Fisheries Research 106 (2010) 141–150

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Biology and meso-scale distribution patterns of North Sea cephalopods

Daniel Oesterwind[a,*], Remment ter Hofstede[b], Brian Harley[c], Heinz Brendelberger[a], Uwe Piatkowski[d]

[a] *Universität Kiel, Zoologisches Institut, Am Botanischen Garten 1-9, 24118 Kiel, Germany*
[b] *IMARES (Institute for Marine Resources and Ecosystem Studies), P.O. Box 68, 1970 AB Ijmuiden, The Netherlands*
[c] *CEFAS, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, United Kingdom*
[d] *Leibniz-Institut für Meereswissenschaften, Universität Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany*

ARTICLE INFO

Article history:
Received 11 April 2010
Received in revised form 4 May 2010
Accepted 4 June 2010

Keywords:
Cephalopods
North Sea
Abundance
Distribution
Migration

ABSTRACT

Between 2007 and 2009, 132,178 cephalopods were sampled in the North Sea during ICES International Bottom Trawl Surveys. Most abundant were the long-finned squids *Alloteuthis subulata* (124,751 animals) and *Loligo forbesii* (3415 animals). Short-finned squids such as *Todaropsis eblanae*, *Todarodes sagittatus* and *Illex coindetii* were rare (195 animals). During winter, *A. subulata* individuals, mostly immature and maturing, were concentrated in the central and northern parts of the North Sea. In summer, the abundance of *A. subulata*, mostly maturing and mature, increased in the southeastern part suggesting a southward migration to spawning grounds. *L. forbesii* individuals, some fully mature, were abundant in the northwestern part of the North Sea during winter indicating spawning areas in this region. In summer, *L. forbesii* individuals, mostly immature, occurred in lower numbers throughout the North Sea. Our data provide new information on abundance, distribution, migration, and possible recruitment areas of North Sea cephalopods.

1. Introduction

Annual cephalopod landings have increased globally since the 1950s from about 500,000 tons to more than 4 million tons in 2007 (FAO, 2009). With growing stock sizes, marine food chains will be affected with implications on the recruitment of commercially important fish species (Caddy and Rodhouse, 1998; Piatkowski et al., 2001). If such a situation occurs in the central and eastern North Sea, where cephalopods have played a minor role in terms of fisheries so far, improved assessment and management of stocks will be required to ensure an ecosystem-compatible utilization of cephalopod resources (Pierce et al., 1998; Bellido et al., 2001; Young et al., 2004, 2006). In order to achieve this, comprehensive data on biology, distribution, landings, and stock size of major cephalopod species are necessary.

Since the early 1990s, the ICES Working Group on Cephalopod Fisheries and Life History (WGCEPH) has reported annually on the development of cephalopod fisheries and related research in the North East Atlantic (e.g. Anonymous, 2008), and during recent decades knowledge on biology, abundance, and fisheries of North Sea cephalopods has substantially increased (see review of Hastie et al., 2009).

Most studies have concentrated on long-finned squid in Scottish waters or in the English Channel, where major cephalopod fisheries exist. First reports of fishery data of *Loligo forbesii* appeared in the 1960s and 1970s (Thomas, 1969; Thomas and Davidson, 1972; Holme, 1974; Howard, 1979). Further studies focused on life history, stock structure, reproduction, recruitment, and early life stages (e.g. Lum-Kong et al., 1992; Pierce et al., 1994, 1998; Boyle et al., 1995; Collins et al., 1999, 2002; Hastie et al., 2009). More recently, distribution patterns, seasonal migrations, and interannual trends in abundance related to oceanographic factors such as water temperature have also been investigated in North Sea squid (e.g. Waluda and Pierce, 1998; Robin and Denis, 1999; Bellido et al., 2001; Pierce and Boyle, 2003; Zuur and Pierce, 2004; Pierce et al., 2008; Viana et al., 2009). Information on the distribution and abundance of cephalopods in North Sea regions other than the English Channel and around Scotland remained poor and was mostly added to reports on the Scottish squid fishery (Thomas, 1969; Thomas and Davidson, 1972; Howard, 1979; Howard et al., 1987). The most comprehensive description of cephalopod distribution patterns in the entire North Sea and the adjacent western Baltic Sea still dates back to the work of Grimpe (1925). In recent years the cephalopod by-catch of ICES International Bottom Trawl Surveys (IBTS) from central and southeastern parts of the North Sea was investigated to provide more detailed information on biology and distribution of major species (De Heij and Baayen, 1999, 2005; Zumholz and Piatkowski, 2005). The IBTS is a multinational long-term program to monitor the condition of commercially important fish stocks in the North Sea. The surveys take place each quarter of the year at randomized stations in defined geographical rectangles which are sampled by standardized fishing gear. They are repeated annu-

* Corresponding author. Tel.: +49 431 8804136; fax: +49 431 8804747.
E-mail address: doesterwind@ifm-geomar.de (D. Oesterwind).

0165-7836/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.fishres.2010.06.003

Table 1
Cephalopods sampled during IBTS cruise (2007–2009). Participating vessels: WH, FRV Walther Herwig III; En, CEFAS Endeavour; Tr, RV Tridens.

