diets would have been so low that the achievable intake rate from those diets would also have been very low (based on the functional response). However, in other situations in which common scoter may also feed on prey other than bivalves it would probably be unwise to amalgamate bivalve and non-bivalve prey into a single diet. Rather, it will probably be necessary to include one or more non-bivalve diets e.g. worms, crustaceans, echinoderms. It would then be necessary to determine whether each of these could be considered to consist of a single prey type or whether, as in the case of bivalves, variation in the digestible: indigestible ratio between species and size classes necessitates division into two or more resources (see section 14.2.8).

14.4 Factors not included in the current model

14.4.1 Current speeds

It was not possible in the current project to derive predictions for the hour-by-hour variation in current speed in each tidal grid cell across the whole of the study area. Current speeds may affect the rate at which common scoter expend energy while foraging in that they must swim against a current in order to remain over a given foraging location. Empirical data suggests that once the current speed exceeds some threshold value (approximately 0.4 ms^{-1}); the energetic cost of swimming against it rises rapidly. There may also be an upper current speed against which ducks cannot maintain their position at all. Thus, fine scale temporal and spatial variation in current speed may influence the energetics of foraging and the distribution of birds. The effects of current speed on duck energetics can be incorporated in a future version of MORPH. Thus, in any future studies it would be desirable to record, or otherwise predict, using a tidal model, the hour-by-hour variation in current speeds within each patch to be included in the modelled area.

14.4.2 Windfarm maintenance traffic

The construction and presence of offshore windfarms in shallow coastal waters have the potential to affect over-wintering common common scoter populations in a number of different ways. These were discussed in sections 8.3 and 11.8.4.. In this report we have been concerned solely with one of these - the consequences of habitat loss due to the avoidance of man made structures i.e. the windfarms themselves. Thus, the current version of the model MORPH has not incorporated the possibility of an increased mortality due to the collision of ducks with the turbines. The model has also not incorporated the consequences of the fact that birds seem to alter their flight paths to avoid windfarms and so may incur increased flight costs due to the need to take circuitous routes around windfarms. It proved impossible to gather data on the frequency and routes of maintenance traffic associated with each windfarm and so the possible adverse effects of this source of disturbance on birds' feeding opportunities and daily energy expenditure have not been addressed. Finally, the model has not addressed the issue of the consequences of the construction of the windfarms and associated underwater cabling on the seabed and benthic communities. Thus, there are a number of possible mechanisms by which the construction, presence and servicing of offshore windfarms could have adverse effects on common scoter that have not been included in the predictions made here. Ideally, all possible mechanisms should be included in any future modelling work. All of these factors could be incorporated in future versions of the model MORPH. However, the most important of these factors is probably the frequency and routes of maintenance traffic associated with each windfarm in a study area. This is probably also the easiest of the four factors on which to obtain quantitative data. Thus, the routes to be taken by maintenance traffic to and from each windfarm within a study area should be defined as should the frequency with which traffic will pass along these routes. In addition, information should be gathered concerning the avoidance distance (i.e. flush distance) of common scoter from maintenance traffic and the time that they take to return to an area of sea from which they are disturbed by such traffic. This information will enable the possible adverse effects of maintenance traffic on common scoter to be included in any future modelling work.

15. References

Section 1

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Section 2

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Section 9 - none

Section 10

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Section 14

De Leeuw, J. (1997(g)). Wintering Tufted Ducks *Aythya fuligula* diving for Zebra Mussels *Dreissena polymorpha* balance feeding costs within narrow margins of their energy budget. In: Demanding divers. Ecological energetics of food exploitation by diving ducks (de Leeuw J.). Wiskunde en Natuurwetenschappen. Groningen, Rijksuniversiteit Groningen: 109-124.

16. Running the MORPH model

CONTENTS OF DISK

This disk contains all of the files necessary to use the model MORPH to simulate two scenarios presented in the report (i.e. scenarios 1 and 10). You will need a fast PC to run the model. You will also need to create a folder **c:\scotermodeloutput** on the PC in order to store the results files. The two scenario parameter files are set up to: i) use 1000 super-individuals, ii) visually display the results of only a set of selected patches and iii) enter data in the output results files only on the last day of the model run. These options can be altered within each of the two parameter files (scenario1.par and scenario10.par) if desired.

This disk contains the following folders and files:

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Top-level directory

File name:

Morph.exe
This is the executable model code.

UCALC32.dll
This file is a dynamic link library file necessary for model calculations to be performed.

Batch.exe
Double click on this icon to call up a list of files in this directory. This list will include the files *scenario1.run* and *scenario10.run*. Double click on either of these file names to activate a run of scenario 1 or 10 respectively.

Scenario1.run
Double clicking this filename (after activating *Batch.exe*) will set a run of scenario 1 going, opening all the relevant input and output files.

Scenario10.run
Double clicking this filename (after activating *Batch.exe*) will set a run of scenario 10 going, opening all the relevant input and output files.

Folder name: Parameters:

File name:

Scenario1.par
Is a version of the parameter file set up to simulate the existence of the North Hoyle windfarm (i.e. current conditions)

Scenario10.par
Is a version of the parameter file set up to simulate the existence of all 5 windfarms within Liverpool Bay and assuming a 2km buffer zone around each one.

ScoterWatertemp.var
Contains a list of interpolated sea water temperatures on an hour by hour basis from 1st August until 31st May.

Scoter.bmp
Contains an image that acts as the background map of the coastline in the model graphic display.

Folder name: Results

By default the two model runs will write their results to a folder called:

c:\scotermodeloutput.

You will need to create this folder on your PC before running either scenario.run file.

You could copy the results files from there back to this empty results folder on the disk to keep everything together.

Folder Name: Appendices

File name:

Appendices1-20.xls
Contains all of the 20 appendices referred to in section 7 of the final report

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* **Following what is going on while model is running**

The continually changing distribution of birds in space can be seen by observing the map image on the left hand side of the screen. The colour codes for each of the cells are described in the legends to various figures in this report. While the model is running you can use the buttons at the lower right corner of the screen to change the speed with which it runs and also pause, resume and quit the simulation at any time.

At the top of the right side of the screen are a number of tabs labelled: Variables, Resources, Foragers, Details and Parameters. By clicking on the tab headers you can bring up the information on each.

The **Variables tab** displays the continually changing values of the global variables and of the patch variables on a select number of grid cells.

The **Resources tab** displays the changing abundance of each of the 14 resources available on several selected grid cells.

The **Foragers tab** displays the continually changing number of foragers that are: yet to immigrate into the system, present and alive in the system, already emigrated from the system, died from starvation or disturbance effects and the total number dead. The numbers of foragers present on several selected patches are also displayed.

The **Details tab** reveals a number of tables. Global variables are displayed in the top table. Patch variables for all patches are displayed in the second table. Values relating to resource densities in all patches are displayed in the third table. Aggregated values relating to the diets in all patches are displayed in the fourth table. The details concerning each forager are displayed in the fifth table.

It is possible to navigate around all but the first table using the scroll bars at the bottom and side of each.

With the model paused, it is possible to double click on any of the dots representing super-individuals in the image. The dot for this individual will then be enlarged and its details highlighted in the Forager table on the **Details tab**. With the model resumed again the changing location and details of this super-individual can be tracked.

With the model paused it is also possible to double-click on any of the column headings in any of the tables on the **Details tab** and to sort records in either ascending or descending order.

The **Parameters tab** displays the contents of the parameter file used to run the simulation in which every value of every parameter used can be found.

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Calculating common scoter mortality during a simulation

The mortality of scoter during a simulation can be tracked as the model is running by viewing the screen display and clicking on the *Foragers* tab at the top of the screen to activate the page displaying Forager details. Here, there is a bar labelled *Starvation* which gives the cumulative number of birds that have died from starvation as the model runs. Mortality can also be calculated from data stored in the model output files rather than watching the screen until the model has finished running.

The output files that the model generates are as follows: Diet.xxx, Forager.xxx, Global.xxx, Log.xxx, Patch.xxx, Resource.xxx

For the purposes of calculating the % overwinter mortality at the end of a run, the file Forager.xxx is the only one that is necessary. This output file should be opened in a text editor. Each column has a heading and each row represents the information pertaining to one particular super individual at a particular point in time. For calculating total over-winter mortality, the time of interest is the last hour of the last day of the model run. This is when the variable TimeStep reaches its maximum value. Thus, first, the header row should be cut and pasted out to a package such as Excel. Then, all the rows at the foot of the file where TimeStep is at its maximum value (n=1000 rows when the model is run with 1000 super-individuals) should be cut and pasted out as well. The % overwinter mortality can then be calculated in Excel as:

100 * (Sum column (Starvation) / Sum columns (Immig, Present, Starvation, Disturbance and Emig))

17. Appendices

The entries under the heading ‘Source’ in each appendix refer to the publication from which the information in the other columns is derived. The full details of each source can be found by consulting the lists of publications under the headings of ‘References’ and ‘Other studies consulted during literature review’ which are given at the end of section 7. Entries under the heading ‘Comment’ are usually notes taken directly from the text of the source publication, although some may have been modified slightly for brevity or have additional explanatory notes.

Appendix 1 Notes concerning the foraging behaviour of diving ducks

record	source	species	season	parameter	comments
40	Degraer et al 1999	common scoter		habitat	possibly a combination of food availability and the lack of disturbance, by fishing activities for instance, determines their spatial distribution
49	Fox 2003	scoter spp		habitat	there is more to habitat selection than just benthic community and sediment type
60	Brager et al 1995	common eider		habitat	decrease in numbers in late winter due to abandonment of shallow reef areas with previously high densities of mussels
62	Brager et al 1995	common eider		foraging efficiency	for immature seaducks this might mean that their diving abilities are not yet fully developed to compete with the adults for food in deeper water. Eiders less able to compete successfully were probably seeking the (coastal) habitat offering a stable but less profitable intake (than offshore) to improve their survival probability. This could be compared to the results of Guillemette et al 1992 who found that individual eider feeding in small flocks were in bad condition compared to individuals feeding in large flocks.
70	Kirby et al 1993	common scoter		movements	No regular dawn or dusk movements have been described and it is presumed that they remain to roost in or close to their daytime feeding areas
71	Kirby et al 1993	common scoter		movements	At least some flocks appear to remain faithful to the same areas throughout the winter; even in the Moray Firth where there are at least three alternative sites in close proximity, there has been NO EVIDENCE of any regular interchange
93	Lovvorn & Gillingham 1996			habitat	detailed mapping of benthic foods on a scale relevant to the foraging energetics of highly mobile birds is currently not feasible, despite the importance of food dispersion to their foraging profitability and sustainable population levels.
96	Lovvorn & Gillingham 1996	canvasbacks		habitat choice	waterfowl in the field did not find high density loci and deplete them disproportionately, but appeared to feed in all loci encountered with profitable food densities
104	Giles 1990	tufted duck(lings)		foraging behaviour	it seems likely that both diving ducklings and adult diving ducks can respond rapidly to changes in the benthic invert food supply by concentrating their foraging over areas of the highest habitat quality
115	Mori & Boyd 2004	fur seal		numerical response	fur seals were able to adjust their behaviour to track highly variable prey distributions and densities
116	Mori & Boyd 2004	fur seal		foraging behaviour	diving time budgets were consistent with the hypothesis of rate maximisation of energy intake during dives
121	Mori & Boyd 2004	fur seal		foraging behaviour	it appears that rate maximisation operates at all scales and leads to a set of behaviours that can result in the maximisation of fitness across a wide range of environmental variability.
172	Tome 1988	ruddy ducks		foraging behaviour	these results provide quantitative support for the prediction that ruddy ducks maximise their rate of net energy intake while foraging.
177	Phillips 1991	pochard		habitat choice	pochard prefer to feed in shallow water and can select prey rich areas, thus maximising their food intake whilst minimising their energy expenditure
178	Phillips 1991	pochard		habitat choice	the feeding areas were significantly shallower than the unused areas
179	Phillips 1991	pochard		habitat choice	both the numbers and dry weights of larval chironomids were, however, found to be significantly higher in the preferred feeding areas than in the rest of the lake.
180	Phillips 1991	pochard		habitat choice	the birds were selecting feeding habitat within the favoured depth range
181	Phillips 1991	pochard		habitat choice	chironomid numbers in the areas where pochard were feeding were significantly greater than in the rest of the Main lake. The mean numbers of larvae per sample in the feeding area was 61.3 compared to 47.2 in the unused areas ie a 17% difference was detected

183	Meissner & Brager 1990	common scoter		distribution	it has been proposed that their distribution in the Keil Bay primarily depends upon the depth of water and the zonation of the macrofauna
188	Pedroli 1982	tufted ducks	winter	distribution	…which are the main feeding and resting areas of the ducks because of the high density of Dreissena.
198	Giles 1989	tufted duck(lings)	captive	habitat choice	…demonstrates the ability of very young birds to locate and exploit small food patches within a novel environment over the course of a relatively few experimental replicates
231	Stott & Olson 1973	scoter		habitat	These highly productive bivalve areas concentrated scoter from September to May
272	Carbone & Houston 1994	pochard	captive	habitat preferences	when offered two options the birds changed their mean preference from a patch with higher food density to one with a lower food density as the depth of the higher density patch was increased. However, they switched their preference earlier than expected based on estimates of the net rates of gain. This suggests that FACTORS OTHER THAN ENERGETICS INFLUENCE THE CHOICE OF FORAGING AREAS. it is possible that there are certain risks involved in diving at greater depths which offset the otherwise greater energetic profitability of deeper patches in the expts.
351	Guillemette et al 1996	common eider	winter	numerical response	distribution closely coincides with locations where prey densities are highest
355	Guillemette et al 1996	common eider		numerical response	cumulative utilisation of most reefs was proportional to their surface area. This suggests that eiders tend to deplete each patch equally during the winter.
373	de leeuw 1997b	tufted duck/pochard	winter	giving up densities	diving ducks apparently adjust their foraging effort at the level of patches with respect to the relative benefit of the patch in relation to that of the environment generally,.
374	de leeuw 1997b	tufted duck/pochard	winter	patch use	we showed underuse of some rich patches. This is probably due to imperfect knowledge of the environment (night time foraging underwater).
375	de leeuw 1997b	tufted duck/pochard	winter	patch use	The choice of a certain foraging area by a flock of several thousand birds is probably influenced by the average quality of the site rather than by peak densities which only a limited number of birds will experience in a patchy envt.
376	de leeuw 1997b	tufted duck/pochard	winter	giving up densities	The giving up density is likely to be determined by the average food density of the site (several km2) and local food QUALITY. In such a system, the relatively scarce rich patches will be underexploited.
377	de leeuw 1997b	tufted duck/pochard	winter	patch use	patch exploitation by individual birds is subservient to the flock's attendance to a site.
378	de leeuw 1997b	tufted duck/pochard	winter	patch use	the results indicate that the ducks are not only able to recognise and to respond to differences in mussel density, but also to different quality over short distances
380	de leeuw 1997b	tufted duck/pochard	winter	patch use	diving ducks seem to choose their foraging and roosting sites from the perspective of MINIMISATION OF ENERGY COSTS FOR TRANSPORT (SHORT FLIGHT TRACKS AND COSTS FOR EXTRA LOCOMOTION AT THE ROOST.. Secondly, individual decisions are made with respect to the exploitation at the level of patches and sites WITHIN A REGION. These decisions are apparently taken from the perspective of MAXIMISATION OF ENERGY INTAKE.
388	de leeuw 1997b	diving ducks		patch use	areas with highly profitable mussels received more attention from the ducks, which could be ascertained at various levels of scale: lake, region, site and patch,. Size selection only operated at shallow depths indicating a time constraint on the ducks set by water depth.
433	de leeuw 1997i	diving ducks		food density	the fine grain or first order patchiness of the food supply as perceived by the ducks could not be exactly assessed because bottom samples with a VV grab (0.04 sq m) cover a much smaller area than a diving duck can scan in a single dive. (at least 1 sq m). therefore diving ducks may perceive a more homogeneous distribution of mussels than expected from the variation in bottom samples. Hence considering larger scale variation at the level of patches is more appropriate for diving ducks.

441	de leeuw 1997i	scaup		numerical response	In lake Ijsselmeer the number of scaup bird days in a 2x2km grid cell correlated best with biomass in those grid dells where the probability of encountering mussels was at least 70% (ie >=7 out of 10 grab samples contained mussels). If cells with lower probabilities were included, the relationship between bird days and cell biomass becomes weaker. Similarly, the number of scaup correlated well with the number of grid cells within an area that meet the profitability criteria of sufficiently high biomass (ie above the threshold denity of 50gfw/sqm) and shallow depths
445	de leeuw 1997i	tufted ducks/scaup		patch quality	Also, the probability of finding food (ie its patchiness as opposed to fine scale density) both at the level of patches and of larger units of profitable area for feeding flocks seems an important criterion for habitat selection. Sampling programs of patchiness at levels relevant to diving ducks linked to field measurements of foraging effort and habitat use of indiv birds could further enhance our understanding of where and how diving ducks can forage profitably

Appendix 2 Notes concerning the amount of time spent in various phases of the dive cycle

record	source	species	parameter	comment
62	Carbone 1995	pochard	foraging time (on bottom)	increases with water depth until it approaches a maximum asymptote in deeper water
63	Carbone 1995	pochard & tufted duck	proportion of time spent feeding over the dive cycle (including surface time)	decreases with increasing water depth in two datasets (due to increases travel time ascent and descent) and increased time spent on surface recovering
104	Bevan et al 1992	tufted ducks	dive duration	the dive durations of tufted ducks are proportional to the depth of the water.
114	Mori & Boyd 2004	fur seal	foraging time (on bottom)	time spent at the bottom of dives was used as an indicator of patch quality and was well correlated (p=0.045 n=5) with independent measures of prey abundance.
147	Stephenson et al 1986	tufted duck	dive duration (s)	linearly correlated with dive depth
152	Stephenson et al 1986	tufted duck	surface time	was not correlated with duration or with distance of the previous or following dive. Pause duration was very variable and appeared to depend very much on factors other than dive durations or feeding time on the bottom.
153	Stephenson et al 1986	tufted duck	dive durations (s)	mean 19.8 secs
154	Stephenson et al 1986	tufted duck	dive durations	during normal feeding dives the ducks probably remain fully aerobic and in this case feeding time on the bottom may be influenced by a number of other factors such as food density, particle selection time and handling time and or by the rate of food ingestion (as opposed to physiological factors such as changes in blood gas levels or acid-base disturbances that may be involved in terminating feeding in (artificially) extended dives)
161	Nilsson 1972	scoter	dive:pause ratios	in shallow water
186	Reynolds 1987	long-tailed duck	dive duration	male dive times were significantly longer than those of females. This may be a consequence of physiological differences in diving ability. The latter has been shown to be very closely linked to body size in vertebrates.
187	Reynolds 1987	long-tailed duck	dive duration	Site related variations in the abundance and availability of potential prey items may also be of importance in determining dive durations
204	kramer 1988		dive duration	frequently increase with depth. The depth-time relationship in diving birds was noted by Dewar (1924)
205	kramer 1988		surface time	surface times also increase with diving depth in a number of species as predicted. Species in which surface times show a positive relationship to diving depth include many diving birds studied by Dewar 1924, cormorants and tufted ducks
262	de Leeuw 1997d	tufted duck	surface time	increases roughly in proportion with depth up to 3.5m and thereafter increases more rapidly. Such trends have been used to indicate a decline in aerobic efficiency and a reliance on anaerobic respiration.
264	de Leeuw 1997d	tufted duck	surface time	surface time should increase with increasing underwater costs for all depths
276	Carbone & Houston 1994	pochard	foraging time (on bottom)	neither foraging time nor surface time was significantly affected by the density of food