	Summer 2007		Winter 2008		Summer 2008		Winter 2009	
	WH	En	WH	Tr	WH	En	WH	Tr
Rectangles	29	72	63	67	24	73	72	56
Trawls (30 min)	134	75	63	67	37	75	72	67
Sepiidae								
Sepia elegans	0	0	1	0	0	0	3	0
Sepia officinalis	0	0	1	0	0	0	0	0
Sepiola atlantica	1	0	54	263	1	0	36	0
Sepietta oweniana	0	0	46	0	0	0	10	0
Rossia macrosoma	1	0	7	0	0	0	11	0
Sepiolidae indet.	0	0	0	0	0	0	0	39
Loliginidae								
Alloteuthis subulata	5,750	3,170	19,471	30,788	2,643	2,410	32,881	27,638
Loligo forbesii	700	636	635	53	214	529	570	78
Loligo vulgaris	5	0	7	3,228	16	3	5	10
Loliginidae indet.	30	0	26	0	4	0	2	0
Ommastrephidae								
Todaropsis eblanae	23	37	29	15	0	6	32	12
Todarodes sagittatus	0	0	2	0	0	0	18	0
Illex coindetii	3	0	3	0	0	0	15	0
Octopodidae								
Eledone cirrhosa	1	0	3	0	1	0	3	0
Total	6,514	3,843	20,285	34,347	2,878	2,948	33,586	27,777

ally, coordinated by ICES, and shared by all countries surrounding the North Sea. Detailed information on sampling techniques and strategies is given in the IBTS manual (Anonymous, 2006).

Collecting the cephalopod by-catch of the IBTS samples provides a unique resource to record temporal and geographical changes of abundance and distribution patterns of cephalopods—prerequisites to assess cephalopod stock structure and its fluctuations. In our study we have analyzed the cephalopod by-catch of German, English and Dutch surveys from 2007 to 2009. The comprehensive dataset provides new information on biology, abundance, distribution and migration of major cephalopod species in various parts of the North Sea.

2. Materials and methods

A total of 132,178 cephalopods were sampled in the North Sea from ICES International Bottom Trawl surveys (IBTS) during winter (January/February) of 2008 and 2009, and from German Small Scale Bottom Trawl Survey (GSBTS) and IBTS during summer (July/August) of 2007 and 2008 (Table 1). Sampling followed ICES IBTS standards in defined Roundfish Areas (RFA) and Rectangles (RA) of about 30 × 30 nautical miles (see Anonymous, 2006). All stations were sampled with a GOV bottom trawl and hauls lasted 30 min.

All cephalopods were identified to the lowest possible taxon. For more detailed analysis 11,062 specimens were selected (10,715 individuals from FRV Walther Herwig III samples and 347 specimens from RV Tridens samples). Dorsal mantle length (DML) was measured to the nearest 1 mm; animals were sexed and maturity stages were estimated (0, immature; I–III, maturing; IV–V, mature).

Cephalopod catch data were converted into number of specimens caught per hour trawling time. If more than one haul was performed in one rectangle, the total number of specimens caught per hour was divided by the number of hauls. The numbers of investigated RAs during each survey are listed in Table 1. Distribution maps were created with ArcView Gis 3.2 software (Environmental Systems Research Institute, USA).

Water temperature and salinity data were only available from FRV Walther Herwig III cruises, where they had been recorded by a Seabird CTD during the sampling stations. Spearman's rank correlation coefficients were calculated with *R*-Statistics to test the correlation between environmental factors and the abundance of *Alloteuthis subulata* and *L. forbesii*.

Significant length cohorts were determined with FISAT II 1.2.2 (FAO-ICLARM stock assessment tools II) (Gayanilo et al., 2006). For this purpose, specimens of *A. subulata* and *L. forbesii* were grouped into 5 mm size classes. Sexes (maturing and matured individuals) were separated and together with juveniles (immature individuals) analyzed by NORMSEP, a modified Bhattacharya's method (Bhattacharya, 1967; Pauly and Caddy, 1985).

3. Results

Cephalopod catch data from the four surveys are summarized in Table 1. In total, twelve species were found which were dominated by the long-finned squids *A. subulata* and *L. forbesii*. Short-finned squids such as *Illex coindetii*, *Todaropsis eblanae* and *Todarodes sagittatus* appeared in low numbers. The bobtail squids (Sepiolidae) like *Sepiola atlantica*, *Sepietta oweniana* and *Rossia macrosoma* were mainly caught during winter surveys. The family Sepiidae was represented by a few individuals of *Sepia officinalis* and *Sepia elegans*, while *Eledone cirrhosa* was the only octopod found in the samples.

3.1. *A. subulata*

The European common squid, *A. subulata*, dominated all surveys (Table 1). During winter, *A. subulata* was most abundant in the central part of the North Sea (Fig. 1). During the winter cruises all animals were caught between 5.5 and 8.5 °C water temperature, 18 and 171 m depth and 34.04 and 35.38 psu salinity (Fig. 2) with depth (p-value < 0.0002, rho = −0.314) and salinity (p-value < 0.0001, rho = −0.340) showing a negative significant relationship with abundance of *A. subulata*. In summer, *A. subulata* were mainly caught in the southeastern part of the North Sea while in the central part no *A. subulata* were present. All specimens occurred between 8.8 and 13.8 °C, 15 and 54 m depth and 32.75 and 35.04 psu salinity. Thereby depth (p-value < 0.0001, rho = −0.782) and salinity (p-value < 0.0001, rho = −0.813) showed a negative