277	Carbone & Houston 1994	pochard	foraging time (on bottom)	a novel prediction of the models is that foraging time (on the bottom) first increases and then decreases with increasing water depth. Initially as the water depth increases, the travel time increases and so the diver increases the size of its O2 stores to allow for more foraging time, in order to reduce the number of trips between the surface and the foraging site. As depth increases further and the diver approaches its max dive duration, foraging time must decrease to compensate for increasing travel time.
278	Carbone & Houston 1994	pochard	dive duration	increased significantly with depth
279	Carbone & Houston 1994	pochard	travel time	increased significantly with depth
280	Carbone & Houston 1994	pochard	foraging time (on bottom)	did not significantly change with increasing food concentration. So, scarcity of food did not necessitate longer time periods on the bottom even though the rate of feeding on the bottom was c three times lower at the low food density
281	Carbone & Houston 1994	pochard	foraging time (on bottom)	increasing sand depth significantly reduced time on the bottom
290	Carbone et al 1996	tufted duck/pochard	surface time	Interdive intervals up to 35secs may be considered to be within a bout. If > 35secs then this equals the end of a foraging bout.
292	Carbone et al 1996	tufted duck/pochard	foraging time (on bottom)	Mean foraging time was also highly correlated with water depth in both spp- but both significantly non-linear (tended to level off at c 3m)
293	Carbone et al 1996	tufted duck/pochard	surface time	in both spp were highly correlated with water depth and significantly non-linear, kicking up at 3.5-4m. This kick may indicate a decline in aerobic efficiency and a reliance on anaerobic respiration.
296	Carbone et al 1996	tufted duck	foraging time (on bottom)	tufties significantly reduced the time spent foraging in response to increasing sand depth. Consumption rates declined significantly as sand depth increased
298	Carbone et al 1996	tufted duck/pochard	surface time	increased significantly in response to decreasing water temperatures.
304	Carbone et al 1996	tufted duck	foraging time (on bottom)	Sand depth of the prey had a strong affect on rates of mealworm consumption. However, rates of consumption did not, however, affect foraging times in the pochard (Carbone & Houston 1994) nor did intake rates have a significant effect on the predicted foraging times (in the model of Houston & Carbone 1992).
310	Beauchamp et al 1992	common eider	dive duration	total dive duration and bottom time increase with depth. The fact that bottom time increases with depth can be readily explained by the MVT. As divers forage deeper, time spent travelling and energy cost increase. Consequently, the expected foraging gain that follows the end of a dive decreases with increasing depth. Animals must therefore increase time spent foraging with increasing depth in order to maximise expected foraging gain over the complete feeding bout.
341	Draulans 1982	tufted duck	dive duration	significantly affected by both prey density (declines up to 944mussels/sq m and then increase again (due to increasing selectivity? Above 1000 per sq m) and diving depth (increased up to 4m depth and then levelled off)
380	Guillemette et al 1992	spider crabs	dive duration	crab feeding bouts also had the longest dive durations. This was expected as crabs were sparsely scattered on the bottom. Searching effort was probably an important part of diving time when feeding on crabs. In contrast, diving duration was the shortest when feeding on urchins. This was not surprising given that urchins were ubiquitous in the sub tidal zone (90 per sq m) .**Thus in these cases low prey density leads to longer bottom times as birds have to search for longer to find prey. However, the longer duration of dives for mussels compared to those for urchins was because a high number of prey was collected during each dive , whereas only a single urchin could be captured per dive.**

391	de Leeuw 1997b	tufted ducks	foraging time (on bottom)	time spent foraging at the bottom increased with diving depth
392	de Leeuw 1997b	tufted ducks	foraging time (on bottom)	Wilson & Wilson (1988) regard diving birds as central place foragers and predicted that they should increase their foraging time under water at greater depths in order to use their dive time most efficiently. We suggest therefore that selectivity for small size classes increased with diving depth because in deeper dives more time was spent in taking small mussels in a run before a large one was picked up at the end.
393	de Leeuw 1997d	tufted ducks	foraging time (on bottom)	we assume that divers aim to maximise the proportion of time of the dive cycle devoted to foraging (as opposed to return travel time and surface recovery time).
394	de Leeuw 1997d	tufted ducks/pochard	travel time	strongly linearly correlated with water depth suggesting rates of travel approx constant
395	de Leeuw 1997d	tufted ducks/pochard	foraging time (on bottom)	highly positively correlated with water depth - spend longer on bottom in deeper water up to 6m. However, correlations were non-linear in both spp. Third order polynomials best fit in both cases ie bottom time levels off at greater depths with minor oscillations.
396	de Leeuw 1997d	tufted ducks/pochard	surface time	highly positively correlated with water depth - and significantly non-linear in both cases with a third order polynomial giving best fit initial increase then level off then another increase
397	de Leeuw 1997d	tufted ducks/pochard	foraging time (on bottom)	significant decline in the PROPORTION of dive cycle spent on bottom foraging with increasing water depth
398	de Leeuw 1997d	tufted ducks	foraging time (on bottom)	tufties significantly reduced the time spent foraging on bottom in response to increasing sand depth in which prey buried
399	de Leeuw 1997d	tufted ducks	surface time	surface time increased significantly in response to decreasing water temperature (except in the shallowest dives)
400	de Leeuw 1997f	tufted ducks	descent time	increased with diving depth (1.5m-5.5m)
401	de Leeuw 1997f	tufted ducks	foraging time (on bottom)	increased with diving depth (1.5m-5.5m)
403	de Leeuw 1997f	tufted ducks	surface time	increased with diving depth (1.5m-5.5m)
404	de Leeuw 1997f	tufted ducks	recovery time (mins)	increased with diving depth (1.5m-5.5m)
410	de Leeuw 1997f	tufted ducks	recovery time (mins)	increased with bout dive duration and its square term after backward deletion of depth and depth sq
411	de Leeuw 1997f	tufted ducks	recovery time (mins)	most diving ducks do indeed prefer to rest during the day time hours at sheltered areas. From an energetic point of view, resting periods thus seem to be of great importance in order to balance the energy budget (when cooled body temperatures can be recovered)
453	Guillemette et al 1992	common eider	dive duration	prey density also influences the duration of dive cycles. For example, when prey density is high, as when eiders feed in kelp beds and urchin barrens, dive duration is low compared to when eiders feed on the scattered crabs in the agarum beds. Similarly, Draulans 1982 and Tome 1988 demonstrate experimentally that diving duration in benthic diving ducks increases as prey density decreases - SEARCHING TIME REQUIRED

Appendix 3 Notes concerning the speed of swimming while underwater

record	source	species	parameter	ascent/ descent	min	value	max	comments
61	Carbone 1995	pochard	travel speed	both		0.88		travel time increases linearly with water depth, suggesting that travel speeds are constant. This constancy appears to be a reasonable assumption under most conditions. Observed changes in travel speed are small and probably only cause slight error in the estimates of travel time.
87	Stephenson 1994	lesser scaup	travel speed	descent		0.63		in descent
148	Stephenson et al 1986	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.57		
149	Stephenson et al 1986	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		0.61		
191	Lovvorn & Jones 1991	lesser scaup	diving speed (m/sec) (descent)	descent		0.67		
192	Lovvorn & Jones 1991	lesser scaup	diving speed (m/sec) (ascent)	ascent		0.69		
248	Lovvorn et al 1991	canvasback	speed of descent (m/sec)	descent		0.93		
249	Lovvorn et al 1991	redhead	speed of descent (m/sec)	descent		0.91		
250	Lovvorn et al 1991	lesser scaup	speed of descent (m/sec)	descent		0.68		
251	de Leeuw 1997d	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.748		upper part of dive in 3.3m of water
252	de Leeuw 1997d	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.69		lower part of dive in 3.3m of water
253	de Leeuw 1997d	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.782		upper part of dive in 5.5m of water
254	de Leeuw 1997d	tufted duck	swimming speed (vertical descent) (m/s)	descent		0.694		lower part of dive in 5.5m of water
255	de Leeuw 1997d	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		1.67		upper part of dive in 3.3m of water
256	de Leeuw 1997d	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		0.822		lower part of dive in 3.3m of water
257	de Leeuw 1997d	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		1.16		upper part of dive in 5.5m of water
258	de Leeuw 1997d	tufted duck	swimming speed (vertical ascent) (m/s)	ascent		0.94		lower part of dive in 5.5m of water
266	Guillemette 1998	common eider	speed of descent (m/sec)	descent		0.952		
273	Carbone & Houston 1994	pochard	diving speed					durations of descent and ascent were linearly related with depth suggesting that both stages of travel were at a constant speed
274	Carbone & Houston 1994	pochard	diving speed (m/sec)	both		0.476		at depth of 0.5m, this is the average of ascent and descent speeds
275	Carbone & Houston 1994	pochard	diving speed (m/sec)	both		0.79		at depth of 3.0m, this is the average of ascent and descent speeds

279	Carbone & Houston 1994	pochard	travel time					increased significantly with depth
291	Carbone et al 1996	tufted duck/pochard	travel speed average over up and down (m/sec)	both		1.31		changes in return travel time with depth were strongly linear suggesting that rates of travel were approx constant.
297	Carbone et al 1996	tufted duck/pochard	ascent duration					birds ascend more rapidly when the water is colder.
299	Carbone et al 1996	tufted duck/pochard	descent speeds					significantly faster at the surface near the start of a dive then deeper later in a dive.
300	Carbone et al 1996	tufted duck/pochard	ascent speeds					significantly faster at the surface near the end of a dive then deeper earlier in the ascent.
309	Beauchamp et al 1992	common eider	descent speeds					assumed here that the speed at which an eider travels to and from the bottom is constant
311	Beauchamp et al 1992	cormorant	descent speeds					travel speed at the bottom increases with depth ie birds descend faster the deeper they go
358	Hawkins et al 2000	common eider	descent method					beating still partly folded wings AND stroking with the feet which beat simultaneously.
359	Hawkins et al 2000	common eider	ascent method					entirely passive- the duck stopped beating her wings and feet and floated to the surface.
383	Lovvorn et al 1991	canvasback	swimming speed of descent (m/sec)	descent		0.93		
384	Guillemette 1998	common eider	swimming speed of descent (m/sec)	descent		0.952		
385	Lovvorn et al 1991	lesser scaup	swimming speed of descent (m/sec)	descent		0.68		
386	Lovvorn et al 1991	redhead	swimming speed of descent (m/sec)	descent		0.91		
394	de Leeuw 1997d	tufted ducks/pochard	travel time (to and from bottom)					strongly linearly correlated with water depth suggesting rates of travel approx constant
400	de Leeuw 1997f	tufted ducks	descent time					increased with diving depth (1.5m-5.5m)
402	de Leeuw 1997f	tufted ducks	ascent time					increased with diving depth (1.5m-5.5m)
405	de Leeuw 1997f	tufted ducks	diving speeds (descent) m/s	descent		0.66		did not vary between depths
406	de Leeuw 1997f	tufted ducks	diving speeds (ascent) m/s	ascent	0.65		1	increased with water depth

Appendix 4 Notes concerning the daytime and nightime feeding activity of diving ducks

record	source	species	season	parameter	value	comments
5	Cramp & Simmons 1977	common scoter		day/night	day	mainly a daytime feeder often in closely grouped flocks with regular massed dives
13	Cramp & Simmons 1977	common scoter		day/night	day	mainly diurnal feeder so roosts nocturnally as well as loafing periodically during day
20	Cramp & Simmons 1977	velvet scoter		day/night	day	normally daytime feeder, often gregarious with synchronised diving
25	Cramp & Simmons 1977	velvet scoter	all year	day/night	day	at all times, essentially diurnal feeder, roosting nocturnally with periods of loafing during day.
30	Durinck et al 1993	common scoter		day/night	night?	birds caught in bottom set nets laid out overnight
72	Kirby et al 1993	velvet scoter	winter	day/night	day	
189	Pedroli 1982	tufted ducks	winter	day/night	night	during the night the birds have their diving activity. Between 30% and 50% of the night time was devoted to diving (cf daytime when feeding occurred only seldom
191	Pedroli 1982		winter	day/night	night	Nilsson (1970 thesis) in Sweden concluded that tufties, pochard and greater scaup had a nocturnal feeding activity.
192	Pedroli 1982		winter	day/night	night	most species of diving ducks feed during the night and rest during the day. In the great number of cases nocturnal feeding was attributed to human disturbance on feeding grounds during the day, mostly near the shore
194	Draulans 1987	tufted duck		day/night	night	nocturnal tactile feeders
195	Draulans 1987	pochard		day/night	night	nocturnal tactile feeders
207	Systad et al 2000	seaducks		day/night	diurnal	
219	Goudie & Ankney 1986	common scoter		day/night	day	
232	Systad & Bustnes 2001	stellers eider		day/night	mostly day	most likely to feed during daylight and twilight, but they also fed during darkness
235	Systad & Bustnes 2001	seaducks		day/night	mainly diurnal	night feeding is thought to be rare amongst sea ducks ALTHOUGH THE EVIDENCE IS POOR
236	Systad & Bustnes 2001	common eider		day/night	DAY	NO NIGHT FEEDING AMONG COMMON EIDERS
264	Guillemette 1998	common eider		day/night	day BUT	although some authors have stated that eiders and sea ducks in general are diurnal birds, NONE HAS PRESENTED EVIDENCE TO SUPPORT THIS
265	Guillemette 1998	common eider	winter	day/night	day	THUS IT MAY BE CONSIDERED THAT COMMON EIDERS IN WINTER FORAGE MOSTLY DURING THE DAY AND THAT NIGHT FORAGING IF ANY IS RARE.
270	Guillemette 1998	common eider		day night		night feeding is related to the digestion constraint and ingestion of a large bulk of shell material associated with eating large molluscs
424	de Leeuw 1997h	diving ducks		day/night	night	in the wild, diving ducks usually feed at night and rest during the day.

Appendix 5 Notes concerning the depletion of resources by diving ducks

record	source	species	season	parameter	min	value	max	comments
120	Mori & Boyd 2004	fur seal		depletion				we found that the index of patch quality declined during a bout, suggesting that there was a resource depletion during foragaing.
144	Guillemette & Larsen 2002	common eider		depletion	40%		70%	eiders may deplete their food substantially (40-70%) during the winter and may track food over large spatial and temporal scales (refs)
149	Guillemette & Larsen 2002	common eider		depletion	11%		37%	this suggests that other predators and other factors played a role in the disappearance of Cardium and Spisula during the winter
152	Guillemette & Larsen 2002	common eider		depletion				prey depletion drives the seasonal distribution of eiders (refs)
162	Nilsson 1972	diving ducks		depletion		5%		the total food intake of all the diving ducks was about 5% of the observed decrease in standing crop between Nov and April
163	Nilsson 1972	diving ducks		depletion				The highest rates of exploitation occurred in the richest areas
164	Nilsson 1972	diving ducks		depletion				In all areas the calculated exploitation (depletion) was small in relation to the standing crop of potential food species
229	Stott & Olson 1973	scoter		depletion		yes		Glude 1967 found that an increase in the number of scoter in a coastal shellfish area of Washington caused a reduction in numbers of commercial soft shelled clams.
230	Stott & Olson 1973	scoter		depletion		no		superficially it appeared that the food resource had not been severely depleted by the scoter population
268	Guillemette 1998	common eider		depletion	40%		60%	eiders removed 40%-60% of the biomass in the course of the winter
282	Sekiya et al 2000	tufted duck	winter	depletion		yes		after the mussel biomass decrease in late winter, tufties switched their diet to manila clams and crustaceans
283	Sekiya et al 2000	pochard	winter	depletion		yes		after the mussel biomass decrease in late winter, pochard switched their diet to manila clams only
286	Sekiya et al 2000	tufted duck/pochard	winter	depletion		yes		large mussels are exhausted by duck predation
317	Lovvorn 1989	canvasbacks	non-breeding	depletion				sequential use of tubers and then clams appears to result from initially high foraging efficiency for tubers which declines as tubers are depleted
318	Lovvorn 1989	canvasbacks	non-breeding	depletion				clam populations (Macoma) fluctuate widely among years and different areas. Thus, effects of the loss of plant tubers (the preferred food) on canvasback populations probably depends on the frequency and extent of shortages of ALTERNATIVE clam foods
320	Lovvorn 1989	canvasbacks	non-breeding	depletion				Along two of four transects numbers and biomass of Vallisneria tubers declined substantially over the waterfowl staging period. On one other transect, and at deeper sediment layers on another, numbers and biomass of tubers increased indicating the plants were still growing after initial sampling. Thus, losses not due to die back but due to consumption by ducks especially of near surface tubers.
322	Lovvorn 1989	canvasbacks	non-breeding	depletion				depletion of tubers results in a shift to a clam diet in December
323	Lovvorn 1989	canvasbacks	non-breeding	depletion				intake rate for tubers is probably greater than for clams when canvasbacks arrive in autumn, This is probably influenced by the much lower mass-ingestion requirements of tubers than clams for producing body fat (higher assimilable energy per gram ingested???)

325	Lovvorn 1989	canvasbacks	non-breeding	depletion				The effects of the loss of tubers on canvasbacks at the population level depend primarily upon the frequency and extent of shortages of clams throughout the region. Thus, the highly publicised concern over submerged aquatic plants in this area should be extended in efforts to monitor and understand variations in clam abundance.
333	Cantin et al 1974	common eider	breeding	depletion	10%		30%	between 10 and 30% of the standing crop biomass of Littorina alone is removed by the ducklings and the females accompanying them.
334	Cantin et al 1974	common eider		depletion (% of stock removed)		15%		Littorina in Russia
335	Cantin et al 1974	common eider		depletion (% of stock removed)		2.70%		Mytilus in Russia
336	Cantin et al 1974	common eider		depletion (% of stock removed)				in depths less than 30m, common eider predation was sufficient to balance the annual production of Chlamys islandica
337	Cantin et al 1974	common eider		depletion (% of stock removed)		30%		all of the annual production by Mytilus edulis in the Ythan may be accounted for in terms of predation, of which eiders represented 30%
343	Draulans 1982	tufted duck	winter	depletion				predation was most intense in the areas with the highest prey densities. The increase in predation rate with increasing mussel density was highly significant
344	Draulans 1982	tufted duck	winter	depletion				mussel density decreased as a consequence of duck predation at all five depths. Predation was however significantly higher at the shallowest depth.
345	Draulans 1982	tufted duck	winter	depletion				birds feed more where mussel densities are high and the water is shallow. Depletion is greater in such places
348	Guillemette et al 1996	common eider	winter	depletion	21%	45%	69%	of the autumn biomass is removed when feeding on mussels. Eiders substantially deplete mussel beds in winter which in turn seems to affect their distribution
349	Guillemette et al 1996	common eider	winter	depletion	3%		6%	of the autumn biomass is removed when feeding on sea urchins
352	Guillemette et al 1996	seaducks	all year	depletion		6%		of the biomass of Mytilus edulis is consumed annually by the entire sea duck community in the Baltic
353	Guillemette et al 1996	common eider		depletion		12.50%		of the biomass of Mytilus edulis and Cerastoderma present is consumed annually by eider ducks
360	Nehls & Ketzenberg 2002	common eider	all year	depletion		20%		on mussels
362	Nehls & Ketzenberg 2002	common eider	all year	depletion		80%		depletion to an extent where a resource is no longer exploitable is a common feature and has been noted for…and eiders which may remove more than 80% of their food stocks in areas where densities are high.
363	Nehls & Ketzenberg 2002	common eider	all year	depletion		12%		consumption by eiders only reaches 12% of the average production of their prey spp ie mussels and cockles in the Wadden sea
364	Nehls & Ketzenberg 2002	common eider	all year	depletion		40%		of the annual mussel production

365	Nehls & Ketzenberg 2002	common eider	all year	depletion		55%		on mussel beds
381	de Leeuw 1997b	tufted duck/pochard		depletion	10%	18%	44%	of the food stock is consumed each winter
382	de Leeuw 1997b	diving ducks	winter	depletion	5%		35%	on Mytilus
383	de Leeuw 1997b	common eider	winter	depletion		13%		mussels and cockles
384	de Leeuw 1997b	common eider		depletion	48%		69%	Mytilus
385	de Leeuw 1997b	diving ducks		depletion		22%		Dreissena
386	de Leeuw 1997b	diving ducks		depletion		57%		Dreissena
387	de Leeuw 1997b	diving ducks		depletion		95%		Dreissena
429	de Leeuw 1997i	tufted ducks/scaup		depletion				depletion of the profitable shallow areas will reduce intake rate when mussel densities become low, thereby increasing the foraging costs to maintain energy balance. Eventually it will pay the ducks to shift to deeper water.