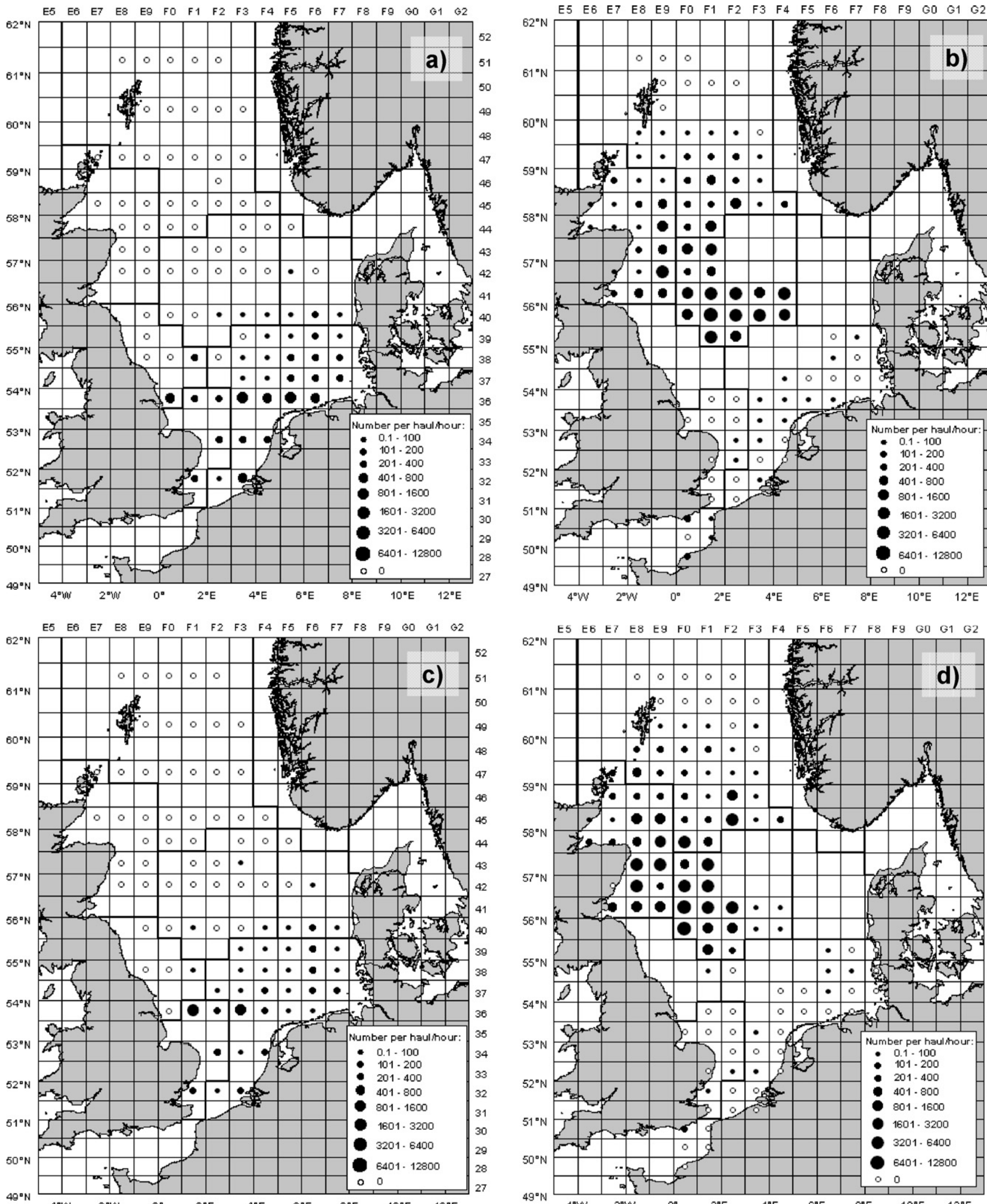

Fig. 1. *Alloteuthis subulata*. Distribution and abundance in summer 2007 (a), winter 2008 (b), summer 2008 (c), and winter 2009 (d).

significant correlation whereas SBT (p-value < 0.0001, rho = 0.817) showed a positive significant correlation with the occurrence of the squid.

Females and males showed different length frequency patterns (Fig. 3), both in summer and winter; with males attaining larger maximum sizes. Length frequency analysis indicates that four female size classes were present in summer versus two in winter, while five male size classes were present in summer versus two in winter (Bhattacharya's and NORMSEP analysis; Tables 2 and 3). In the different RFAs mean water temperature varied, both in winter and in summer (Table 4). Accordingly, there was a tendency that the mean DML of *A. subulata* changed, with