Appendix 6 Notes concerning the diving depth of diving ducks

record	source	species	season	parameter	min (m)	value (m)	max (m)	comments
4	Cramp & Simmons 1977	common scoter	winter	water depth		not more than 10-20m	20	
6	Cramp & Simmons 1977	common scoter		water depth		2.95	6.7	81% of dives in 2.2-3.7m
7	Cramp & Simmons 1977	common scoter		water depth			6.4	maximum
8	Cramp & Simmons 1977	common scoter		water depth		15		usual is 10-20m
9	Cramp & Simmons 1977	common scoter		water depth		14	30	maximum
10	Cramp & Simmons 1977	common scoter	breeding	water depth	1		3	normally in Iceland
11	Cramp & Simmons 1977	common scoter		water depth	1.5		3.5	preferred
15	Cramp & Simmons 1977	surf scoter		water depth			9	inshore marine waters rarely beyond 9m depth, often within zones of breaking waves, rests in flocks further out
17	Cramp & Simmons 1977	velvet scoter		water depth		5		normal foraging depth, occasionally much more
18	Cramp & Simmons 1977	velvet scoter	breeding	water depth	2	5	7	more rarely up to 7m (Finland)
19	Cramp & Simmons 1977	velvet scoter		water depth	14		30	Danish waters
29	Durinck et al 1993	common scoter		water depth		10		
32	Durinck et al 1993	velvet scoter	winter	water depth			20	generally use waters less than 20m deep
34	Durinck et al 1993	scoter		water depth			20	most of the food items found belong to spp distributed in waters less than 20m deep
38	Degraer 1999	common scoter		water depth				groups of seaducks can be found on places where it is too deep to dive for food
45	Fox 2003	scoter		water depth	5		15	preference in the Wadden Sea
46	Fox 2003	scoter	summer	water depth		5.93		aerial survey results from the Kattegat, Denmark. Mean depth of water over which bird recorded fell in a predictable fashion through each of the winter months to reach a max depth of 9.4m by following April (depletion?????)
47	Fox 2003	scoter	spring	water depth			9.4	aerial survey results from the Kattegat, Denmark
48	Fox 2003	scoter	spring	water depth			20	only 0.015% of 568,000 scoter observed at positions with depths > 20m
54	Brager et al 1995	common scoter		water depth			10	in this wintering area seaducks prefer shallow waters (<10m deep) for feeding
58	Brager et al 1995	common eider		water depth	5	8.4	9	immature eider

59	Brager et al 1995	common eider		water depth	9	11.2	20	adult eider
74	Kirby et al 1993	velvet scoter		water depth			10	commonly feed at depths of less than 10m
77	Owen et al 1986	common scoter	winter	water depth		10	20	often in depths of 10-20m, though usually less than 10m
81	Owen et al 1986	velvet scoter		water depth		10	30	accomplished diver feeding at depths up to 30m though most commonly under 10m
87	Richman & Lovvorn 2003	spectacled eider		water depth		40-70		
95	Lovvorn & Gillingham 1996	canvasbacks		water depth	0.5		3.5	
98	Lovvorn & Gillingham 1996			water depth				several field studies have noted the importance of water depth in feeding site selection by diving ducks.
105	Lovvorn et al 2003	spectacled eider		water depth		40-70m		
184	Meissner & Brager 1990	common scoter		water depth	6		22	6-10m depths are of major importance to the ducks , although the significance of deeper water areas as feeding grounds (where Arctica islandica occurs) was not appreciated
185	Reynolds 1987	long-tailed duck		water depth		3m-10m	55	introductory comments gleaned from other sources
193	Mitchell 1992	redhead	winter	water depth				predicting redhead flock locations and amount of time spent there, based solely on the percent of time water was 12-30cm deep, accurately reflected where redheads were found
220	Goudie & Ankney 1986	common scoter		water depth			15	
224	Stott & Olson 1973	scoter		water depth	9		12	these were the depths in the areas where most seaducks (especially scoter) were observed
239	Systad & Bustnes 2001	stellers eider		water depth			5	90% of birds fed in waters <5m deep
241	Lovvorn & Jones 1991	long-tailed duck		water depth			60	
242	Lovvorn & Jones 1991	common eider		water depth			60	

Appendix 7 Notes concerning individual variation between diving ducks

record	source	species	season	parameter	min	value	max	comments
173	Tome 1988	ruddy ducks		individual variation		No		I compared the slopes and intercepts of the energy gain functions among individual birds within a patch density and found NO DIFFERENCE in slopes or intercepts.
174	Tome 1988	ruddy ducks		individual variation		Yes		However, optimal foraging efficiency (in terms of when birds chose to leave patches) differed between individuals-some birds behaved closer to optimality than others
196	Draulans 1987	tufted duck		individual variation		Yes		the optimal mussel size curves indicate LARGE DIFFERENCES BETWEEN ALL INDIVIDUALS tested. The data suggest that individual variability in SKILL in dealing with mussels could be important in determining the shapes of optimality curves
347	Draulans 1984	tufted duck	winter	individual variation		Yes		the calculated profitability curves were QUIITE DIFFERENT for the four ducks. The most profitable size class varied from mussels of 12.5-15mm to 20-22.5mm. This variation can only stem from variation in the speed with which different birds handled mussels of different sizes.

Appendix 8 Notes concerning the existence of interference competition between diving ducks

record	source	species	season	parameter	min	value	max	comments
65	Schenkeveld & Ydenberg 1985	surf scoter		interference				we commonly observed glaucous winged gulls stealing mussels from diving birds. By attacking them as they surface from foraging dives.
99	Lovvorn & Gillingham 1996	canvasbacks		interference		yes		foraging canvasbacks are often displaced from profitable loci by other individuals that observe their success
103	Giles 1990	tufted duck(lings)		interference		no		I have not observed any instances of intraspecific aggression either within or between broods of tufted ducklings which could reduce foraging efficiency either under natural conditions or in the lab.
169	Hohman 1993			interference				competition between the sexes and age classes during winter is assumed to be deleterious to females and immatures, however, effects of competition on survival and reproductive performance have not yet been demonstrated.
170	Hohman 1993	canvasbacks		interference				aggression associated with feeding was commonly observed in wintering canvasbacks
171	Hohman 1993	canvasbacks		interference				this difference might have resulted from INTERFERENCE competition with adults.
361	Nehls & Ketzenberg 2002	common eider	all year	interference		yes		social interactions limit the density of feeding eiders on their preferred feeding grounds below a level which would lead to prey exhaustion
366	Nehls & Ketzenberg 2002	common eider	all year	interference		yes		a negative effect of density on the food intake has indeed been found in Scottish eiders
367	Nehls & Ketzenberg 2002	common eider	all year	interference		yes		although eiders may gather in large and dense flocks, interference within these groups apparently is higher than in other waterfowl eg geese. In the Wadden sea, aggressive interactions between feeding or resting eiders occur frequently
443	de Leeuw 1997i	diving ducks		interfernce				although interspecific aggressive behaviour is rarely observed in free living ducks the segregation of the species might well be a result of interference competition….this phenomenon can also explain the tendency for segregation between males, females and juveniles within the species

Appendix 9 Notes concerning the diet of diving ducks

record	source	species	season	location	habitat	taxonomic group eaten	species eaten	min size (mm)	size (mm)	max size (mm)	comment	quantity (%)	method	sample size of birds
1	Cramp & Simmons 1977	common scoter				molluscs					mainly			
2	Cramp & Simmons 1977	common scoter			marine and brackish water areas	molluscs					predominantly			
3	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Mytilus edulis			40				
4	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Cerastoderma spp			40				
5	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Mya							
6	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Spisula							
7	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Venus							
8	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Tellina							

9	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	macoma							
10	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Solen							
11	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Venerupis							
12	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Cyprina							
12	Cramp & Simmons 1977	common scoter									availability of food items may be prime factor in diet composition (horse bean episode)			
13	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Nucula							
14	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Saxicava							
15	Cramp & Simmons 1977	common scoter			marine and brackish water areas	gastropods	Nassa reticulata							
16	Cramp & Simmons 1977	common scoter			marine and brackish water areas	gastropods	Littorina spp							

17	Cramp & Simmons 1977	common scoter			marine and brackish water areas	gastropods	Hydrobia spp							
18	Cramp & Simmons 1977	common scoter			marine and brackish water areas	crustaceans					occasionally			
19	Cramp & Simmons 1977	common scoter			marine and brackish water areas	crustaceans	Idotea							
20	Cramp & Simmons 1977	common scoter			marine and brackish water areas	crustaceans	Gammarus							
21	Cramp & Simmons 1977	common scoter			marine and brackish water areas	crustaceans	Carcinus			small				
22	Cramp & Simmons 1977	common scoter			marine and brackish water areas	annelids	polychaetes							
23	Cramp & Simmons 1977	common scoter			marine and brackish water areas	echinoderms								
24	Cramp & Simmons 1977	common scoter			freshwater	molluscs								
25	Cramp & Simmons 1977	common scoter			freshwater	bivalves	Anodonta							
26	Cramp & Simmons 1977	common scoter			freshwater	gastropods	Lymnaea							

27	Cramp & Simmons 1977	common scoter			freshwater	insects and larvae								
28	Cramp & Simmons 1977	common scoter			freshwater	annelids								
29	Cramp & Simmons 1977	common scoter			freshwater	fish				small				
30	Cramp & Simmons 1977	common scoter			freshwater	fish eggs								
31	Cramp & Simmons 1977	common scoter			freshwater	plant material					roots, tubers and seeds			
32	Cramp & Simmons 1977	common scoter	winter	Denmark	marine areas	molluscs						95.90%	freq of birds found in	219
33	Cramp & Simmons 1977	common scoter		Denmark	marine areas	bivalves	Mytilus edulis					50.70%	freq of birds found in	219
34	Cramp & Simmons 1977	common scoter		Denmark	marine areas	bivalves	Cardium spp.					42.50%	freq of birds found in	219
35	Cramp & Simmons 1977	common scoter		Denmark	marine areas	gastropods	dogwhelk					10.90%	freq of birds found in	219
36	Cramp & Simmons 1977	common scoter		Denmark	marine areas	crustaceans	amphipods					10.90%	freq of birds found in	219
37	Cramp & Simmons 1977	common scoter		Denmark	marine areas	annelids	Pectinaria (tubeworms)					12.80%	freq of birds found in	219
38	Cramp & Simmons 1977	common scoter		Denmark	brackish areas	bivalves	blue mussel					100%		8
39	Cramp & Simmons 1977	common scoter		Spitsbergen		gastropods	Margarita helicina							
40	Cramp & Simmons 1977	common scoter	winter	USSR	marine	bivalves	Mytilus spp.					especially		
41	Cramp & Simmons 1977	common scoter	winter	Denmark	freshwater	caddisfly	Phryganea spp				larvae			1

41	Fox 2003	common scoter									the local distribution and abundance of scoter is likely to be strongly influenced by the local abundance and availability of benthic bivalves			
42	Cramp & Simmons 1977	common scoter		USSR	freshwater	caddisfly					larvae			
43	Cramp & Simmons 1977	common scoter		USSR	freshwater	dragonfly					larvae			
44	Cramp & Simmons 1977	common scoter		USSR	freshwater	molluscs						less		
45	Cramp & Simmons 1977	common scoter		USSR	freshwater	fish	minnow					and still less		
46	Cramp & Simmons 1977	common scoter	autumn	USSR	freshwater	bivalves						50% by volume		
47	Cramp & Simmons 1977	common scoter	autumn	USSR	freshwater	chironomid					larvae	2% by volume		
48	Cramp & Simmons 1977	common scoter	autumn	USSR	freshwater	caddisfly					larvae	126.3% by volume		
49	Cramp & Simmons 1977	common scoter	summer	Iceland	freshwater	chironomid					larvae	mainly		81 females
50	Cramp & Simmons 1977	common scoter	summer	Iceland	freshwater	fish eggs						some		81 females
51	Cramp & Simmons 1977	common scoter	summer	Iceland	freshwater	molluscs	Lymnaea					some		81 females
52	Cramp & Simmons 1977	common scoter	summer	Iceland	freshwater	plant material	Potamogeton				seeds	some		81 females
53	Cramp & Simmons 1977	common scoter	summer	Iceland	freshwater	fish					eggs	mainly		12 males
54	Cramp & Simmons 1977	common scoter	summer	Iceland	freshwater	chironomid					larvae	some		12 males

55	Cramp & Simmons 1977	common scoter	summer	Iceland	freshwater	crustaceans	Cladocera					some		12 males
56	Cramp & Simmons 1977	common scoter	summer	Iceland	freshwater	plant material					seeds	some		12 males
57	Cramp & Simmons 1977	velvet scoter	winter		marine	bivalves	mytilus				sometimes attracted inshore by large inshore mussel beds in estuaries and inlets			
58	Cramp & Simmons 1977	velvet scoter				molluscs					chiefly molluscs			
59	Cramp & Simmons 1977	velvet scoter									similar to common scoter but more varied probably because more often feeds near coasts			
60	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	mytilus edulis	5		20	especially			
61	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	cardium spp			20	especially			
62	Cramp & Simmons 1977	velvet scoter			marine and brackish	gastropods	Nassa			25	especially			
63	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Mya			40	less often			
64	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	macoma				less often			
65	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Spisula				less often			
66	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Mactra				less often			
67	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Venus				less often			
68	Cramp & Simmons 1977	velvet scoter			marine and brackish	gastropods	Nucula				less often			

69	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Astarte				less often			
70	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Cyprina				less often			
71	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Modiolaria				less often			
72	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Leda				less often			
73	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Solen				less often			
74	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Tellina				less often			
75	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Donax				less often			
76	Cramp & Simmons 1977	velvet scoter			marine and brackish	gastropods	Littorina				less often			
77	Cramp & Simmons 1977	velvet scoter			marine and brackish	gastropods	Buccinium			60	less often			
78	Cramp & Simmons 1977	velvet scoter			marine and brackish	crustaceans	Carcinus maenas		small		less often			
79	Cramp & Simmons 1977	velvet scoter			marine and brackish	crustaceans	Eupagarus bernhardus		small		less often			
80	Cramp & Simmons 1977	velvet scoter			marine and brackish	crustaceans	Idotea				less often			
81	Cramp & Simmons 1977	velvet scoter			marine and brackish	crustaceans	Gammarus				less often			
82	Cramp & Simmons 1977	velvet scoter			marine and brackish	crustaceans	Pallasea				less often			
83	Cramp & Simmons 1977	velvet scoter			marine and brackish	echinoderms	Echinocardium				less often			

84	Cramp & Simmons 1977	velvet scoter			marine and brackish	echinoderms	Asterias				less often			
85	Cramp & Simmons 1977	velvet scoter			marine and brackish	annelids	Pectinaria (tubeworms)				less often			
86	Cramp & Simmons 1977	velvet scoter			marine and brackish	annelids	Arenicola			120	less often			
87	Cramp & Simmons 1977	velvet scoter			marine and brackish	annelids	Nereis spp				less often			
88	Cramp & Simmons 1977	velvet scoter			marine and brackish	fish			small		rarely			
89	Cramp & Simmons 1977	velvet scoter			freshwater	molluscs	Bithynia							
90	Cramp & Simmons 1977	velvet scoter			freshwater	molluscs	Valvata							
91	Cramp & Simmons 1977	velvet scoter			freshwater	molluscs	Anodonta							
92	Cramp & Simmons 1977	velvet scoter			freshwater	molluscs	Unio							
93	Cramp & Simmons 1977	velvet scoter			freshwater	molluscs	Dreissena							
94	Cramp & Simmons 1977	velvet scoter			freshwater	molluscs	Pectunculus							
95	Cramp & Simmons 1977	velvet scoter			freshwater	insects								
96	Cramp & Simmons 1977	velvet scoter			freshwater	annelids								
97	Cramp & Simmons 1977	velvet scoter			freshwater	fish			small					
98	Cramp & Simmons 1977	velvet scoter			freshwater	plant material					seeds, roots,tubers,buds and leaves			

99	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	molluscs					by frequency	97%		144 stomachs
100	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	molluscs					by volume	83%		144 stomachs
101	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	crustaceans					by frequency	16%		144 stomachs
102	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	crustaceans					by volume	6%		144 stomachs
103	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	echinoderms					by frequency	9.70%		144 stomachs
104	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	echinoderms					by volume	6%		144 stomachs
105	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	annelids					by frequency	8.30%		144 stomachs
106	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	annelids					by volume	4%		144 stomachs
107	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	fish					by frequency	4.20%		144 stomachs
108	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	fish					by volume	2%		144 stomachs
109	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	gastropods	dogwhelk				main item			144 stomachs
110	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	bivalves	Cardium spp				main item			144 stomachs
111	Cramp & Simmons 1977	velvet scoter	winter	Denmark	marine	bivalves	Mytilus spp.				main item			144 stomachs
112	Cramp & Simmons 1977	velvet scoter		Denmark	brackish areas						similar to marine stomach contents			13 stomachs
113	Cramp & Simmons 1977	velvet scoter		Switzerland	freshwater	fish					roe (when other foods scarce)	100%		7 stomachs

114	Cramp & Simmons 1977	velvet scoter		Lower Saxony	freshwater	amphibians					frogspawn			
115	Cramp & Simmons 1977	velvet scoter		Germany	freshwater	bivalves	Dreissena							
116	Cramp & Simmons 1977	velvet scoter		Germany	freshwater	molluscs	Unio							
117	Cramp & Simmons 1977	velvet scoter		Germany	freshwater	molluscs	Anodonta							
118	Cramp & Simmons 1977	velvet scoter		Germany	freshwater	molluscs	Viviparus viviparus							
119	Cramp & Simmons 1977	velvet scoter		Germany	freshwater	molluscs	Bulimus tentaculata							
120	Cramp & Simmons 1977	velvet scoter	autumn	USSR	freshwater	molluscs					mainly			
121	Cramp & Simmons 1977	velvet scoter	autumn	USSR	freshwater	insecta	caddisfly larvae				fewer			
122	Cramp & Simmons 1977	velvet scoter	autumn	USSR	freshwater	plant material	Potamogeton				fewer			
123	Cramp & Simmons 1977	velvet scoter	autumn	USSR	freshwater	animal food					predominant (by volume)	99.50%		
124	Cramp & Simmons 1977	velvet scoter	autumn	USSR	freshwater	molluscs	Unio & Anodonta				by volume	62.50%		
125	Cramp & Simmons 1977	velvet scoter	autumn	USSR	freshwater	insecta	caddisfly larvae				by volume	30%		
126	Cramp & Simmons 1977	velvet scoter	autumn	USSR	freshwater	fish			small		by volume	7%		
126	Bourne 1984	scoter									clams were ingested whole and some rather large ones were consumed			
127	Cramp & Simmons 1977	velvet scoter	spring/summer	Finland	marine	bivalves	Mytilus edulis				by volume	71%		38 stomachs

128	Cramp & Simmons 1977	velvet scoter	spring/summer	Finland	marine	bivalves	Macoma balthica					less		38 stomachs
129	Cramp & Simmons 1977	velvet scoter	spring/summer	Finland	marine	gastropods	Hydrobia spp					less		38 stomachs
130	Cramp & Simmons 1977	velvet scoter	spring/summer	Finland	marine	crustaceans	Gammarus					less		38 stomachs
131	Cramp & Simmons 1977	velvet scoter	summer	Norway		crustaceans	Pallasea							
132	Cramp & Simmons 1977	velvet scoter	summer		freshwater	insecta						mainly		
133	Cramp & Simmons 1977	velvet scoter	summer		freshwater	insecta	caddisfly larvae					especially		
134	Cramp & Simmons 1977	velvet scoter	summer		freshwater	crustaceans						some		
135	Cramp & Simmons 1977	velvet scoter	summer		freshwater	fish						some		
136	Cramp & Simmons 1977	velvet scoter	summer		freshwater	plant material						some		
137	Durinck 1993	common scoter		Denmark (kattegat)	marine	molluscs						77%		
138	Durinck 1993	common scoter		Denmark (kattegat)	marine	bivalves						66% of 77%		
139	Durinck 1993	common scoter		Denmark (kattegat)	marine	bivalves	Mytilus edulis				main species			
140	Durinck 1993	common scoter		Denmark (kattegat)	marine	bivalves	Cardium edule				main species			
141	Durinck 1993	velvet scoter		Denmark (kattegat)	marine	molluscs						83%		
142	Durinck 1993	velvet scoter		Denmark (kattegat)	marine	bivalves						53% of 83%		
143	Durinck 1993	velvet scoter		Denmark (kattegat)	marine	bivalves	Mytilus edulis					in equal quantities ie 1/3 of 53% of 83%		
144	Durinck 1993	velvet scoter		Denmark (kattegat)	marine	bivalves	Cardium edule					in equal quantities ie 1/3 of 53% of 83%		

145	Durinck 1993	velvet scoter		Denmark (kattegat)	marine	gastropods	Nassa reticulata					in equal quantities ie 1/3 of 53% of 83%		
146	Durinck 1993	common scoter	winter	Denmark (north sea)	marine	bivalves	Spisula subtruncata	9	15.3	19	by frequency	97%	freq of items	n=1824 items
147	Durinck 1993	common scoter	winter	Denmark (north sea)	marine	bivalves	Cardium edule	8	11.4	15	by frequency	3%	freq of items	n=1824 items
148	Durinck 1993	common scoter	winter	Denmark (north sea)	marine	bivalves	Solenidae spp				1 item out of 1824 identified	1 item	freq of items	n=1824 items
149	Durinck 1993	common scoter	winter	Denmark (north sea)	marine	annelids	Pectinaria (tubeworms)				1 item out of 1824 identified	1 item	freq of items	n=1824 items
150	Durinck 1993	velvet scoter	winter	Denmark (north sea)	marine	bivalves	Spisula subtruncata	10	15.2	19	by frequency	94%		n=594 items
151	Durinck 1993	velvet scoter	winter	Denmark (north sea)	marine	bivalves	Cardium edule	9	11.6	14	by frequency	6%		n=594 items
152	Durinck 1993	common scoter	winter	Denmark (kattegat)	marine	molluscs					10-20 the preferred size			
153	Durinck 1993	velvet scoter	winter	Denmark (kattegat)	marine	bivalves	spisula spp	10		12	smaller than 30mm			
154	Durinck 1993	common scoter		Poland	marine	bivalves	Mya arenaria				most important items			
155	Durinck 1993	common scoter		Poland	marine	bivalves	Macoma balthica				most important items			
156	Durinck 1993	common scoter		Poland	marine	bivalves	Cardium lamarckii				most important items			
157	Durinck 1993	velvet scoter		Poland	marine	bivalves	Mya arenaria				most important items			
158	Durinck 1993	velvet scoter		Poland	marine	bivalves	Macoma balthica				most important items			
159	Durinck 1993	velvet scoter		Poland	marine	bivalves	Cardium lamarckii				most important items			
160	Durinck 1993	common scoter		Netherlands	marine	bivalves	Spisula subtruncata				main food			
161	Degraer 1999	common scoter		Netherlands	marine	bivalves	Donax vittatus				likely to be eaten			
162	Degraer 1999	common scoter		Netherlands	marine	bivalves	Abra alba				likely to be eaten			
163	Degraer 1999	common scoter		Netherlands	marine	bivalves	Tellina fabula				likely to be eaten			
164	Degraer 1999	common scoter		Netherlands	marine	bivalves	Tellina tenuis				likely to be eaten			
165	Degraer 1999	common scoter		Netherlands	marine	bivalves	Macoma balthica				likely to be eaten			

166	Degraer 1999	common scoter		Netherlands	marine	bivalves	Spisula subtruncata				likely to be eaten			
167	Degraer 1999	common scoter		Netherlands	marine	bivalves	Barnea candida				doubtful if eaten (lives in compact muddy sediment)			
168	Fox 2003	common scoter		Belgium, Britain, Danish Baltic, Sweden, Lithuania, German Baltic, Danish Baltic		bivalves	Macoma balthica				7 studies cited			
169	Fox 2003	common scoter		Danish wadden sea, Britain, Poland, German Baltic, Danish Baltic		bivalves	Cardium edule				5 studies			
170	Fox 2003	common scoter		Danish Baltic, Britain, White Sea, German Baltic		bivalves	Mytilus edulis				4 studies			
171	Fox 2003	common scoter		Lithuania, Poland, German Baltic, Danish Baltic		bivalves	Mya arenaria				4 studies			
172	Fox 2003	common scoter		Belgium, Netherlands, Danish wadden sea		bivalves	Spisula subtruncata				3 studies			
173	Fox 2003	common scoter		German Baltic, Danish Baltic, Danish wadden sea		bivalves	Cyprina islandica				3 studies			
174	Fox 2003	common scoter		Belgium, Britain		bivalves	Donax vittatus				2 studies			
175	Fox 2003	common scoter		Belgium, Britain		bivalves	Tellina tenuis				2 studies			
176	Fox 2003	common scoter		Danish baltic, Britain		gastropods	Littorina spp				2 studies			
177	Fox 2003	common scoter		Danish baltic, Britain		bivalves	Venus gallina				2 studies			

178	Fox 2003	common scoter		Netherlands, Britain		bivalves	Mactra corralina				2 studies			
179	Fox 2003	common scoter		Britain		bivalves	Pharus legumen				1 study			
180	Fox 2003	common scoter		Britain		bivalves	Spisula elliptica				1 study			
181	Fox 2003	common scoter		Britain		bivalves	Lutraria lutraria				1 study			
182	Fox 2003	common scoter		Britain		bivalves	Scobicularia plana				1 study			
183	Fox 2003	common scoter		Britain		gastropods	Gibbula cineraria				1 study			
184	Fox 2003	common scoter		Britain		bivalves	Cardium echinatum				1 study			
185	Fox 2003	common scoter		Belgium		bivalves	Abra alba				1 study			
186	Fox 2003	common scoter		Belgium		bivalves	Tellina fabula				1 study			
187	Fox 2003	common scoter		Belgium		bivalves	Barnea Candida				1 study			
188	Fox 2003	common scoter		Danish Baltic		gastropods	Nassarius reticulatus				1 study			
189	Fox 2003	common scoter		Danish Baltic		bivalves	Cardium scarbrum				1 study			
190	Fox 2003	common scoter		Danish Baltic		gastropods	Nucella spp.				1 study			
191	Fox 2003	common scoter		Danish Baltic		gastropods	Neretina fluviatilis				1 study			
192	Fox 2003	common scoter		Danish Baltic		bivalves	Musculus nigra				1 study			
193	Fox 2003	common scoter		German Baltic		bivalves	Mya truncata				1 study			
194	Fox 2003	common scoter		Poland		bivalves	Cardium lamarckii				1 study			
195	Fox 2003	common scoter		Danish wadden sea		bivalves	Ensis spp				1 study			
196	Fox 2003	velvet scoter		Danish wadden sea, Danish Baltic		bivalves	Spisula subtruncata				2 studies			
197	Fox 2003	velvet scoter		Danish wadden sea, Danish Baltic		bivalves	Cardium edule				2 studies			
198	Fox 2003	velvet scoter		Danish Baltic		bivalves	Macoma balthica				Madsen 1954			

199	Fox 2003	velvet scoter		Danish Baltic		bivalves	Mytilus edulis				Madsen 1954			
200	Fox 2003	velvet scoter		Danish Baltic		gastropods	Nassarius reticulatus				Madsen 1954			
201	Fox 2003	velvet scoter		Danish Baltic		gastropods	Littorina litorea				Madsen 1954			
202	Fox 2003	velvet scoter		Danish Baltic		bivalves	Venus gallina				Madsen 1954			
203	Fox 2003	velvet scoter		Danish Baltic		gastropods	Bittium reticulatum				Madsen 1954			
204	Fox 2003	velvet scoter		Danish Baltic		gastropods	Gibbula cineraria				Madsen 1954			
205	Fox 2003	velvet scoter		Danish Baltic		gastropods	Buccinium undulatum				Madsen 1954			
206	Fox 2003	velvet scoter		Danish Baltic		bivalves	Nucula nitida				Madsen 1954			
207	Fox 2003	velvet scoter		Danish Baltic		bivalves	Macoma calcarea				Madsen 1954			
208	Fox 2003	velvet scoter		Danish Baltic		bivalves	Mya truncata				Madsen 1954			
209	Fox 2003	velvet scoter		Danish Baltic		gastropods	Bela turricula				Madsen 1954			
210	Fox 2003	velvet scoter		Danish Baltic		gastropods	Nassarius pygmaea				Madsen 1954			
211	Fox 2003	velvet scoter		Danish Baltic		gastropods	Lunatia nitida				Madsen 1954			
212	Fox 2003	velvet scoter		Danish Baltic		bivalves	Nucula nitida				Madsen 1954			
213	Fox 2003	velvet scoter		Danish Baltic		bivalves	Cyprina islandica				Madsen 1954			
214	Fox 2003	velvet scoter		Danish Baltic		gastropods	Aporrhais pes pelicani				Madsen 1954			
215	Fox 2003	common scoter				bivalves					most frequently			
216	Fox 2003	common scoter				gastropods	Nassarius				lesser degree			
217	Fox 2003	common scoter				gastropods	Littorina				lesser degree			
218	Fox 2003	common scoter				crustaceans	isopods				also figure in oesophagus			
219	Fox 2003	common scoter				crustaceans	amphipods				also figure in oesophagus			
220	Fox 2003	common scoter				crustaceans	crabs		small		also figure in oesophagus			

221	Fox 2003	common scoter				annelids					also figure in oesophagus			
222	Fox 2003	common scoter				echinoderms					also figure in oesophagus			
223	Fox 2003	scoter				molluscs					by frequency	95%		
224	Fox 2003	scoter				molluscs					by volume	80%		
225	Fox 2003	common scoter		Lithuania	marine	bivalves	Macoma balthica				most frequently			
226	Fox 2003	common scoter		Lithuania	marine	annelids	polychaetes				relatively high proportions			
227	Fox 2003	common scoter		Lithuania	marine	crustaceans	isopods				relatively high proportions			
228	Fox 2003	velvet scoter		Lithuania	marine	bivalves	Mya arenaria				mainly			
229	Fox 2003	scoter		Poland	marine	bivalves	Mya arenaria				most important items			
230	Fox 2003	scoter		Poland	marine	bivalves	Macoma balthica				most important items			
231	Fox 2003	scoter		Poland	marine	bivalves	Cardium lamarckii				most important items			
232	Fox 2003	scoter		Denmark & netherlands noerth sea coast	marine	bivalves	Spisula spp.				dominant			
233	Fox 2003	scoter		Denmark (east Jutland)	marine	bivalves	Musculus nigra				dominant in 86/87 to 87/88			
234	Fox 2003	scoter		Denmark (east Jutland)	marine	bivalves	Mya arenaria				dominant in 86/87 to 87/88			
235	Fox 2003	scoter		Denmark (east Jutland)	marine	bivalves	Cardium edule				dominant in 89/90			
236	Fox 2003	scoter		Denmark (east Jutland)	marine	bivalves	Macoma balthica				dominant in 89/90			
237	Fox 2003	scoter		Denmark (east Jutland)	marine	bivalves	Cyprina islandica				dominant in 89/90			
238	Fox 2003	common scoter		Danish Kattegat	marine	bivalves	Cardium edule				dominant			
239	Fox 2003	common scoter		Danish wadden sea	marine	bivalves	Cyprina islandica				dominant			
240	Fox 2003	common scoter		Danish wadden sea	marine	bivalves	Ensis spp				dominant			
241	Fox 2003	common scoter		Poland	marine	bivalves	Mya arenaria				fed selectively upon			
242	Fox 2003	common scoter		Poland	marine	bivalves	Cardium edule				fed selectively upon			

243	Fox 2003	common scoter		Poland	marine	bivalves	Mytilus edulis				avoided in preference to Mya and cardium			
244	Fox 2003	common scoter			marine	annelids	polychaetes				significant proportions			
245	Fox 2003	common scoter			marine	crustaceans	isopods				significant proportions			
246	Fox 2003	common scoter			marine	bivalves		5 to 10		20				
247	Fox 2003	common scoter			marine	bivalves	Mytilus edulis			30				
248	Fox 2003	common scoter			marine	bivalves	Mya spp			40				
249	Fox 2003	velvet scoter			marine	gastropods	Buccinium undulatum			60				
250	Fox 2003	velvet scoter			marine	molluscs				50				
251	Fox 2003	common scoter			marine	bivalves	Mya arenaria	5		30				
252	Fox 2003	common scoter	winter	Wales	marine	bivalves	Donax vittatus		28					
253	Fox 2003	common scoter		Germany	marine	bivalves	Cyprina islandica		15.3	30	very few specimens larger than 30			
254	Fox 2003	scoter		Denmark	marine	bivalves	in study by Durinck et al 1993 there were significant differences in the sizes of Cardium and Spisula eaten by both common and velvet scoter suggesting neither scoter spp selects for a specific size class of prey but take a subset of what is available to them							
255	Fox 2003	common scoter	winter	Denmark	marine	molluscs		3		9	the presence of large numbers of very small prey items in the sample from Helgenaes suggests that there is not an obvious lower critical threshold that limits prey size since none of the abundant prey was found to exceed 10mm.			
256	Fox 2003	common scoter	summer	Denmark	marine	molluscs		8		15	it would seem likely that there is an upper limit to the size of hard prey taken which seems to be around 30-40mm			
257	Fox 2003	scoter	it also seems likely that the wide range of prey sizes within the range taken reflects the local conditions in some way.											
258	Fox 2003	scoter	scoter take the most abundant bivalve mollusc species known to be present in the substrate in areas where the birds feed. Diet appears simply to reflect local abundance, the major constituents of the benthic communities dominating the diet in most studied situations.											
259	Fox 2003	scoter	difficult to differentiate between the hypotheses that scoter select for specific prey size or simply take prey in proportion to their availability											
260	Brager et al 1995	common scoter	winter	Germany	marine	…when using these shallow coastal waters, common scoter feed on different prey species than eiders. They still seem to be able to find sufficient food even if the stock of benthic macrofauna has been depleted during the winter								
261	Brager et al 1995	common scoter	winter	Germany	marine	The infauna eg cockles and Mya consumed by common scoter are possibly less affected by hydrodynamical abrasion (than epibenthic mussels) or can even become more easily available to predators								
262	Schekeveld & Ydenberg 1985	surf scoter				bivalves	Mytilus edulis				feed primarily on the edible mussel and other bivalves			

263	Kirby et al 1993	common scoter	winter	Britain	marine	bivalves	Mytilus edulis				mainly			
264	Kirby et al 1993	common scoter	winter	Britain	marine	crustaceans								
265	Kirby et al 1993	common scoter	winter	Britain	marine	fish			small					
266	Kirby et al 1993	velvet scoter	winter		marine	molluscs					mainly. But diet more varied than common scoter			
267	Owen et al 1986	common scoter	winter		marine	bivalves	Mytilus edulis				predominates in their diet. Concentrate their feeding over mussel beds			
268	Owen et al 1986	velvet scoter									takes larger prey items than the common scoter, stays closer to the shore and has a more varied diet			
269	Owen et al 1986	velvet scoter	winter	Denmark	marine	molluscs					predominate but more cockles and gastropods (periwinkles and whelks) are taken than by common scoter			
270	Owen et al 1986	velvet scoter	spring/summer	Finland	marine	shellfish					taken roughly in proportion to their availability in the Fucus zone over which the birds feed			
278	Toba et al 1992	scoter		Washington	marine	bivalves	T. phillipinarum	6		20	Three duck species (ie all 3 scoter spp) are known to be significant predators on manila clams within the 6-20mm size range (Toba et al 1992).			
279	Toba et al 1992	scoter		Japan	marine	bivalves	T.phillipinarum			25	In Japan, scoter were seen to consume as many as 52 small clams (<25mm mean shell length) per bird per day for 150 consecutive days (Cahn 1951 in Toba et al 1992).			
280	Bourne 1984	scoter		Washington	marine	molluscs					dominant food item			219
281	Bourne 1984	scoter		Washington	marine	bivalves					90% of ducks			219
282	Bourne 1984	scoter		Washington	marine	gastropods					25% of ducks mainly small and formed a minor part of the inorganic matter in the gut			219
283	Bourne 1984	scoter		Washington	marine	bivalves	Saxidomus giganteus					2%		219
284	Bourne 1984	scoter		Washington	marine	bivalves	Protothaca staminea					43%		219
285	Bourne 1984	scoter		Washington	marine	bivalves	Tapes phillipinarum					56%		219
286	Bourne 1984	common scoter		Washington	marine	molluscs					94%	94	freq of birds found in	16
287	Bourne 1984	common scoter		Washington	marine	bivalves					88%	88	freq of birds found in	16

288	Bourne 1984	common scoter		Washington	marine	gastropods					12%	12	freq of birds found in	16
289	Bourne 1984	common scoter		Washington	marine	bivalves	Tapes phillipinarum				12%	12	freq of birds found in	16
290	Bourne 1984	common scoter		Washington	marine	bivalves	Protothaca staminea				19%	19	freq of birds found in	16
291	Bourne 1984	common scoter		Washington	marine	bivalves	Mytilus edulis				88% the most important food item for common scoter	88	freq of birds found in	16
292	Bourne 1984	common scoter		Washington	marine	gastropods	Littorina scutulata				6%	6	freq of birds found in	16
293	Bourne 1984	common scoter		Washington	marine	gastropods	Mitrella gausaoata				6%	6	freq of birds found in	16
294	Bourne 1984	common scoter		Washington	marine	barnacles					56% possibly incidentally eaten attached to mussels	56	freq of birds found in	16
295	Bourne 1984	common scoter		Washington	marine	echinoderms	Echinicarius excentricus				6%	6	freq of birds found in	16
296	Bourne 1984	scoter		Washington	marine	crustaceans	crabs				minor part of the diet			
297	Bourne 1984	scoter		Washington	marine	worms					minor part of the diet			
298	Bourne 1984	scoter		Washington	marine	echinoderms					minor part of the diet			
299	Bourne 1984	scoter		Washington	marine	stones				25mm				
300	Bourne 1984	scoter		Washington	marine	bivalves	Mytilus edulis			30mm				
301	Bourne 1984	velvet scoter		Washington	marine	bivalves	Mytilus edulis			45mm				
302	Bourne 1984	velvet scoter		Washington	marine	bivalves	clams	10		>40mm				
303	Bourne 1984	surf scoter		Washington	marine	bivalves	clams	<10		40mm				
304	Bourne 1984	velvet scoter		Washington	marine	bivalves	Saxidomus giganteus	20		40				
305	Bourne 1984	scoter				bivalves	cockles				important food item of scoter in some areas			