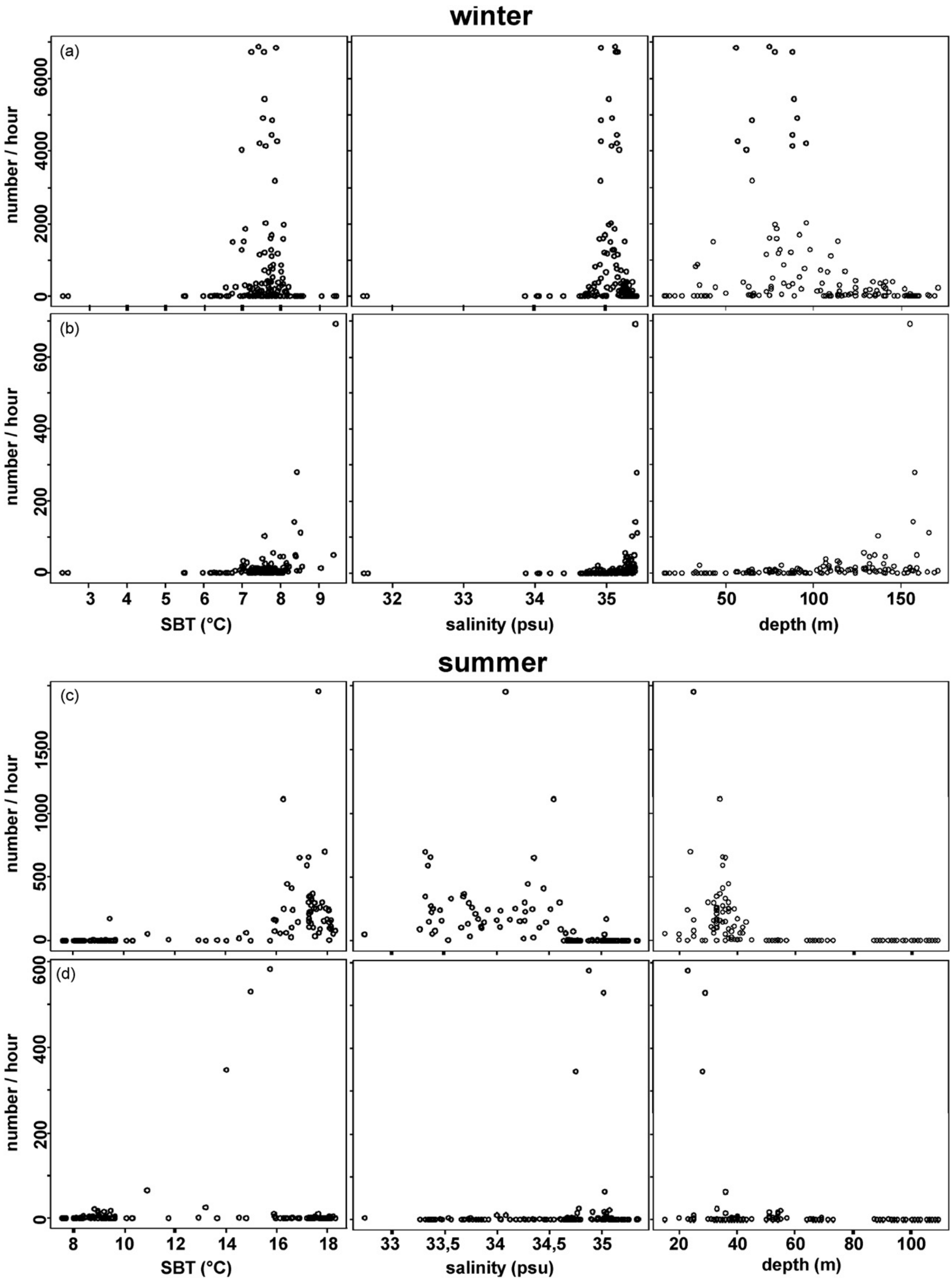

Fig. 2. Scatter plots between numbers of trawled squid during IBTS survey 2007–2009 and sea bottom temperature (SBT), salinity and depth for winter and summer. Line a, c: *Alloteuthis subulata*; line b, d: *Loligo forbesii*.

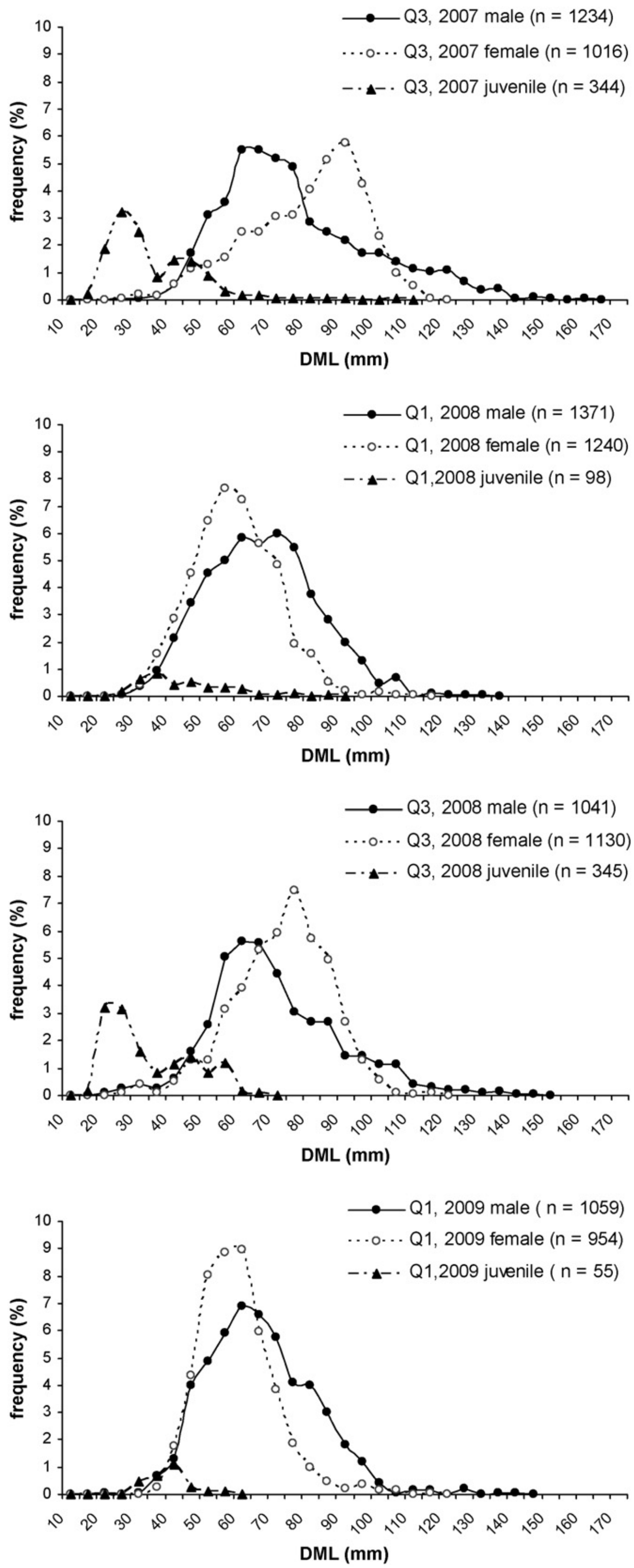

Fig. 3. *Alloteuthis subulata*. Percentage length frequency distribution (DML in mm) of juveniles, females and males sampled during the IBTS surveys 2007–2009 (Q1: winter; Q3: summer).

longer DML at higher water temperatures in the winter season (Table 4).

The percentage of mature individuals for both sexes was higher in summer than in winter with male maturity being more advanced than female in winter and in summer (Table 5). Females tend to have a faster growth rate than males, while males mature earlier than females. The data on maturity stages and size-frequency distributions suggest that main spawning takes place in summer when *A. subulata* is distributed in the southeastern part of the North Sea.

Table 2
Alloteuthis subulata females. Length cohorts in mm and standard deviation.

Summer				Winter			
2007 (n = 1337)		2008 (n = 1468)		2008 (n = 1259)		2009 (n = 1009)	
Mean	SD	Mean	SD	Mean	SD	Mean	SD
23.5	±4.7	21.7	±4.2	53.7	±10.4	55.3	±12.0
41.0	±5.0	41.3	±5.9	96.9	±3.4	90.0	±5.8
62.3	±10.5	53.0	±2.5				
82.7	±8.8	71.5	±11.6				

Table 3
Alloteuthis subulata males. Length cohorts in mm and standard deviation.

Summer				Winter			
2007 (n = 1555)		2008 (n = 1379)		2008 (n = 1390)		2009 (n = 1144)	
Mean	SD	Mean	SD	Mean	SD	Mean	SD
22.8	±4.3	21.4	±4.0	62.7	±13.3	61.0	±15.4
61.1	±15.2	57.8	±12.9	110.0	±4.8	119.5	±10.5
95.8	±9.2	81.3	±3.0				
116.3	±10.0	95.2	±8.8				
138.2	±10.8	123.4	±9.4				

3.2. *L. forbesii*

In winter, most *L. forbesii* were caught in the northern parts of the North Sea near the Shetland Islands (Fig. 4). All animals were caught between 33 and 171 m depth, 6.3 and 9.4 °C water temperature and 34.7 and 35.4 psu salinity (Fig. 2). All three factors showed a positive significant correlation (p-value < 0.0001; rho-factors: depth = 0.510, salinity = 0.646, SBT = 0.431) with the abundance of the species.

In summer *L. forbesii* occurred in low numbers throughout the whole North Sea (Fig. 4), between 8.1 and 18.2 °C, 20 and 92 m depth, and 32.75 and 35.34 psu salinity. Only depth showed a negative significant influence (p-value = 0.001, rho = −0.271) on the occurrence (Fig. 2).

Table 4
Alloteuthis subulata. Mean DML and mean temperature ± standard deviation for winter and summer in different RFAs and years.

RFA	Mean DML (mm)	SD	n	Mean temperature (°C)	SD	n
Winter 2008						
1	65.40	±14.09	1037	7.93	±0.55	31
2	55.59	±13.15	1612	7.89	±0.13	14
3	59.34	±17.60	562	7.79	±0.38	12
6	53.00	±20.11	10	6.51	±0.12	4
Winter 2009						
1	60.78	±12.98	790	7.60	±0.45	38
2	57.05	±13.74	683	6.99	±0.67	16
3	60.95	±16.39	581	7.41	±0.36	12
6	56.22	±7.93	10	4.66	±1.78	6
Summer 2007						
2	78.11	±15.87	27	12.96	±2.87	2
6	70.11	±23.06	2811	16.27	±2.22	33
7	67.07	±25.26	181	9.71	±2.03	18
Summer 2008						
2	63.15	±24.62	72	11.23	±2.81	2
6	53.94	±25.75	646	16.67	±2.53	27
7	60.59	±31.38	75	14.64	±4.79	3

Table 5
Maturity stages of *Alloteuthis subulata* and *Loligo forbesii* sampled during the IBTS surveys 2007–2009.

Maturity stage	*Alloteuthis subulata*				*Loligo forbesii*			
	Winter		Summer		Winter		Summer	
	Male $n=2430$	Female $n=2193$	Male $n=2273$	Female $n=2146$	Male $n=311$	Female $n=260$	Male $n=268$	Female $n=145$
1	8.68%	7.16%	6.16%	4.94%	44.05%	16.15%	37.31%	30.34%
2	17.45%	64.34%	11.83%	21.30%	21.54%	43.08%	54.10%	68.97%
3	54.16%	27.36%	29.21%	27.35%	8.04%	15.00%	5.22%	0.69%
4	19.51%	1.09%	30.71%	41.80%	24.76%	25.38%	0.37%	0.00%
5	0.21%	0.05%	22.09%	4.61%	1.61%	0.38%	2.99%	0.00%

Greater abundance of mature and larger *L. forbesii* was sampled in winter than in summer suggesting main spawning in late winter and spring (Fig. 5 and Table 5). Bhattacharya's and NORMSEP analysis identified a maximum of five different length cohorts of females in summer and a maximum of eight length cohorts in winter. There were four length classes of male *L. forbesii* in summer and seven in winter (Tables 6 and 7). In *L. forbesii* mean DML increased significantly ($p = 0.017$) with higher water temperatures in summer 2007 in the RFAs (Table 8). In summer 2008 there is a similar trend observable. In winter such an effect was not evident.