306	Bourne 1984	scoter				bivalves	macoma				important food item of scoter in some areas			
307	Nilsson 1972	velvet scoter	winter	Baltic	marine	bivalves	Macoma balthica				4/5 birds	80%		5
308	Nilsson 1972	velvet scoter	winter	Baltic	marine	bivalves	Mytilus edulis				1/5 birds	20%		5
309	Nilsson 1972	common scoter	winter	Baltic	marine	bivalves	Mytilus edulis				46%	46	freq of items	13
310	Nilsson 1972	common scoter	winter	Baltic	marine	bivalves	Macoma balthica				49%	49	freq of items	13
315	Leopold et al 1995	common scoter	winter	Netherlands	marine	bivalves	Spisula subtruncata	a rich supply of S.s was present at all locations where common scoter wintered in large numbers since 1987, and this bivalve is now the most important food item for the ducks						
316	Ferns 1984	common scoter		Bristol Channel		bivalves	Mytilus edulis				subtidal and intertidal			
317	Ferns 1984	common scoter		Bristol Channel		bivalves	Pharus spp.				subtidal and intertidal			
318	Ferns 1984	common scoter		Bristol Channel		bivalves	Donax spp.				subtidal and intertidal			
319	Ferns 1984	common scoter		Bristol Channel		crustaceans	Corystes spp.				subtidal and intertidal			
320	Ferns 1984	common scoter		Bristol Channel		crustaceans	Carcinus spp.				subtidal and intertidal			
321	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Mytilus edulis					2.70%	% wet weight	157
322	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Cerastoderma spp					34.70%	% wet weight	157
323	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Macoma balthica					4.60%	% wet weight	157
324	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Mya arenaria					33.80%	% wet weight	157
325	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Mya truncata					5.70%	% wet weight	157
326	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Arctica islandica	3.5	15.3	31.8		18.50%	% wet weight	157
327	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Cerastoderma spp					44.60%	% wet weight	134
328	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Macoma balthica					4.90%	% wet weight	134
329	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Mya arenaria					43.50%	% wet weight	134
330	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	other spp					7.30%	% wet weight	134

331	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	other spp					7.50%	% wet weight	36
332	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Mya truncata					22.20%	% wet weight	36
333	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Arctica islandica					70.30%	% wet weight	36
334	Meissner & Brager 1990	common scoter	winter	Baltic	marine	With the exception of some Asterias and very few polychaetes ands crustaceans (taken by eider) the diets of both seaducks consists of molluscs								
335	Meissner & Brager 1990	common scoter	winter	Baltic	marine	in shallow waters scoter preferred cerastoderma and Mya arenaria to Mytilus which the eiders ate much more of. In deeper water scoter took more Mya truncata than did eiders and less Arctica islandica								
336	Meissner & Brager 1990	common scoter	winter	Baltic	marine	In deeper water the proportion of Mya truncata in the diet (22% in common scoter) are remarkable too since this species usually lives rather deep in the sediment. The small Abra alba which is also very common in deep waters is hardly used by the birds at all.								
337	Meissner & Brager 1990	common scoter	winter	Baltic	marine	within scoter there seems to be NO INTRASPECIFIC DIFFERENCES BETWWEEN AGES OR SEXES in their diet in either shallow or deep water.								
342	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	fish	Ammodytidae spp. (sandeels)				%of food content (by mass)	23.40%		200 stomachs
343	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	crustaceans	Mesidothea, Palemon, Crangon, Gammarus				%of food content (by mass)	0.20%		200 stomachs
344	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Macoma balthica				%of food content (by mass)	22.50%		200 stomachs
345	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Mya arenaria			52mm	%of food content (by mass)	41.50%		200 stomachs
346	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Mytilus edulis				%of food content (by mass)	2.20%		200 stomachs
347	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Cardium lamarckii				%of food content (by mass)	10.20%		200 stomachs
348	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	fish	Ammodytidae spp. (sandeels)				% occurrence (N stomachs found in)	44.00%		200 stomachs
349	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	crustaceans	Mesidothea, Palemon, Crangon, Gammarus				% occurrence (N stomachs found in)	4.50%		200 stomachs
350	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Macoma balthica				% occurrence (N stomachs found in)	76.50%		200 stomachs
351	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Mya arenaria				% occurrence (N stomachs found in)	86.70%		200 stomachs
352	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Mytilus edulis				% occurrence (N stomachs found in)	15.30%		200 stomachs

353	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Cardium lamarckii				% occurrence (N stomachs found in)	32.10%		200 stomachs
354	Stempniewicz 1986	common scoter	winter	Baltic	marine	fish	Ammodytidae spp. (sandeels)				%of food content (by mass)	6.20%	% wet weight	52 stomachs
355	Stempniewicz 1986	common scoter	winter	Baltic	marine	crustaceans					%of food content (by mass)	0.00%	% wet weight	52 stomachs
356	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Macoma balthica				%of food content (by mass)	24.70%	% wet weight	52 stomachs
357	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Mya arenaria				%of food content (by mass)	34.00%	% wet weight	52 stomachs
358	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Mytilus edulis				%of food content (by mass)	0.20%	% wet weight	52 stomachs
359	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Cardium lamarckii				%of food content (by mass)	35.00%	% wet weight	52 stomachs
360	Stempniewicz 1986	common scoter	winter	Baltic	marine	fish	Ammodytidae spp. (sandeels)				% occurrence (N stomachs found in)	19.20%	freq of birds found in	52 stomachs
361	Stempniewicz 1986	common scoter	winter	Baltic	marine	crustaceans					% occurrence (N stomachs found in)	0.00%	freq of birds found in	52 stomachs
362	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Macoma balthica				% occurrence (N stomachs found in)	51.00%	freq of birds found in	52 stomachs
363	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Mya arenaria				% occurrence (N stomachs found in)	72.50%	freq of birds found in	52 stomachs
364	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Mytilus edulis				% occurrence (N stomachs found in)	3.90%	freq of birds found in	52 stomachs
365	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Cardium lamarckii				% occurrence (N stomachs found in)	56.90%	freq of birds found in	52 stomachs
366	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Mya, macoma and cardium				made up over 90% of the average weight of food			
367	Stempniewicz 1986	common scoter	winter	Baltic	marine	bivalves	Mytilus				was of no great significance			
368	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Mya, macoma and cardium				made up over 70% of the average weight of food			
369	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Mytilus				was on no great significance			

370	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	fish	Ammodytidae spp. (sandeels)				was the next most important constituent of the scoter diet (next to bivalves)			
371	Stempniewicz 1986	common scoter	winter	Baltic	marine	fish	Ammodytidae spp. (sandeels)				was the next most important constituent of the scoter diet (next to bivalves)			
372	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	crustaceans					eaten only occasionally			
373	Stempniewicz 1986	common scoter	winter	Baltic	marine	crustaceans					not eaten at all			
374	Stempniewicz 1986	scoter	winter	Baltic	marine						velvet scoter ate considerably more fish and Mytilus than did common scoter but less cardium.			
375	Stempniewicz 1986	scoter	winter	Baltic	marine	although bivalves were prevalent in both cases, the proportions of particular spp were totally dissimilar between this study in Gdansk and that of Madsen 1954 in Kattegat and western Baltic. These dietary differences result from the dissimilar food resources available in the two regions								
376	Stempniewicz 1986	scoter	winter	Baltic	marine	bivalves	Mya and cardium	make up 15% of the bivalve biomass in Gdansk but 70% of the scoter diet				70%		
377	Stempniewicz 1986	scoter	winter	Baltic	marine	bivalves	Mytilus edulis	make up 40% of the bivalve biomass in Gdansk but are quite an insignificant constituent of the scoter diet (velvet 2.7%, common 0.2%)				0.20%		
378	Goudie & Ankney 1986	common scoter	winter	Newfoundland	marine	bivalves	Mytilus edulis		6.3		% of mass in gullet	>95%	% of mass in gullet	15 birds
379	Goudie & Ankney 1986	common scoter	winter	Newfoundland	marine	gastropods	Littorina obtusata				% of mass in gullet	<5%	% of mass in gullet	15 birds
380	Goudie & Ankney 1986	common scoter	winter	Newfoundland	marine	gastropods	Lacuna vincta				% of mass in gullet	<5%	% of mass in gullet	15 birds
381	Goudie & Ankney 1986	common scoter	winter	Newfoundland	marine	bivalves	Mytilus edulis				areas of extensive mussel beds at Cape St Mary's are used predominantly by black scoter			
382	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa			50mm	% by volume	54%		166 birds
383	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	Mytilus edulis				% by volume	5%		166 birds
384	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	Mesodesma arctatum				% by volume	20%		166 birds
385	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	gastropods	Lunatia heros				% by volume	5%		166 birds
386	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	barnacles	Balanus spp				% by volume	<1%		166 birds
387	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	echinoderms	Echinarachnius parma				% by volume	3%		166 birds
388	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	crustaceans	Idotea baltica				% by volume	<1%		166 birds
389	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	unident spp.				% by volume	8%		166 birds
390	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa			<50mm	% by volume	24%		133 birds

391	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	Mytilus edulis				% by volume	8%		133 birds
392	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	Mesodesma arctatum				% by volume	60%		133 birds
393	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	gastropods	Lunatia heros				% by volume	1%		133 birds
394	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	barnacles	Balanus spp				% by volume	<1%		133 birds
395	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	echinoderms	Echinarachnius parma				% by volume	<1%		133 birds
396	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	crustaceans	Idotea baltica				% by volume	1%		133 birds
397	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	unident spp.				% by volume	2%		133 birds
398	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa			<50mm	% by volume	55%	% by volume	42 birds
399	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	Mytilus edulis				% by volume	19%	% by volume	42 birds
400	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	Mesodesma arctatum				% by volume	23%	% by volume	42 birds
401	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	gastropods	Lunatia heros				% by volume	1%	% by volume	42 birds
402	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	barnacles	Balanus spp				% by volume	1%	% by volume	42 birds
403	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	echinoderms	Echinarachnius parma				% by volume	<1%	% by volume	42 birds
404	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	crustaceans	Idotea baltica				% by volume	0%	% by volume	42 birds
405	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	unident spp.				% by volume	<1%	% by volume	42 birds
406	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa				% by occurrence	61%		166 birds
407	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	Mytilus edulis				% by occurrence	11%		166 birds
408	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	Mesodesma arctatum				% by occurrence	8%		166 birds
409	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	gastropods	Lunatia heros				% by occurrence	35%		166 birds
410	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	barnacles	Balanus spp				% by occurrence	0%		166 birds
411	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	echinoderms	Echinarachnius parma				% by occurrence	11%		166 birds
412	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	crustaceans	Idotea baltica				% by occurrence	0%		166 birds

413	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	unident spp.				% by occurrence	42%		166 birds
414	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa				% by occurrence	55%		133 birds
415	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	Mytilus edulis				% by occurrence	19%		133 birds
416	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	Mesodesma arctatum				% by occurrence	16%		133 birds
417	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	gastropods	Lunatia heros				% by occurrence	15%		133 birds
418	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	barnacles	Balanus spp				% by occurrence	0%		133 birds
419	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	echinoderms	Echinarachnius parma				% by occurrence	0%		133 birds
420	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	crustaceans	Idotea baltica				% by occurrence	5%		133 birds
421	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	unident spp.				% by occurrence	32%		133 birds
422	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa				% by occurrence	62%	% by occurrence	42 birds
423	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	Mytilus edulis				% by occurrence	33%	% by occurrence	42 birds
424	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	Mesodesma arctatum				% by occurrence	12%	% by occurrence	42 birds
425	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	gastropods	Lunatia heros				% by occurrence	12%	% by occurrence	42 birds
426	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	barnacles	Balanus spp				% by occurrence	21%	% by occurrence	42 birds
427	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	echinoderms	Echinarachnius parma				% by occurrence	0%	% by occurrence	42 birds
428	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	crustaceans	Idotea baltica				% by occurrence	0%	% by occurrence	42 birds
429	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	unident spp.				% by occurrence	0%	% by occurrence	42 birds
430	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves					% of volume	89%		166 birds
431	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves					% of volume	96%		133 birds
432	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves					% of volume	97%	% of volume	42 birds
433	Stott & Olson 1973	velvet scoter		Rhode Island	marine	bivalves	Mercenaria mercenaria (mostly)				% of volume	90.70%		18 birds

434	Stott & Olson 1973	scoter		New England	marine	bivalves	Modiolus modiolus (mussel)							
435	Stott & Olson 1973	scoter		New England	marine	bivalves	Spisula solidissima							
436	Stott & Olson 1973	scoter		New England	marine	bivalves	Pecten concentricus							
437	Stott & Olson 1973	scoter		New England	marine	bivalves	Siliqua costata (razor shell)	25mm		38mm				
438	Stott & Olson 1973	velvet scoter		California	marine	bivalves	Solen sicarius				% of volume	92%		21 birds
439	Stott & Olson 1973	velvet scoter		California	marine	bivalves	Solen sicarius				% occurrence	91%		21 birds
440	Stott & Olson 1973	scoter		Massach-Maine	marine	bivalves	Yoldia spp				these seaducks had mainly taken three species of Yoldia			43 birds
441	Stott & Olson 1973	scoter		Massach-Maine	marine	bivalves	Spisula solidissima				very abundant in the benthos but not eaten at all by any of the three scoter species			
442	Stott & Olson 1973	scoter		Massach-Maine	marine	crustaceans	various species				abundant in the benthos but not eaten at all by any of the three scoter species			
443	Stott & Olson 1973	velvet scoter		California	marine	bivalves	Solen sicarius				the major proportion of the diet			
498	de Leeuw 1997c	velvet scoter			marine	bivalves	Mytilus edulis				white winged scoter feeding at the water surface chose smaller blue mussels than when diving			

Appendix 10 Notes concerning the sizes of prey consumed by diving ducks

record	source	species	season	location	habitat	taxonomic group eaten	species eaten	min (mm)	size (mm)	max (mm)	comment
3	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Mytilus edulis			40	
4	Cramp & Simmons 1977	common scoter			marine and brackish water areas	bivalves	Cerastoderma spp			40	
21	Cramp & Simmons 1977	common scoter			marine and brackish water areas	crustaceans	Carcinus			small	
29	Cramp & Simmons 1977	common scoter			freshwater	fish				small	
60	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Mytilus edulis	5		20	especially
61	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	cardium spp			20	especially
62	Cramp & Simmons 1977	velvet scoter			marine and brackish	gastropods	Nassa			25	especially
63	Cramp & Simmons 1977	velvet scoter			marine and brackish	bivalves	Mya			40	less often
77	Cramp & Simmons 1977	velvet scoter			marine and brackish	gastropods	Buccinium			60	less often
78	Cramp & Simmons 1977	velvet scoter			marine and brackish	crustaceans	Carcinus maenas		small		less often
79	Cramp & Simmons 1977	velvet scoter			marine and brackish	crustaceans	Eupagarus bernhardus		small		less often
86	Cramp & Simmons 1977	velvet scoter			marine and brackish	annelids	Arenicola			120	less often
88	Cramp & Simmons 1977	velvet scoter			marine and brackish	fish			small		rarely
97	Cramp & Simmons 1977	velvet scoter			freshwater	fish			small		
109	Lovvorn et al 2003	spectacled eider	winter	eiders selected N. radiata of 18-24mm (this size class was far more common in the diet in % number terms than it was in the benthic samples. Eiders ate few if any small specimens despite their high abundance. The largest size class 24-30 was rare in the benthos and in the birds diet but was more prevalent in the birds than in the benthic samples - ie birds take the bigger size classes. The consumption of N radiata in greater proportion than available, the lack of other prey taken and selection by length class suggest that eiders developed a search image for N radiata of 18-24mm long.							
112	Lovvorn et al 2003	spectacled eider	winter	N. radiata eaten by spectacled eiders were of intermediate length. Several studies have shown size selection of bivalves by diving ducks and especially common eider eating mussels. Size selection has been explained by differential handling times, effects on meat/shell ratios on nutrient gain relative to passage rates or as a means of avoiding the risk of ingesting prey that are too large.							

113	Lovvorn et al 2003	spectacled eider	winter	Eiders probably consumed N radiata of intermediate length because most of the biomass was in that range and because energy intake per unit handling time (profitability) was greater than for smaller clams.							
126	Cramp & Simmons 1977	velvet scoter	autumn	USSR	freshwater	fish			small		by volume
146	Durinck 1993	common scoter	winter	Denmark (north sea)	marine	bivalves	Spisula subtruncata	9	15.3	19	by frequency
147	Durinck 1993	common scoter	winter	Denmark (north sea)	marine	bivalves	Cardium edule	8	11.4	15	by frequency
150	Durinck 1993	velvet scoter	winter	Denmark (north sea)	marine	bivalves	Spisula subtruncata	10	15.2	19	by frequency
151	Durinck 1993	velvet scoter	winter	Denmark (north sea)	marine	bivalves	Cardium edule	9	11.6	14	by frequency
152	Durinck 1993	common scoter	winter	Denmark (kattegat)	marine	molluscs					10-20 the preferred size
153	Durinck 1993	velvet scoter	winter	Denmark (kattegat)	marine	bivalves	Spisula spp	10		12	smaller than 30mm
220	Fox 2003	common scoter				crustaceans	crabs		small		also figure in oesophagus
246	Fox 2003	common scoter			marine	bivalves		5 to 10		20	
247	Fox 2003	common scoter			marine	bivalves	Mytilus edulis			30	
248	Fox 2003	common scoter			marine	bivalves	Mya spp			40	
249	Fox 2003	velvet scoter			marine	gastropods	Buccinium undulatum			60	
250	Fox 2003	velvet scoter			marine	molluscs				50	
251	Fox 2003	common scoter			marine	bivalves	Mya arenaria	5		30	
252	Fox 2003	common scoter	winter	Wales	marine	bivalves	Donax vittatus		28		
253	Fox 2003	common scoter		Germany	marine	bivalves	Cyprina islandica		15.3	30	very few specimens larger than 30
254	Fox 2003	scoter		Denmark	marine	bivalves	in study by Durinck et al 1993 there were significant differences in the sizes of Cardium and Spisula eaten by both common and velvet scoter suggesting neither scoter spp selects for a specific size class of prey but take a subset of what is available to them				

255	Fox 2003	common scoter	winter	Denmark	marine	molluscs		3		9	the presence of large numbers of very small prey items in the sample from Helgenaes suggests that there is not an obvious lower critical threshold that limits prey size since none of the abundant prey was found to exceed 10mm.
256	Fox 2003	common scoter	summer	Denmark	marine	molluscs		8		15	it would seem likely that there is an upper limit to the size of hard prey taken which seems to be around 30-40mm
257	Fox 2003	scoter	it also seems likely that the wide range of prey sizes within the range taken reflects the local conditions in some way.								
259	Fox 2003	scoter	difficult to differentiate between the hypotheses that scoter select for specific prey size or simply take prey in proportion to their availability								
265	Kirby et al 1993	common scoter	winter	Britain	marine	fish			small		
268	Owen et al 1986	velvet scoter	takes larger prey items than the common scoter, stays closer to the shore and has a more varied diet								
278	Toba et al 1992	scoter		Washington	marine	bivalves	Tapes phillipinarum	6		20	Three duck species (ie all 3 scoter spp) are known to be significant predators on manila clams within the 6-20mm size range (Toba et al 1992).
279	Toba et al 1992	scoter		Japan	marine	bivalves	Tapes phillipinarum			25	In Japan, scoter were seen to consume as many as 52 small clams (<25mm mean shell length) per bird per day for 150 consecutive days (Cahn 1951 in Toba et al 1992).
282	Bourne 1984	scoter		Washington	marine	gastropods					25% of ducks. Mainly small and formed a minor part of the inorganic matter in the gut
299	Bourne 1984	scoter		Washington	marine	stones				25	
300	Bourne 1984	scoter		Washington	marine	bivalves	Mytilus edulis			30	
301	Bourne 1984	velvet scoter		Washington	marine	bivalves	Mytilus edulis			45mm	
302	Bourne 1984	velvet scoter		Washington	marine	bivalves	clams	10		>40mm	
303	Bourne 1984	surf scoter		Washington	marine	bivalves	clams	<10		40mm	
304	Bourne 1984	velvet scoter		Washington	marine	bivalves	Saxidomus giganteus	20		40	
312	Hamilton et al 1999	common eider	all year	preferred smaller mussels than those that would have been the most energetically profitable. During most of the year (spring summer and autumn) they select relatively small mussels that MINIMISED SHELL INGESTION. In winter, differences among length classes in shell ingestion became small and birds switched to feeding on larger prey that provided more energy per unit work and probably were more profitable.							