During winter, mature *L. forbesii* were caught in all parts of the North Sea except the south. The highest percentage of mature *L. forbesii* was found in the central parts and off the Scottish coast, while the highest numbers of mature *L. forbesii* were caught close to the Shetland Islands. Because no mature females were caught in summer it can be supposed that spawning begins in winter in areas near the Shetland Islands.

3.3. Loligo vulgaris

L. vulgaris was rare in the North Sea compared to *A. subulata* and *L. forbesii*. In summer there were fewer *L. vulgaris* than in winter (Table 1). *L. vulgaris* was completely absent in the northern part of the North Sea and was more concentrated in the southern and central parts. A total of 3233 specimens were sampled in winter 2008 in the central North Sea. DML was between 18 and 60 mm in summer, and between 72 and 368 mm in winter. In summer maturity stages were low (0–1), while in winter the maturity stages varied between two and five, suggesting the main spawning season in winter to spring.

3.4. Ommastrephidae

In winter 2009, 15 *I. coindetii* were caught in the northern and central parts of the North Sea (Table 1). During all other surveys the species was absent or occurred only sporadically. The length frequency distribution revealed small and large *I. coindetii* in winter (DML: 39–312 mm; mean: 76 mm, ±59 mm), while the three specimens from summer 2007 were medium sized (DML: 98–148 mm; mean: 115 mm, ±20 mm). The small squids in winter had a maturity stage between zero and two, the large-sized animals were mature.

T. eblanae was the most abundant ommastephid in our samples (Table 1). In winter the species was more common in the central and northern part of the North Sea. DML ranged from 58 to 212 mm in winter and from 66 to 205 mm in summer. Summer caught specimens were more mature than those caught in winter suggesting an autumn spawning season.

T. sagittatus was very rare in the North Sea (Table 1). In summer *T. sagittatus* was absent while in winter this species occurred seldom but constantly in the northern parts. In winter 2008 *T. sagittatus* was caught near the Shetlands Islands. *T. sagittatus* specimens had DML between 165 and 360 mm (mean: 267 mm, ±45 mm), and most were maturing.

Table 6
Loligo forbesii females. Length cohorts in mm and standard deviation.

Summer				Winter			
2007 ($n=188$)		2008 ($n=56$)		2008 ($n=174$)		2009 ($n=275$)	
Mean	SD	Mean	SD	Mean	SD	Mean	SD
45.8	±4.2	72.3	±10.1	43.8	±9.0	36.8	±8.7
74.4	±18.0	93.7	±2.5	77.0	±9.5	112.5	±15.1
112.8	±2.5	111.3	±5.5	110.5	±5.8	158.5	±6.9
135.9	±14.9	136.2	±9.7	130.6	±11.7	185.0	±5.0
		212.5	±2.5	191.0	±26.0	217.1	±14.5
				255.6	±18.2	289.1	±13.2
				334.7	±24.4		
				527.5	±3.7		

Table 7
Loligo forbesii males. Length cohorts in mm and standard deviation.

Summer				Winter			
2007 ($n=292$)		2008 ($n=72$)		2008 ($n=173$)		2009 ($n=327$)	
Mean	SD	Mean	SD	Mean	SD	Mean	SD
52.0	±9.4	63.5	±8.5	38.8	±7.2	33.4	±5.6
77.4	±7.8	78.7	±3.2	53.6	±2.5	48.5	±6.8
107.1	±17.7	93.6	±5.6	84.4	±21.5	114.6	±13.9
221.2	±15.3	190.8	±68.1	135.0	±14.7	152.6	±8.3
				180.0	±11.7	181.4	±16.5
				264.7	±51.8	300.1	±50.5
				441.2	±61.7	492.5	±4.9

Table 8
Loligo forbesii. Mean DML and mean temperature ± standard deviation for winter and summer in different RFAs and years.

RFA	Mean DML (mm)	SD	*n*	Mean temperature (°C)	SD	*n*
Winter 2008						
1	121.31	±82.53	279	7.93	±0.55	31
2	182.90	±85.62	39	7.89	±0.13	14
3	210.69	±96.31	45	7.79	±0.38	12
Winter 2009						
1	90.05	±64.06	409	7.60	±0.45	38
2	166.85	±112.56	26	6.99	±0.67	16
3	173.43	±115.96	14	7.41	±0.36	12
Summer 2007						
1	54.00	±7.55	3	7.87	±0.30	21
2	82.23	±16.75	156	12.96	±2.87	2
4	56.60	±11.54	15	8.32	±0.17	14
6	108.57	±26.02	101	16.27	±2.22	33
7	57.35	±20.20	88	9.71	±2.03	18
Summer 2008						
2	76.14	±22.61	21	11.23	±2.81	2
6	89.71	±33.55	92	16.67	±2.53	27
7	98.00	±31.76	4	14.64	±4.79	3