314	Hamilton et al 1999	common eider	all year	for most of the year, ducks selected prey that allowed them to MINIMISE SHELL INGESTION when large differences between shell length classes were evident. However, when shell mass was least variable among mussel length classes, common eiders appeared to switch tactics in an attempt to maximise short term energy intake by taking large mussels (when really pushed for energy???)							
315	Hamilton et al 1999	red knot		birds selected Macoma balthica that minimised shell intake relative to the amount of tissue ingested.							
316	Hamilton et al 1999	common eider		energy INTAKE maximisation appears NOT to be the primary factor influencing prey selection by common eider (although maybe maximisation of assimilated energy is given the higher efficiency with which they can probably digest meals consisting of a lower % of shell??)							
326	Bustnes 1998	common eider		the results of this study strongly indicate that reducing the amount of indigestible shell is an important factor for eiders selecting among mussels of different lengths							
326	Meissner & Brager 1990	common scoter	winter	Baltic	marine	bivalves	Arctica islandica	3.5	15.3	31.8	18.50%
327	Bustnes 1998	common eider		Length had a highly significant effect on the % of mussels eaten within 6 size classes (negative).							
329	Bustnes 1998	common eider		Nehls 1995 showed that eiders selected large mussels (55mm) during winter but during the summer after the large mussels had spawned (much higher relative shell content) they fed predominantly on the smaller non-spawning mussels							
330	Bustnes & Erikstad 1990	common eider		common eiders select mussels below the mean size found in the mussel beds (refs) as do other duck spp (ref)							
331	Bustnes & Erikstad 1990	common eider		eiders select (smaller) mussels to minimise the ratio of shell to flesh weight in their daily intake of food							
338	Draulans 1982	tufted duck	captive	the ducks did not prefer the most profitable prey (caloric yield per unit handling time) but took significantly smaller mussels							
339	Draulans 1982	tufted duck	captive	increasing prey density and decreasing depth caused an increase in selectivity (less time spent travelling to and from bottom and less time needed to find each mussel means more time to assess and consume/reject mussels)							
340	Draulans 1982	tufted duck	captive	increasing prey density caused a transition towards preference for smaller mussels							
342	Draulans 1982	tufted duck	captive	not perfect - the greater the differences in the sizes of mussels offered the more the birds will select for one size class							
345	Stempniewicz 1986	velvet scoter	winter	Baltic	marine	bivalves	Mya arenaria			52mm	%of food content (by mass)
346	Draulans 1984	tufted duck	winter	an increasing risk of taking unprofitable mussels caused a decrease in mean mussel size eaten							
378	Goudie & Ankney 1986	common scoter	winter	Newfoundland	marine	bivalves	Mytilus edulis		6.3		% of mass in gullet
382	Stott & Olson 1973	velvet scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa			50mm	% by volume
390	Stott & Olson 1973	surf scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa			<50mm	% by volume
398	Stott & Olson 1973	common scoter	winter	Massach-Maine	marine	bivalves	Siliqua costa			<50mm	% by volume
413	de Leeuw 1997g	diving ducks		selection for small sizes would become less profitable in winter (because takes longer underwater, and the heat generated by crushing big shells will help to offset thermoregulatory requirements)							
425	de Leeuw 1997h	diving ducks		may be limited by the short time available for selection while diving at high energetic costs							
437	Stott & Olson 1973	scoter		New England	marine	bivalves	Siliqua costata	25		38	
498	de Leeuw 1997c	velvet scoter			marine	bivalves	Mytilus edulis	white winged scoter feeding at the water surface chose smaller blue mussels than when diving			

Appendix 11 Notes concerning the instantaneous intake rates and functional responses of diving ducks

record	source	species	food item	prey size	prey depth (cm)	equation	dependent/ independent variables	min	value	max	comments
1	Richman & Lovvorn 2003	a type II functional response (limited by handling time)…often typifies diving duck foraging on benthic foods									
2	Richman & Lovvorn 2003	effects of prey depth have seldom been studied for diving ducks									
3	Richman & Lovvorn 2003	nutrient and energy content, digestibility and crushing resistance of shells can vary with both species and size of bivalves and various studies have shown size selection of bivalves by diving ducks (none of these are on scoter though, all being of tufted ducks or eiders). In these studies, preference for smaller bivalves than expected was explained by differential availability, handling times, effects of meat: shell ratios on nutrient gain relative to passage rates or as a means to avoiding prey that are too large to swallow. Resistance of shells to crushing in the gizzard may also affect selection of species and sizes of bivalve prey									
4	Richman & Lovvorn 2003	velvet scoter	Macoma balthica	18-24mm	4	I=0.7483X/(591+X)	I=clams consumed per sec on the bottom and X=clams per sq m	intake rates of smaller clams 18-24mm were limited by clam density up to at least 2000/sq m			
5	Richman & Lovvorn 2003	velvet scoter	Macoma balthica	24-30mm	4	I=0.496X/(209+X)	I=clams consumed per sec on the bottom and X=clams per sq m	intake rates of larger clams 24-30mm were more limited by handling time at densities >400/sq m			
6	Richman & Lovvorn 2003	velvet scoter	Macoma balthica	18-24mm	7	I=0.5396X/(682+X)	I=clams consumed per sec on the bottom and X=clams per sq m	intake rates of smaller clams 18-24mm were limited by clam density up to at least 2000/sq m			
7	Richman & Lovvorn 2003	velvet scoter	Macoma balthica	24-30mm	7	I=0.2955X/(139+X)	I=clams consumed per sec on the bottom and X=clams per sq m	derived from the other 3 measured responses			
8	Richman & Lovvorn 2003	velvet scoter	Nuculana radiata					not significantly different to the Macoma FR			
9	Richman & Lovvorn 2003	spectacled eider	Macoma balthica					not significantly different to the Macoma FR of the velvet scoter			
10	Richman & Lovvorn 2004	a type 2 functional response in which IR increases with prey density up to an asymptote where intake is limited by handling time, often typifies diving duck foraging on benthic foods (Takekawa 1987 thesis, Giles 1990, Lovvorn & Gillingham 1996 and Richman & Lovvorn 2003)									

11	Richman & Lovvorn 2004	scaup (lesser)	Potamogeton pectinatus tubers	<6 and 6-12mm	3	I=3.752X(3260+X)	I=tuber pieces consumed per sec on the bottom and X=tuber pieces per sq m	At depths of both 3cm and 6cm intake rates continued increasing with increasing tuber density up to at least 4000 tubers/sq m			
12	Richman & Lovvorn 2004	scaup (lesser)	Potamogeton pectinatus tubers	< 6mm	6	I=0.657X/(4018+X)	I=tuber pieces consumed per sec on the bottom and X=tuber pieces per sq m	At depths of both 3cm and 6cm intake rates continued increasing with increasing tuber density up to at least 4000 tubers/sq m			
13	Richman & Lovvorn 2004	scaup (lesser)	Nuculana radiata	<12mm	3	intake rates by two scaup feeding on freshly thawed clams at densities of 100, 250, 500 and 1000 clams/sq m did not differ from those of four scaup feeding on tubers at the same densities. These results indicate that functional responses based on feeding trials with tubers can be extrapolated to freshly thawed clams.					
14	Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)			our analyses indicate that foraging profitability and amount of viable habitat are most affected by variations in FOOD-ITEM SIZE (MASS PER BUD) AND IN LOCOMOTOR COSTS OF DESCENT AS INFLUENCED BY WATER DEPTH. The gradient and asymptote of the FR (buds eaten per sec v buds per sq m) were much less important **probably because unlike our functional responses, the x axis is not truly biomass**					
15	Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)			variations in water temperature above 0 have relatively little effect on foraging costs					
16	Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)			variations in mass per prey item (bud) alter profitability much more than do variations in bud metabolisable energy, mean bud density or intake rates at different bud densities					
17	Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)			variations in bud dispersion have relatively minor effects on profitability in this habitat					
18	Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)								
19	Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)		2.5-6.4	I=0.193X/(29.5+X)	I=buds consumed per second at the bottom and X=number of buds per sq m				fitted to the empirical data of Takekawa's 1987 thesis
20	Lovvorn & Gillingham 1996	canvasback	Vallisneria americana (buds)								assume canvasbacks search for buried winter buds by touch
21	Lovvorn 1994	canvasback	Vallisneria americana (buds)			I=0.0727X**0.552	I=tubers eaten PER DIVE and X = tubers per sq m				based on data from Takekawa 1987

22	Carbone 1995	pochard	mealworms		2.5	I=0.0814+0.0014*X	I=mealworms consumed per second at the bottom, X=mealworms per sq m				both food density and substrate depth influenced the rate of consumption
23	Carbone 1995	pochard	mealworms		1.25		I=mealworms consumed per second at the bottom		0.67		both food density and substrate depth influenced the rate of consumption
23	Carbone 1995	pochard	mealworms		3.75		I=mealworms consumed per second at the bottom		0.3		both food density and substrate depth influenced the rate of consumption
24	Giles 1989	tufted duck(lings)	chironomid larvae			I=-0.51+0.00087*X	I=chironomids consumed per dive, X= chironomid larve per sq m				range of prey densities from 2000-16,000 per sq m yielded a linear response
25	Giles 1989	tufted duck(lings)	chironomid larvae	4.4mgdryweight		I=0.6152+0.0003*X	I=chironomids consumed per second on the bottom, X= chironomid larve per sq m	range of prey densities from 2000-16,000 per sq m yielded a linear response. The point of levelling of the curve was not reached in the present study. **This is perhaps not surprising since natural chironomid densities can reach at least 4-5 times this value**			
26	Giles 1989	tufted duck(lings)	chironomid larvae	while the food density remained at 2000 per sq m ducklings achieved a feeding success rate of c 1 larvae per dive; this increased to > 2 larvae per dive when the density of chironomids was doubled to 4000 per sq m. The doubling of food density had no obvious effect upon either dive duration or the proportion of dives made on to the food tray							
27	Systad et al 2000	common eider		ingestion of food per unit time was higher in midwinter than in spring and gizzard size increased to cope with the higher processing rates during the coldest period							
28	Carbone & Houston 1994	pochard	mealworms			I=0.0814+0.0014*X	I=mealworms consumed per second at the bottom, X=mealworms per sq m				rsq=0.9996 (three density values used (125, 375 and 500 worms per sq m)
29	Carbone & Houston 1994	pochard	mealworms		1.25		mealworms consumed per sec on the bottom		0.67		rates of consumption (while on the bottom) were significantly affected by sand depth in which mealworms were buried
30	Carbone & Houston 1994	pochard	mealworms		3.75		mealworms consumed per sec on the bottom		0.3		rates of consumption (while on the bottom) were significantly affected by sand depth in which mealworms were buried
31	Carbone et al 1996		mealworms	0.087g/ worm							26g live weight of worms = 300 worms

32	Carbone et al 1996		mealworms	0.087g/ worm							100g live weight of worms = 1150 worms
33	Lovvorn 1989	canvasback	clams	we lack information on… minimum clam densities required for diving ducks to forage efficiently… More work is needed on clam abundance and its determinants but also on… foraging efficiency of diving ducks.							
34	Guillemette et al 1996			a reduction in prey availability can affect the profitability of foraging since diving ducks react promptly to changes in prey density							
35	de Leeuw 1997d	tufted ducks	mealworms		2		mealworms consumed per sec (on the bottom)		0.46		consumption rate of mealworms declined significantly as the depth of the sand in which the prey were buried increased
36	de Leeuw 1997d	tufted ducks	mealworms		4		mealworms consumed per sec (on the bottom)		0.14		consumption rate of mealworms declined significantly as the depth of the sand in which the prey were buried increased
37	de Leeuw 1997d	tufted ducks	mealworms	rates of consumption did not affect foraging time (on bottom) in Pochard (Carbone & Houston 1994) nor did intake rate have a strong effect on the predicted foraging time (Houston & carbone 1992). ie higher or lower IR does NOT affect how long birds spend foraging on the bottom!!!!!!!							
38	de Leeuw 1997f	tufted ducks	mealworms				gFW consumed per sec diving		0.04		maximum intake rate recorded
39	de Leeuw 1997g	tufted ducks	Dreissena	due to the low flesh content of mussels, daily consumption was extremely high (up to 3times the birds body mass of 600g)							
40	de Leeuw 1997h	tufted ducks/ scaup	Dreissena	daily consumption of mussels (on the basis of fresh mass) was about 2-3 times the body mass of the birds because of the large water content and shell content and consequently low nutritional value of the mussels							
41	de Leeuw 1997h	tufted ducks/scaup	Dreissena	scaup proved more efficient foragers at low mussel density than tufted ducks but intake rates seemed unaffected at densities of mussels higher than c 100gFW per sq m							
42	de Leeuw 1997h	scaup	Dreissena				gFW per sec underwater		0.46		at 1m depth
43	de Leeuw 1997h	scaup	Dreissena				gFW per sec underwater		0.42		at 3m depth
44	de Leeuw 1997h	scaup	Dreissena				gFW per sec underwater		0.36		at 5m depth
45	de Leeuw 1997h	scaup	Dreissena	7-30mm		I=0.45X/(7.4+X)	gFW per sec underwater (1.5m deep)	apparent intake rate while underwater based on timing and counting of dives and before and after measurement of mussel densities etc. The max value of 0.45 was determined from intake rates observed in scaup feeding in diving cages at mussel densities of > 2000 gfw per sq m. The searching coefficient is the only parameter fitted here having forced in the asymptotic value first			
46	de Leeuw 1997h	tufted duck	Dreissena	7-30mm		a type 3 sigmoid curve was fitted but the eqn is not given	gFW per sec underwater (1.5m deep)			0.35	this is the asymptotic value determined as described above for scaup (i.e. record No 45)

47	de Leeuw 1997h	tufted ducks/ scaup	although the food intake rate itself is usually NOT LIMITING the energy procurement, the efficiency of food gathering may indirectly influence the amount of food to be processed, and thus the time needed for food processing, owing to the high feeding costs in these birds. Diving costs contribute c 25% to the DEE of scaup and tufties in winter, while the energy costs of food processing account for a similar proportion. A decrease in INTAKE RATE results in higher diving costs to obtain a GIVEN QUANTITY of food. This extra diving cost must be compensated by a higher DAILY food intake, which also increases the food processing costs per day and in turn, further increases diving cost to obtain this EXTRA FOOD. Thus, diving ducks face the problem that any adverse effect on feeding performance will disproportionately increase total feeding effort on a daily basis and consequently increases in DEE and foraging times.		
48	de Leeuw 1997h	scaup	Dreissena	7-30mm	depletion reduces, however, the density of the food source and this will increase the searching effort. From the functional response curves, it appeared that scaup were feeding very efficiently at low mussel densities. This suggests that searching for food is only limiting at EXTREMELY LOW DENSITIES while handling prey is usually limiting.
49	de Leeuw 1997h	scaup	Dreissena	7-30mm	the result of the patch experiment suggests that scaup prefer to deplete patches SEQUENTIALLY rather than constantly searching for sites with high food densities. This is in accordance with the expectation that handling time mainly determines intake rate and only at very low densities will high searching effort per prey item affect the intake rate. **With a flat functional response and a limited perceptive ability the model should indeed predict that birds stay put and deplete patches a lot before moving to another patch.**
50	de Leeuw 1997h	tufted duck	Dreissena	7-30mm	intake rates of tufties were considerably lower at low mussel densities than the intake rates of scaup
51	de Leeuw 1997h				as a consequence of increasing searching effort with depletion, diving may become too costly for further exploitation of the food source and ducks may have to give up foraging in that patch (BASED ON NET ENERGETIC REWARD RATHER THAN JUST INTAKE RATE)
52	de Leeuw 1997i	tufted duck	Dreissena		a reduction in foraging success (apparent intake rate per sec underwater) of 20% from the maximum (asymptotic value) will incur an increment in DEE of 25% in tufted duck. Because of these extremely narrow margins we may expect that diving ducks favour areas with high densities of mussels and a high probability of encountering mussels.
53	de Leeuw 1997i	tufted ducks/ scaup			tufted duck also seem more sensitive to variation in mussel density than scaup probably because searching efficiency is lower (ie a shallower functional response) and a reduction in density more strongly reduces AIR and hence increased DEE

Appendix 12 Notes concerning the constraints on rates of food intake by diving ducks

record	source	species	parameter	units	min	value	max	comment
42	Richman & Lovvorn 2003	common eider	gut capacity (gizzard)	grams		20		
43	Richman & Lovvorn 2003	common eider	meal size	grams		60-100		
55	Lovvorn & Gillingham 1996	canvasback	gut capacity	g dry mass		4.65		maximum content of oesophagus which limits prey items consumable per foraging bout
91	Richman & Lovvorn 2004	scaup (lesser)	gut capacity					time required to clear the oesophagus-proventriculus may limit intake rate by scaup over short periods, but intake rate does not seem to be directly constrained by mean retention time
124	Bourne 1984	scoter	gut capacity	g fresh mass		80		crop and gizzard
201	Stempniewicz 1986	velvet scoter	gut capacity	g fresh mass		18.5+/-15.3		stomach contents (mean +/1sd)
202	Stempniewicz 1986	common scoter	gut capacity	g fresh mass		9.7+/-6.9		stomach contents (mean +/1sd)
203	Stempniewicz 1986	velvet scoter	gut capacity					the average weight of the contents of adult females was much smaller than that of adult males, and being smaller than males, had a diet that was rather more like that of common scoter (ie fewer fish and more Cardium)
263	Guillemette 1998	common eider	gut capacity (of gizzard)	g fresh mass		20		ingestion rate of shells is approx twice as high as the defecation rate and concluded that energy assimilation is constrained by digestion in this species
271	Guillemette 1998	common eider	gut processing rate	g fresh mass per min	2.4		6.1	the rate at which the shells are processed in the gizzard. This is the ultimate factor limiting digestion and hence energy assimilation in this species
323	de Leeuw 1997h	tufted duck	MMEI (kj/hr)	kJ/hr		40		from Kirkwood 1983 allometric equation
324	de Leeuw 1997h	scaup	MMEI (kj/hr)	kJ/hr		50		from Kirkwood 1983 allometric equation
326	de Leeuw 1997h	tufted duck	MMEI (kj/day)	kJ/day		1185		
327	de Leeuw 1997h	scaup	MMEI (kj/day)	kj/day		1435		
328	Bustnes 1998	common eider	gut processing rate					Guillemette (1994) found that eiders ingested blue mussels TWICE AS FAST as they were able to digest them, showing the importance of the digestive constraint. The general problem for these birds is thus not to find food (fast enough) but to locate prey with sufficient energy density to fulfil the daily requirement
332	Bustnes & Erikstad 1990	black duck	gut processing rate					common mussels pass through the digestive tract of black ducks Anas rubripes in about 30-40 mins
339	de Leeuw 1997i	tufted duck	mean increase in fat mass per day (g)	grams		3		
340	de Leeuw 1997i	scaup	mean increase in fat mass per day (g)	grams		4		

412	de Leeuw 1997g	Dreissena	constituents					zebra mussels comprise c 56% water, 6% dry flesh mass and 38% shell
416	de Leeuw 1997h	tufted duck/ scaup	gut capacity					the limited capacity to store food in the body and long digestive pauses imply that diving ducks have to spend a large fraction of the day on the feeding grounds
419	de Leeuw 1997h	scaup	gut capacity	g fresh mass		35	40	per feeding bout c 35gFW of mussels were ingested. This is close to the 40gfw of mussels found in the oesophagi of 2322 drowned wild scaup. It appears that the oesophagus is filled during a feeding bout and mussels are crushed in the gizzard later
420	de Leeuw 1997h	scaup	gut capacity	g fresh mass		55		the amount that can be in the gizzard and intestines (as opposed to the 35g in the oesophagus)
421	de Leeuw 1997h	scaup	gut capacity	g fresh mass		90		the amount in the oesophagus, gizzard and intestines combined
422	de Leeuw 1997h	scaup	gut processing rate	mins		25		the rate of food processing is apparently the factor that limits crude intake rate over a period of several hours
423	de Leeuw 1997h		gut processing rate	mins				the timing of diving activity is structured by the rate of food processing
447	Ball 1994	canvasback	gut capacity	g fresh mass				the total volume of food eaten must be less than or equal to the capacity of the upper digestive tract multiplied by the number of times the upper digestive tract is emptied during the period concerned.
448	Ball 1994	canvasback	gut capacity	ml		33		of the upper intestinal tract only
449	Guillemette et al 1992	common eider	gut capacity	g fresh mass	64		93	oesophagus only. Corresponds to 3.5%-5% of body mass
452	Guillemette et al 1992	common eider	gut processing rate (mins)					…digestion rate is much slower than the ingestion rate. We suggest that resting after a meal provides time to process a part of the food ingested and to lose mass by defecation and excretion. It follows that resting bouts can be considered as an obligatory part of the foraging behaviour of the eider. Together these considerations stress the importance of measuring the intake rate at THE SCALE OF A FORAGING CYCLE OR A DAY IN ORDER TO TAKE INTO ACCOUNT THE HIDDEN HANDLING TIME THAT IS OCCURRING WITHIN THE DIGESTIVE SYSTEM.