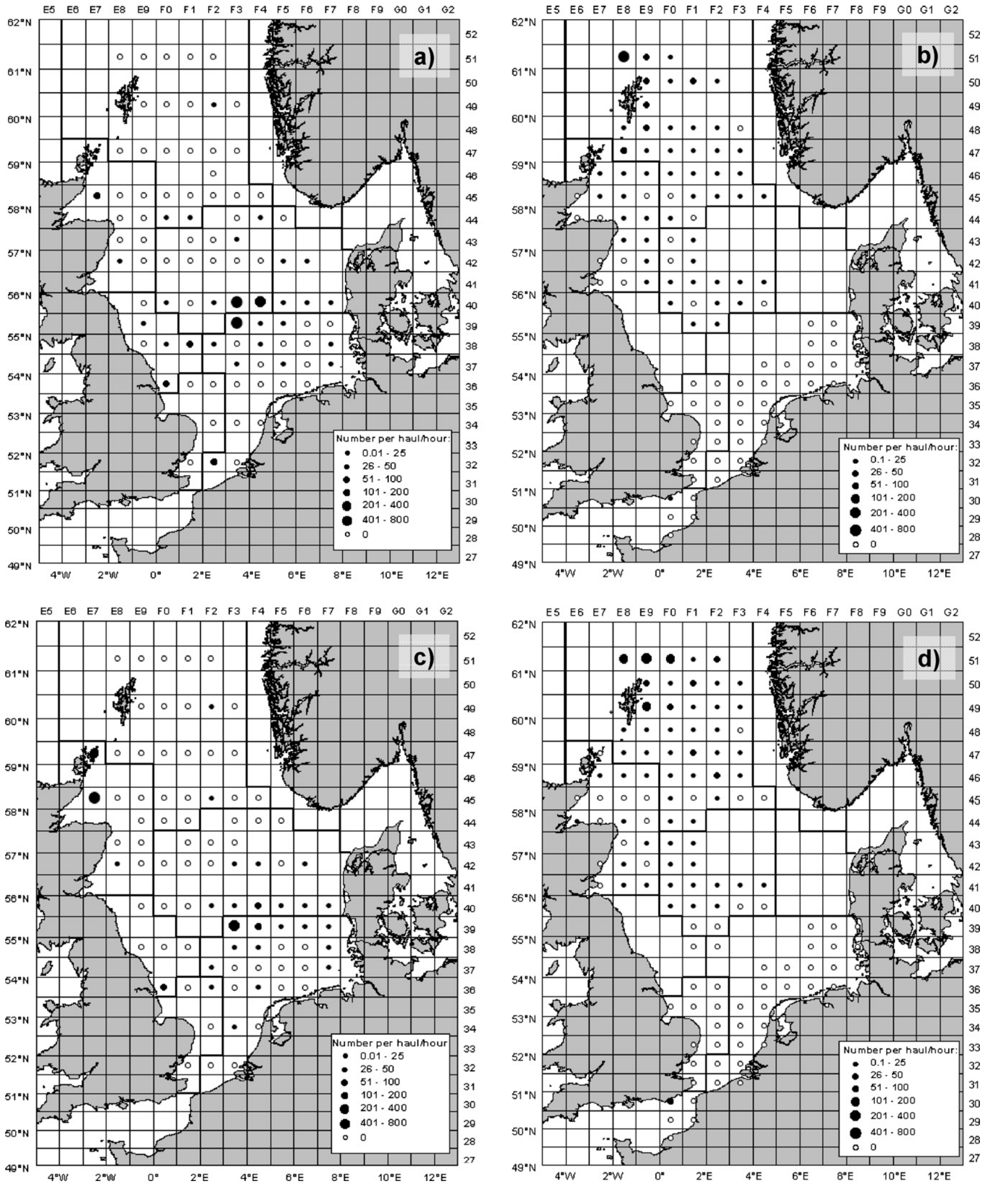

Fig. 4. *Loligo forbesii*. Distribution and abundance in summer 2007 (a), winter 2008 (b), summer 2008 (c), and winter 2009 (d).

3.5. Sepiolidae

Only Sepiolidae sampled during FRV Walther Herwig III cruises were identified to species level. In general, the most abundant Sepiolidae from these cruises was *S. atlantica* (52%) followed by *S. oweniana* (35%) and *R. macrosoma* (12%) (Table 1). In summer there were fewer Sepiolidae sampled in the North Sea than in winter. In winter catches were scattered throughout the whole North Sea, but tended to be more common in coastal waters, especially in the northwestern part of the North Sea.