Appendix 13 Notes concerning the efficiency of assimilation by diving ducks

record	source	species	parameter	min	value	max	comment
37	Richman & Lovvorn 2003	eider	assimilation efficiency when eating Nuculana radiata		0.573		including shells (Nuculana radiata)
38	Richman & Lovvorn 2003	eider	assimilation efficiency when eating Macoma calcarea		0.544		including shells (Macoma calcarea)
46	Richman & Lovvorn 2004	scaup (lesser)	assimilation efficiency		0.505		including shells (Potamocorbula amurensis)
47	Richman & Lovvorn 2004	scaup (lesser)	assimilation efficiency		0.45		including shells (Macoma balthica)
48	Richman & Lovvorn 2004	black ducks	assimilation efficiency				Jorde & Owen (1988) found higher digestibility for blue mussels than for soft shelled clams (Mya arenaria) when the ash content of mussels was about 12% lower.
49	Richman & Lovvorn 2004		assimilation efficiency				variations in digestibility between these and other species may be partly explained by differences in the relative fractions of structural and soluble carbohydrate

Appendix 14 Notes concerning the energy density of the prey species of diving ducks

record	source	location	season	species	parameter	value	age/size	comment
39	Richman & Lovvorn 2003	Canada	august	Macoma calcarea	energy density (kJ/gdm)	17.97		without shells
40	Richman & Lovvorn 2003	Canada	august	Nucula minuta	energy density (kJ/gdm)	16.37		without shells
41	Richman & Lovvorn 2003	Canada	august	Nucula belloti	energy density (kJ/gdm)	16.83		without shells
69	Lovvorn et al 2003	Bering Sea	march	Nuculana radiata	energy density (kJ/gdm)	2.663	6-12mm	including shells
70	Lovvorn et al 2003	Bering Sea	march	Macoma calcarea	energy density (kJ/gdm)	*	6-12mm	including shells
71	Lovvorn et al 2003	Bering Sea	march	Nucula belloti	energy density (kJ/gdm)	4.189	6-12mm	including shells
72	Lovvorn et al 2003	Bering Sea	march	Nuculana radiata	energy density (kJ/gdm)	3.508	12-18mm	including shells
73	Lovvorn et al 2003	Bering Sea	march	Macoma calcarea	energy density (kJ/gdm)	4.278	12-18mm	including shells
74	Lovvorn et al 2003	Bering Sea	march	Nucula belloti	energy density (kJ/gdm)	4.55	12-18mm	including shells
75	Lovvorn et al 2003	Bering Sea	march	Nuculana radiata	energy density (kJ/gdm)	3.475	18-24mm	including shells
76	Lovvorn et al 2003	Bering Sea	march	Macoma calcarea	energy density (kJ/gdm)	5.645	18-24mm	including shells
77	Lovvorn et al 2003	Bering Sea	march	Nucula belloti	energy density (kJ/gdm)	*	18-24mm	including shells
78	Lovvorn et al 2003	Bering Sea	march	Nuculana radiata	energy density (kJ/gdm)	3.418	24-30mm	including shells
79	Lovvorn et al 2003	Bering Sea	march	Macoma calcarea	energy density (kJ/gdm)	6.324	24-30mm	including shells
80	Lovvorn et al 2003	Bering Sea	march	Nucula belloti	energy density (kJ/gdm)	*	24-30mm	including shells
162	Jorde & Owen 1988			gammarus	energy density (kcal/gdm)	3.52		true metabolisable energy/gram decreased as food intake increased, which indicated differences in the rate or efficiency of digestion (digestion, absorption and passage rates in the alimentary tract of small amounts of food were more efficient than for larger amounts of food ingested)
163	Jorde & Owen 1988			littorina	energy density (kcal/gdm)	0.27		ditto
164	Jorde & Owen 1988			Mya arenaria	energy density (kcal/gdm)	0.22		ditto

165	Jorde & Owen 1988			Mtyilus edulis	energy density (kcal/gdm)	0.52		ditto
167	Dauvin & Joncourt 1989	English Channel	all year round average	polychaeta	energy density (j per mgDW)	18.93		
168	Dauvin & Joncourt 1989	English Channel	all year round average	gastropoda	energy density (j per mgDW)	17.83		
169	Dauvin & Joncourt 1989	English Channel	all year round average	bivalvia	energy density (j per mgDW)	18.03		individual values available for 120spp including Abra alba, Spisula elliptica and various Tellinas and Venus spp.
170	Dauvin & Joncourt 1989	English Channel	all year round average	amphipoda	energy density (j per mgDW)	20.3		
171	Dauvin & Joncourt 1989	English Channel	all year round average	decapoda	energy density (j per mgDW)	19.22		
172	Dauvin & Joncourt 1989	English Channel	all year round average	ophiuroidea	energy density (j per mgDW)	17.02		
173	Dauvin & Joncourt 1989	English Channel	all year round average	polychaeta	energy density (j per mgAFDW)	21.11		
174	Dauvin & Joncourt 1989	English Channel	all year round average	gastropoda	energy density (j per mgAFDW)	19.42		
175	Dauvin & Joncourt 1989	English Channel	all year round average	bivalvia	energy density (j per mgAFDW)	19.73		
176	Dauvin & Joncourt 1989	English Channel	all year round average	amphipoda	energy density (j per mgAFDW)	21.1		
177	Dauvin & Joncourt 1989	English Channel	all year round average	decapoda	energy density (j per mgAFDW)	20.52		
178	Dauvin & Joncourt 1989	English Channel	all year round average	ophiuroidea	energy density (j per mgAFDW)	19.51		
179	Goudie & Ankney 1986			sea urchins	energy density (kj per g live mass)	1.2		
180	Goudie & Ankney 1986			amphipods	energy density (kj per g live mass)	5.9		
181	Goudie & Ankney 1986			Idotea baltica	energy density (kj per g live mass)	4.39		

182	Goudie & Ankney 1986			Mtytilus edulis	energy density (kj per g live mass incl shell)	1.92		
202	Beauchamp et al 1992			mussels	energy density (kj/gram dry mass)	20.51		
222	Bustnes & Erikstad 1990			Mytilus edulis	energy density (kcal per g dry flesh mass)	4.9		
227	Cantin et al 1974			Littorina	energy density (kcal g dry flesh mass)	3.4		
228	Draulans 1982			Mytilus edulis	energy density (kcal g dry flesh mass)	4.5		
307	de Leeuw 1997g			Dreissena	energy density			in Lake Ijsselmeer mussels from deeper water tend to have lower flesh contents up to 40% less at 5m cf 2m. This may limit the exploitation of deeper located mussels in addition to the greater diving efforts in deeper water
310	de Leeuw 1997h			Dreissena	energy density (kJ per g FreshWeight)	0.5		
311	de Leeuw 1997h			Dreissena	energy density (kJ per g FreshWeight)	0.6		
312	de Leeuw 1997h			Dreissena	energy density (kJ per g dry mass of flesh)	22.5		
337	de Leeuw 1997i			diving ducks	energy density of fat stores (kJ/g)	39.3		
377	Guillemette et al 1992			Mytilus edulis	energy density (kJ/gwetmass)	0.966		including the shell/test/carapace
378	Guillemette et al 1992			sea urchins	energy density (kJ/gwetmass)	0.58		including the shell/test/carapace
379	Guillemette et al 1992			spider crabs	energy density (kJ/gwetmass)	3.163		including the shell/test/carapace
381	de Leeuw 1997i			Dreissena	energy density (kj per g live mass)	0.4-0.6		
382	Guillemette & Larsen 2002			Cardium and Spisula	energy density (kj per g wet mass)	1.5		

Appendix 15 Notes concerning Danish studies of the response of birds to offshore windfarms

record	source	site	season	species	data type	parameter	min	value	max	comments
1	Petersen et al 2004	Horns Rev		common scoter	sea survey data	avoidance distance (km)	showed an increased avoidance of the windfarm area (and zones within 2km and 4km of it) after the erection of the turbines			
2	Petersen et al 2004	Horns Rev		common scoter	sea survey data	avoidance distance (km)	showed a difference in the spatial distribution within the study area in 2003 compared to previous years. An area southeast of the windfarm previously used by common scoter especially in Feb-April became less attractive to the species. Simultaneously areas north and west of the windfarm with previously very few scoter supported greater numbers in 2003.			
3	Petersen et al 2004	Horns Rev		common scoter	sea survey data	avoidance distance (km)	The reason for the change in avoidance of the windfarm for…common scoter… is unknown. Disturbance effects from the wind turbines are ONE POSSIBLE REASON. Disturbance from increased human activity associated with maintenance of the wind turbines could be another. BUT CHANGES IN THE DISTRIBUTION OF FOOD RESOURCES IN THE STUDY AREA COULD POTENTIALLY PLAY A ROLE TOO.			
4	Petersen et al 2004	Horns Rev		common scoter	sea survey data	disturbance frequency		150 days/ year		during the fully operational phase, service and maintenance of the turbines are expected to constitute 150 days per year and will be carried out partly from ship and partly from helicopter.
5	Petersen et al 2004	Horns Rev		common scoter	sea survey data	avoidance distance (km)		1.5		no common scoter was observed closer than 1.5km from the wind farm
6	Petersen et al 2004	Horns Rev		common scoter	sea survey data	water depth (m)	2	4 to 6	8	75% of birds were over depths of water between 2 and 8 m
7	Petersen et al 2004	Horns Rev		common scoter	sea survey data	avoidance distance (km)		2	4	common scoter were encountered within the wind farm area as well as the 2 and 4km zones around it SIGNIFICANTLY LESS THAN EXPECTED assuming an even distribution BOTH PRIOR TO AND FOLLOWING THE ERECTION OF THE WINDFARM. THE DEGREE OF AVOIDANCE INCREASED MARKEDLY FROM PRE TO POST CONSTRUCTION IN THE WIND FARM AREA ITSELF, WITHIN 2KM AND WITHIN THE 4KM ZONE.
8	Petersen et al 2004	Horns Rev		common scoter	sea survey data	avoidance distance (km)			8	there was a marked reduction in the post construction utilisation of the windfarm area and its immediate surroundings. This figure indicates a change in the distribution of common scoter out to a distance of approx 8km from the windfarm. Such an effect cannot be explained purely as a result of the visual stimulus of the turbines at such long range. A supplementary explanation involves the patchiness of the habitat exploited by the ducks.
9	Petersen et al 2004	Horns Rev		common scoter	sea survey data	avoidance distance (km)	common scoter were observed to avoid flying between wind turbines. When flying birds avoid turbines this will influence where birds settle to feed or rest. Thus the avoidance patterns shown by flying birds are likely to contribute to the overall avoidance distance shown by the species when counted on the water during aerial survey.			

10	Petersen et al 2004	Horns Rev		common scoter	sea survey data	avoidance distance (km)	the physical presence of the turbines is one major potential factor, but the increased boat traffic associated with maintenance of the wind farm will be another. However, given the lack of data relating to the benthic fauna it cannot be ruled out that changes in the distribution of food resources in the study area played a role in the observed shift in common scoter distribution.			
11	Christensen et al 2004	Horns Rev		all species	flight tracks	avoidance distance (km)	0.4		1	the majority of tracks either changed their orientation and passed around the windfarm, most reacting 400m from the farm (north side) or 1000m (east side) or disappeared from the screen.
12	Christensen et al 2004	Horns Rev		all species	flight tracks	avoidance distance (km)	the loss of tracks on the radar screen reflects an avian behavioural response to the wind farm by approaching birds. Since most tracks disappeared c400m from the outer turbines (north side) or 1000m (east side) these distances may represent the general extent to which flying birds avoid such structures			
13	Christensen et al 2004	Horns Rev		all species	flight tracks	collisions				it is expected that collisions may be very rare
14	Christensen et al 2004	Horns Rev		all species	flight tracks	avoidance distance (km)	0.4	migration orientation (from the north of the farm) changed significantly with distance to the windfarm from a SW direction to a S direction as more and more tracks turned westwards or disappeared so that those left for analyses close to the farm headed straight into it. The most dramatic shift was the significant shift in orientation at 400m from the windfarm		
15	Christensen et al 2004	Horns Rev		all species	flight tracks	avoidance distance (km)	there was a substantial decrease in the number of tracks with decreasing distance to the farm. Thus, few bird flocks actually entered the windfarm. The marked reduction in track numbers close to the windfarm partly reflects a lateral deflection in tracks moving directly west (to avoid the farm) but also the fact that many echoes for unknown reasons disappeared			
16	Christensen et al 2004	Horns Rev		all species	flight tracks	avoidance distance (km)			1.5	this is my take on figure 8 showing the point at which the number of tracks first starts to decline as the windfarm is approached (from the north), even though the biggest change in direction of the remaining tracks occurs at 400m.
17	Christensen et al 2004	Horns Rev		all species	flight tracks	avoidance distance (km)			2	this is my take on figure 9 showing the point at which the number of tracks first starts to decline as the windfarm is approached from the east, This is also the distance at which there is a bit of a jump in the mean direction of the tracks even though the biggest change in direction of the remaining tracks occurs at 400m.
18	Christensen et al 2004	Horns Rev		all species	flight tracks	avoidance distance (km)	as was the case north of the windfarm, the number of tracks declined with decreasing distance to the farm. Thus at the eastern row of turbines few birds/flocks actually entered the farm and those that did entered heading almost parallel with the turbine rows.			
19	Christensen et al 2004	Horns Rev		common scoter	flight tracks	avoidance distance (km)	of 293 scoter recorded during transect observations, 28 were recorded approaching the windfarm from the north. None of these birds were observed to enter the windfarm. Deflection was recorded both westwards and eastwards.			
20	Christensen et al 2004	Horns Rev		common scoter	flight tracks	avoidance distance (km)	0.3		1	…many of these flocks moved towards the windfarm several times before either passing west or east around the windfarm making turns at distances between 300m and 1000m
21	Christensen et al 2004	Horns Rev		common scoter	flight tracks	avoidance distance (km)				a total of 10 (out of 36,000) scoter was recorded in the windfarm itself. These few observations suggest that these species actively avoided the windfarm.
22	Christensen et al 2004	Horns Rev		common scoter	flight tracks	flight altitude (m)	0	4	8	sd = 5.2m n = 2 observations only#

23	Christensen et al 2004	Horns Rev		common scoter	flight tracks	flight speed (km/hr)	46.9	75.3	86.1	sd 10.7km/hr n= 11 obs
24	Kahlert et al 2004	Nysted		waterbirds	flight tracks	avoidance distance (km)				it was not possible to demonstrate a convincing change in migration orientation at a specific distance from the windfarm following its construction (in comparison with that before)
25	Kahlert et al 2004	Nysted	autumn	waterbirds	flight tracks	avoidance distance (km)	1		3	The standard deviation of the migration orientation increased significantly during the daytime at distances closer than 3000m to the windfarm in 2003 and closer than 1000m at night. These results support the hypothesis that migrating birds show a response to the windfarm, specifically reacting by increased lateral avoidance.
28	Kahlert et al 2004	Nysted	autumn	waterbirds	flight tracks	avoidance distance (km)	1		3	daytime observations showed more than twice the standard deviation at distances closer than 30000m to the windfarm in 2003 compared to the baseline years and in particular at distances closer than 1000m SD was MARKEDLY higher during operation compared to base-line.
29	Kahlert et al 2004	Nysted	autumn	waterbirds	flight tracks	avoidance distance (km)			1	During the night the response distance over which a significant increase in SD of migration tracks occurred was at 1000m. This suggested that birds came closer to the windfarm at night before they adjusted their course
30	Kahlert et al 2004	Nysted	autumn	waterbirds	flight tracks	avoidance distance (km)	1			thus, at a distance of 3000m but most markedly at 1000m, birds adjusted their flight course likely to be a response to the windfarm.
31	Kahlert et al 2004	Nysted	autumn	waterbirds	flight tracks	avoidance distance (km)	this means that after the wind turbines were erected in 2003, a flock of birds that approached the windfarm was significantly less likely to pass the eastern gate (and pass into it) compared to baseline years (ie in the absence of turbines).			
32	Kahlert et al 2004	Nysted	spring	waterbirds	flight tracks	avoidance distance (km)				during daytime there was no support for the hypothesis that birds avoided the wind farm area in the construction phase
33	Kahlert et al 2004	Nysted	spring	waterbirds	flight tracks	avoidance distance (km)				However, there were some indications that birds avoided the windfarm area at night during the construction phase
34	Kahlert et al 2004	Nysted	spring	common eider	flight tracks	flight speed (km/hr)	50	55	78	headwind
35	Kahlert et al 2004	Nysted	spring	common eider	flight tracks	flight speed (km/hr)	54	71	122	tailwind
36	Kahlert et al 2004	Nysted	autumn	waterbirds	flight tracks	avoidance distance (km)				track densities were significantly lower in 2003 (post construction) in the eastern part of the wind farm compared to baseline years.
43	Kahlert et al 2004	Nysted	winter-spring	waterbirds	flight tracks	collisions	even those birds entering the windfarm are not necessarily at risk from collision since the tracks clearly showed that many waterbirds are moving along the open corridors between the rows of turbines			
26	Kahlert et al 2004	Nysted	autumn	long-tailed duck	sea survey data	avoidance distance (km)				showed reduced preference for the windfarm area during construction

27	Kahlert et al 2004	Nysted	autumn	comon eider	sea survey data	avoidance distance (km)				showed reduced preference for the windfarm area during construction
37	Kahlert et al 2004	Nysted	winter-spring	long-tailed duck	sea survey data	avoidance distance (km)		no effect		the general distribution pattern based on baseline surveys showed the highest concentrations at Gedser Rev and in a band which extended westwards towards Hyllekrog. This was similar to the distribution found in 2003 (during and after construction)
38	Kahlert et al 2004	Nysted	winter-spring	common eider	sea survey data	avoidance distance (km)		no effect		In 2003 few eiders were recorded in the windfarm area. However, this followed the pattern observed in baseline years. Thus, the general distribution pattern in baseline years and construction years was similar
39	Kahlert et al 2004	Nysted	winter-spring	comon scoter	sea survey data	avoidance distance (km)		no effect		a flock of 12 birds were seen flying between the wind turbines during the Dec 2003 survey. The general distribution did not change much between pre and post construction
40	Kahlert et al 2004	Nysted	winter-spring	long-tailed duck	sea survey data	avoidance distance (km)			4	selectivity indices for the wind farm area plus 2km and 4km zones around it DECREASED DURING THE CONSTRUCTION PHASE indicating a reduced preference for these areas
41	Kahlert et al 2004	Nysted	winter-spring	common eider	sea survey data	avoidance distance (km)			4	selectivity indices for the wind farm area plus 2km and 4km zones around it DECREASED DURING THE CONSTRUCTION PHASE indicating a reduced preference for these areas
42	Kahlert et al 2004	Nysted	winter-spring	long-tailed duck	sea survey data	avoidance distance (km)				at distances of 0-15km from the turbines, 2 baseline years showed higher % of birds in the vicinity of turbines than one other baseline year and during construction (2003). A POSSIBLE EFFECT
44	Kahlert et al 2004b	Nysted	spring	common eider	flight tracks	flight speed (km/hr)	45	61	83	
45	Kahlert et al 2004b	Nysted	spring	waterbirds	flight tracks	avoidance distance (km)	11% OF ALL FLOCKS PASSED THE EASTERN EDGE OF THE WINDFARM IE AFTER FLOCKS MAY POTENTIALLY HAVE PASSED THROUGH THE ENTIRE WIND FARM. However, this was a lower % than during the baseline years but similar to the construction phase (2003)			
46	Kahlert et al 2004b	Nysted	spring	waterbirds	flight tracks	avoidance distance (km)	track densities in the reference area were generally significantly higher compared to the eastern part of the windfarm area. For 2004 this could indicate that birds which avoided the windfarm and passed north and south of it, changed their flight direction just after they had passed the windfarm to cross through the reference area east of the windfarm (on easterly migration)			
47	Kahlert et al 2004b	Nysted	spring	waterbirds	flight tracks	avoidance distance (km)	track densities were significantly lower in spring 2004 (operation) compared to spring 2001,2002 (baseline) and 2003 (construct). This supports the results obtained in autumn 2003 when the flight behaviour of the birds at their approach to the wind farm area (as assessed by the SD of the flight tracks) suggested that birds avoided the windfarm area to some extent. Further support for this conclusion could also be derived from the fact that track densities in the reference area further east of the farm was maintained at a relatively high level throughout the entire study (2001-2004)			
48	Kahlert et al 2004b	Nysted	spring	waterbirds	flying bird counts on transect	avoidance distance (km)	…tended to support the prediction of an avoidance response amongst migrating birds, as migration intensity (flocks seen per 15mins) was almost consistently lower during operation of the farm (2004) compared to baseline years (2000-2002). Migration intensity was lower again during construction.			

49	Kahlert et al 2004b	Nysted	spring	waterbirds	flight tracks	avoidance distance (km)	the results from the operation period in spring 2004 showed that waterbirds appeared less frequently (3-18%) at the eastern edge of the windfarm during most conditions compared to previous years. This was also supported by mean track densities in the eastern part of the windfarm which was generally lower compared to the baseline and construction period. Hence the results from spring 2004 support the conclusions from autumn 2003 when there were strong indications that part of the migrating waterbirds showed an avoidance response to the windfarm.			
51	Petersen 2004	Nysted	spring	common eider	sea survey data	avoidance distance (km)				few eiders were recorded in the windfarm area
54	Petersen 2004	Nysted	spring	common eider	sea survey data	avoidance distance (km)				the distribution pattern in 2004 spring resembled the general pattern observed in previous years.
57	Petersen 2004	Nysted	spring	common eider	sea survey data	avoidance distance (km)	in the operational phase (post construct) the selectivity index for the windfarm itself recovered compared to the construct phase and returned to baseline levels- so no more effect. The reduced selectivity for the 2km and 4km zones when under construction either continued to get worse (individual analysis) or did not improve (cluster analysis) so were still lower than baseline. So, still a significant effect during operation at the wider scales cf baseline conditions			
52	Petersen 2004	Nysted	spring	common scoter	sea survey data	avoidance distance (km)				no common scoter were observed in the vicinity of the windfarm during the four spring surveys in 2004
55	Petersen 2004	Nysted	spring	common scoter	sea survey data	avoidance distance (km)				the distribution pattern in 2004 spring resembled the general pattern observed in previous years.
50	Petersen 2004	Nysted	spring	long-tailed duck	sea survey data	avoidance distance (km)				60 birds were recorded in the windfarm area
53	Petersen 2004	Nysted	spring	long-tailed duck	sea survey data	avoidance distance (km)				the distribution pattern in 2004 spring resembled the general pattern observed in previous years.
56	Petersen 2004	Nysted	spring	long-tailed duck	sea survey data	avoidance distance (km)	in the operational phase (post construct) the selectivity index for the windfarm itself recovered compared to the construct phase but was still lower than under baseline conditions. The reduced selectivity for the 2km and 4km zones when under construction did not improve after construction so were still lower than baseline. So, still a significant effect during operation at all scales cf baseline conditions			
58	Petersen 2004	Nysted	spring	long-tailed duck	sea survey data	avoidance distance (km)			7	At distances of up to 7km from the turbines the cumulative % of LTDs was highest in 2001 and 2002 (pre) and lowest in 2000 (pre) and 2003 (construct). The data for 2004 (post) showed a similar curve to that for 2000 and 2003 ie few birds within 7km. So maybe an effect but 2000 was a baseline year. (Fig 26)
59	Petersen 2004	Nysted	spring	long-tailed duck	sea survey data	avoidance distance (km)			20	In spring 2004, the cumulative % of LTDs seen increased more slowly than in any previous year up to a distance of 20km from the turbines (Fig 26)

60	Petersen 2004	Nysted	spring	long-tailed duck	sea survey data	avoidance distance (km)	within a 4km radius only, the cum % of LTDs seen increased most rapidly in 2001 and 2002 (pre), somewhat less in 2000 (pre), and least rapidly in 2003 (construct). The curve for 2004 (post) was intermediate up to 2km and thereafter more like the baseline years up to 4km. Maybe construction scares birds more thoroughly in the immediate vicinity of the farm than the turbines themselves do later, but the turbines on their own after construction have a more pronounced effect over much larger distances (up to 20km???)			
142	Guillemette & larsen 2002	Tuno Knob	winter-spring	common eider						the wind park did not substantially affect wintering common eiders
143	Guillemette & larsen 2002	Tuno Knob	winter-spring	common eider			any permanent disturbance effects from wind turbines would translate directly into habitat loss….it has been concluded that disturbance to resting/foraging birds is the main problem related to wind parks, whereas collisions are likely to be a minor concern (Brenner et al 1993)			
145	Guillemette & larsen 2002	Tuno Knob	winter-spring	common eider				600m		this was based on observations conducted on three spatial scales suggesting that negative impacts (of wind turbines) were unlikely to occur at larger distances (Guillemette et al 1998)
147	Guillemette & larsen 2002	Tuno Knob	winter-spring	common eider						the operating wind turbines did not appear to affect the abundance or spatial distribution of eider
148	Guillemette & larsen 2002	Tuno Knob	winter-spring	common eider						variation in the eider numbers counted in one zone was almost entirely explained by the amount of bivalve food present, this leaving little variation to be explained by wind turbines.
150	Guillemette & larsen 2002	Tuno Knob	winter-spring	common eider						the wind turbines do not appear to play any role in the exploitation pattern of eiders during the winter
151	Guillemette & larsen 2002	Tuno Knob	winter-spring	common eider			eiders appeared to avoid flying and landing in close proximity (100m) to the wind park. Because the flying and reacting rates were similar for eiders 300m and 500m from the turbines, the impact of the turbines was only in the immediate vicinity of the windpark.			
153	Guillemette & larsen 2002	Tuno Knob	winter-spring	scoter						scoter have a different flock structure and seem to be more easily disturbed than eiders
154	Guillemette & larsen 2002	Tuno Knob	winter-spring							individuals in large flocks are more easily disturbed than those in small flocks, which is apparently true for other waterfowl spp (ref)
155	Guillemette & larsen 2002	Tuno Knob	winter-spring							..strongly suggest that the best way to lessen any potential impact on seaducks is to avoid the building of offshore windfarms on bottoms characterised by large biomass of prey.

Appendix 16 Notes concerning the proportion of time spent feeding by diving ducks

record	source	species	parameter	min	value	max	comments
208	Systad et al 2000	common eider	proportion time diving (below surface only ie excluding interdive pauses on surface)	0.169		0.257	increased as daylength shortens (0.169 in April and 0.257 in December)
209	Systad et al 2000	king eider	proportion time diving (below surface only ie excluding interdive pauses on surface)		0.233		did not change significantly with changing daylength (mean c0.233)
210	Systad et al 2000	long-tailed duck	proportion time diving (below surface only ie excluding interdive pauses on surface)	0.334		0.546	increased as daylength shortens (0.334 in April and 0.546 in November). This (0.53 midwinter) may be close to the max possible rate for the species
211	Systad et al 2000	eiders (common and king)	% time on feeding grounds				birds spent more time in the study area before and after twilight when the days were short than when the days were long
212	Systad et al 2000	common eider	time spent diving per day (mins)	73	100	144	longer total time underwater in daylight when more hours of daylight
213	Systad et al 2000	king eider	time spent diving per day (mins)	57	102	161	longer total time underwater in daylight when more hours of daylight
214	Systad et al 2000	long-tailed duck	time spent diving per day (mins)	148	232	382	longer total time underwater in daylight when more hours of daylight. NB much longer time spent underwater by the smaller long-tailed ducks cf eiders
216	Systad et al 2000	eiders	% dive time per day				..especially in December and January when feeding was extended into the afternoon darkness
217	Systad et al 2000		% time feeding				compared to most other waterfowl, sea ducks spend substantial amounts of time feeding, probably because of their low quality diets
218	Systad et al 2000	common eider	% time feeding				extended feeding after dark by common eiders also has been observed at blue mussel beds exposed at low tide
222	Goudie & Ankney 1986	common scoter	% time feeding (including pauses between dives)		58%		black scoter and common eiders did not differ in the proportion of time spent feeding (but both higher than long-tailed ducks and harlequins)
240	Systad & Bustnes 2001	Stellers eider	time spent feeding (hours)	4.6h		6.3h	estimated feeding time (in total) was about 35% higher in midwinter than in spring
262	Guillemette 1998	common eider	% time feeding (in daylight)	33%	46%	56%	compensated for shorter days by feeding for 56% of the time in mid winter, 46% in late winter and 33% in spring
267	Guillemette 1998	common eider	% of time spent diving (ie underwater)	15%		24%	the % time spent diving (ie underwater) during the day decreased significantly from mid-winter to spring.
269	Guillemette 1998	common eider	% of time spent diving (ie underwater)	17%		22%	in Norway cited from Systad 1995 (thesis)

Appendix 17 Notes concerning the daily consumption of food by diving ducks

record	source	species	season	parameter	min	value	max	comments
130	Bourne 1984	white-winged scoter		daily intake rate		336		whole clams (g) Assuming daily ingestion rate of c 20% of total body weight in whole shellfish (shells included) or 30% of body weight in shellfish flesh only.
131	Bourne 1984	surf scoter		daily intake rate		224		whole clams (g) Assuming daily ingestion rate of c 20% of total body weight in whole shellfish (shells included) or 30% of body weight in shellfish flesh only.
132	Bourne 1984	white-winged scoter		daily intake rate		1008		whole clams (g) Assuming daily ingestion rate of c 60% of total body weight in whole shellfish (shells included)
133	Bourne 1984	surf scoter		daily intake rate		672		whole clams (g) Assuming daily ingestion rate of c 60% of total body weight in whole shellfish (shells included)
203	Beauchamp et al 1992	common eider		Daily requirement (g dry mass)		130		
220	Bustnes & Erikstad 1990	common eider		Daily requirement (g dry mass)		113		assuming 4.9kcal/g dry flesh mass
221	Bustnes & Erikstad 1990	common eider		Daily requirement (kcal per day)		555		
223	Cantin et al 1974	common eider	captive	Daily consumption (kcal per day)		683		adult (n=2)
224	Cantin et al 1974	common eider	captive	Daily assimilation (kcal per day)		516		adult (n=2)
225	Cantin et al 1974	common eider	captive	Daily consumption (kcal per day)		520		on Mytilus
226	Cantin et al 1974	common eider	captive	Daily consumption (kcal per day)		720		on cockles
229	Guillemette et al 1996	common eider		Daily consumption (g fresh weight per day (poss incl shells)		2000		on Mytilus
230	Guillemette et al 1996	common eider		Daily consumption (g fresh weight per day (poss incl shells)		1990		on sea urchins
417	de Leeuw 1997h	scaup		daily consumption gFW per day		2240		
418	de Leeuw 1997h	tufted duck		daily consumption gFW per day		1607		
457	Guillemette 1998	common eider	winter	daily consumption gFW per day	1781	1906	2098	1781g in spring, 1906g in mid winter and 2098g in late winter (eating Mytilus edulis)

Appendix 18 Notes concerning the daily energy expenditure of diving ducks

record	source	species	season	parameter	value	comment
56	Lovvorn & Gillingham 1996	canvasback		DEE	1120kJ	Field Metabolic Rate based on Nagy 1987 allometric equation
244	de Leeuw 1997b	tufted duck	winter	DEE	4.2*BMR	this is close to the upper ceiling of metabolisable energy which can be achieved according to Kirkwood (1983)
245	de Leeuw 1997b	common eider	winter	DEE	4.3*BMR	
300	de Leeuw 1997g	tufted duck		DEE	4.2*BMR	in winter. Costs for thermoregulation and heating up the ingested mussels primarily explained the high DEE in winter. These high costs are probably due to the high costs of feeding on mussels with a low energy density
303	de Leeuw 1997g	common eider		DEE	4.3*BMR	in winter
309	de Leeuw 1997h	diving ducks		DEE		because of the high energetic costs of getting benthic food underwater and the need to heat large quantities of cold prey, food intake rates have a direct implication for energy and time budgets of diving ducks in addition to habitat parameters. Properties of the prey are supposed to be the primary determinants of food intake rates in this study. For example, handling of mussels may depend on prey size and byssal attachment, while searching for mussels depends on the distribution of the prey (density and patchiness). These prey properties in turn depend on properties of the habitat, IN PARTICULAR WATER DEPTH. WATER DEPTH MAY ALSO AFFECT THE ENERGETIC CONTENT OF THE PREY TOO.
318	de Leeuw 1997h	scaup		DEE	1063kJ	
328	de Leeuw 1997i	diving ducks	winter	DEE		foraging costs mainly determine DEE
343	de Leeuw 1997i	tufted duck/ scaup		DEE		minimising DEE at ENERGY BALANCE is here used a currency for habitat selection decisions. DEE is calculated in two steps. First, the daily costs for maintenance and flight are assessed for a certain feeding site and roost (fixed costs) and subsequently, the additive costs are calculated in order to achieve energy balance. For every unit of foraging effort (second spent underwater) energy is gained by food intake (depending on apparent intake rate and energy content of mussels) while the energy costs of diving (per sec) and food processing increase. The energy expenditure at the point where expenses meet the gains equals the DEE at energy balance.
344	de Leeuw 1997i	tufted duck/ scaup		DEE		the increased diving effort with greater water depth has only a moderate effect on DEE when mussel condition is constant with respect to water depth. It is the decline in mussel condition with increasing water depth that leads to the marked increase in DEE with water depth in the Ijsselmeer.

Appendix 19 Notes concerning the body mass of diving ducks

record	source	species	location	season	months	parameter	min	value	max	age	sex	comment
4	Cramp & Simmons 1977	common scoter	Netherlands and Denmark	winter	october-april	weight (g)	964	1165	1339	adult	male	n=14
5	Cramp & Simmons 1977	common scoter	Netherlands and Denmark	winter	october-april	weight (g)	973	1059	1233	adult	female	n=10
6	Cramp & Simmons 1977	common scoter	East germany	spring	april-may	weight (g)	1304	1363	1450	adult	male	n=4
7	Cramp & Simmons 1977	common scoter	East germany	spring	april-may	weight (g)	1231	1250	1268	adult	female	n=2
8	Cramp & Simmons 1977	common scoter	Netherlands	winter	december-march	weight (starvation) (g)	642	752	851	adult	male	n=21
9	Cramp & Simmons 1977	common scoter	Netherlands	winter	december-march	weight (starvation) (g)	636	703	778	adult	female	n=9
10	Cramp & Simmons 1977	common scoter	USSR	winter	october	weight (g)	710	778	818	juv	male	
11	Cramp & Simmons 1977	common scoter	USSR	winter	november	weight (g)	600	735	850	juv	female	
12	Cramp & Simmons 1977	common scoter	Netherlands and Denmark	winter	december-april	weight (g)	878	1126	1380	juv	male	n=17
13	Cramp & Simmons 1977	common scoter	Netherlands and Denmark	winter	december-april	weight (g)	622	979	1227	juv	female	n=13
14	Cramp & Simmons 1977	common scoter	USSR	summer	may	weight (g)	1215	1306	1610	adult	male	
15	Cramp & Simmons 1977	common scoter	USSR	summer	may	weight (g)		990		adult	female	
16	Cramp & Simmons 1977	common scoter	USSR	summer	june	weight (g)	960		1150	adult	male	

17	Cramp & Simmons 1977	common scoter	USSR	summer	june	weight (g)		1000		adult	female	
18	Cramp & Simmons 1977	common scoter	USSR	summer	july	weight (g)	975	1037.5	1100	adult	male	
19	Cramp & Simmons 1977	common scoter	USSR	summer	july/ august	weight (g)		915		adult	female	n=2
20	Cramp & Simmons 1977	common scoter	Netherlands	outside winter		weight (starvation) (g)	510				male	
27	Durinck et al 1993	common scoter	Denmark	winter	march	weight (g)	1150	1294	1490	adult	male	n=47
28	Durinck et al 1993	common scoter	Denmark	winter	march	weight (g)	1110	1249	1360	adult	female	n=22
29	Durinck et al 1993	common scoter	Denmark	winter	march	weight (g)	1090	1199	1290	juv	female	n=7
167	Hohman 1993					body condition	overwinter and annual survival probabilities of waterfowl may be influenced by their relative body mass in winter					
168	Hohman 1993					body condition	…breeding performance of waterfowl is correlated with their physiological condition during winter					
319	Lovvorn 1989	canvasbacks		non-breeding		weight (g)	typically low and declining in winter when canvasbacks eat mostly clams (not necessarily cause and effect in that they may eat clams in mid winter when it is colder)					
451	Guillemette et al 1992	common eider				body condition	individuals in large flocks were heavier than those in small flocks. Large flock eiders were in better condition than individuals in small flocks					
456	Guillemette et al 1992	common eider				body condition	our study indicates that individuals in small flocks both use the habitat differently and are in worse body condition than individuals in large flocks. We suggest that eiders in small flocks behave as risk-prone foragers and seek the *Agarum* beds where crabs live to enhance their chances of survival (because the max possible profitability there exceeds that in other habitats - although the variance is higher).					

Appendix 20 Notes concerning the mortality of diving ducks

record	source	species	parameter	min	value	max	comments
68	Ross 1983	common scoter	mortality		0.65-0.70		assumption: an over wintering mortality range for sub adults of 65-70% cf Bellrose 1978
75	Kirby et al 1993	scoter spp.	mortality				Unfortunately there is very little hard data on any aspects of the population ecology in sea ducks. Relatively little is known about…winter mortality rates.
83	Fox et al 2003	common scoter	annual survival	0.623	0.749	0.843	first year after ringing
84	Fox et al 2003	common scoter	annual survival	0.715	0.783	0.839	following years. This is higher than Tufted duck and Pochard (0.72 and 0.65) but less than for eiders (0.90)
85	Fox et al 2003	common scoter	annual survival		0.77		source (Boyd 1962)
86	Richman & Lovvorn 2003	spectacled eider	mortality				up to 46% of the annual mortality of adult females appears to occur in the non-breeding period when the eiders are at sea. Regardless of the mechanism, modelling indicates that a major limitation on the population is adult mortality much of which occurs away from the breeding area. Source Flint et al 2000
134	Garthe & Huppop 2004	common scoter	annual survival		0.773		source: Krementz, Barker & Nichols 1997
261	Coulson 1984	common eider	annual survival	0.756	0.895	1	
455	Guillemette et al 1992	common eider	mortality				body mass (and reserves) in ducks in winter is positively correlated with the probability of survival. We have no difficulty imagining that starvation could be a major cause of natural mortality in wintering eiders. sources : Haramis et al 1986, Hepp et al 1986