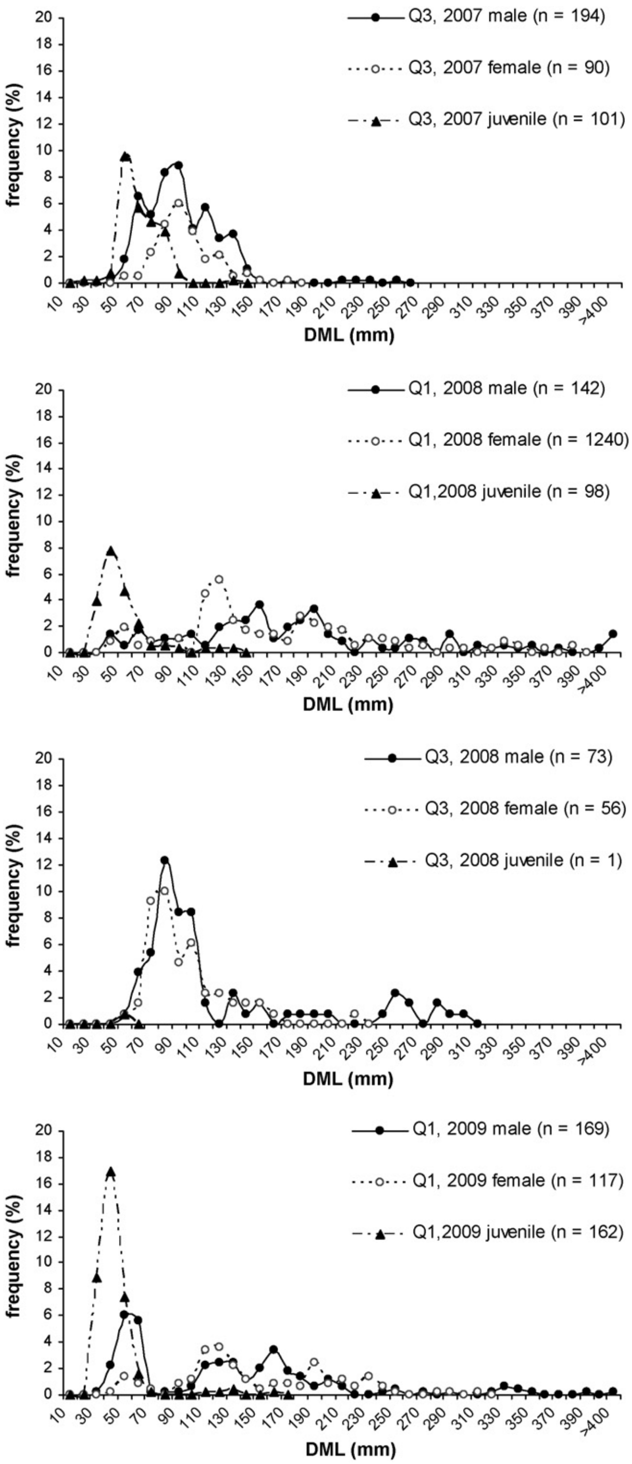

Fig. 5. *Loligo forbesii*. Percentage length frequency distribution (DML in mm) of juveniles, females and males sampled during the IBTS surveys 2007–2009 (Q1: winter; Q3: summer).

3.6. *E. cirrhosa*

E. cirrhosa (8 specimens) was the only octopod caught during the surveys (Table 1). One *E. cirrhosa* was caught in summer and three were sampled in winter for each year. One specimen was caught in the central part of the North Sea; all other specimens occurred in the northern part. The largest animal was a female with 180 mm DML caught in summer. The smallest specimen (DML = 15 mm) was caught in winter.

4. Discussion

During the IBTS surveys, cephalopods were fished with a GOV net with a stretched mesh size of 20 mm in the codend. Hence, it is most likely that small-sized cephalopods such as Sepiolidae and juvenile squid were not caught adequately. Furthermore, attention must be paid to the patchy distribution of some species, which might explain the fluctuations of species with general low densities. Nevertheless, the relatively small-sized loliginid *A. subulata* was the most common cephalopod in our samples, indicating its major position in the North Sea cephalopod fauna. This is in accordance with recent studies of De Heij and Baayen (1999) who reported from the central and southern North Sea that more than 90% of all cephalopods encountered belonged to *A. subulata*. In our study 99.5% of the cephalopods belonged to long-finned squids (94.5% *A. subulata*, 2.4% *L. forbesii* and 2.5% to *L. vulgaris*); short-finned squids accounted for 0.2%, and other cephalopods (Sepiolodae, Octopoda) accounted for 0.4%.

4.1. *A. subulata*

There are different views on distribution and migration patterns of *A. subulata*. Grimpe (1925) noted that *A. subulata* individuals were observed earlier in the year in the German Bight than off the Dutch southwestern coast, suggesting that they return from the north, while Kristensen (1966) supposed that they migrate back from the north and the south. Another opinion is that in response to cooling during late autumn/winter, the juvenile *A. subulata* migrate from the spawning grounds in the southeastern parts of the North Sea to the deeper, in winter relatively warmer, waters in the central parts (De Heij and Baayen, 2005). In spring the young adults return to the warming shallow waters from the Danish to the Belgian coast and southeastern British coast for spawning (De Heij and Baayen, 1999), which is supported by our data (Fig. 1). During summer, a large number of mature and large *A. subulata* was encountered in the southeastern parts of the North Sea, whereas in the central and northern parts this species was not common. In winter, *A. subulata* was caught in large numbers in the central and northern parts, suggesting that it lives permanently in the North Sea with spawning grounds in the southeast in summer and feeding grounds in the central parts in winter. The length frequency distribution (Fig. 3) suggests either slightly different growth rates or slightly different spawning times. This may explain the presence of different micro-cohorts in the North Sea (Tables 2 and 3), which might also be attributed to different water temperatures in subareas (RFAs) where *A. subulata* occurs (Table 4). Likewise, Rodhouse et al. (1988), studying the English Channel, described three spawning groups of females that spawn in spring, summer and autumn, with individuals being recruited to the population in spring and summer.

The differences between summer and winter length frequency are due to a combination of the short life span and hence the growth curve over the season and the part of the population in the North Sea. Rodhouse et al. (1988) suggested that males mature earlier than females. The results from this study indicate that females are larger than males, while males mature earlier than females. This could mean that males invest their energy in maturation earlier than females, while females invest their energy in somatic growth, hence females have a faster growth rate and are larger than males in summer.

4.2. *L. forbesii*

In this study, *L. forbesii* individuals, some fully mature, were concentrated in the northwestern part of the North Sea during winter. In summer, *L. forbesii*, mostly immature, occurred in lower numbers throughout the North Sea (Fig. 4). This reflects earlier results by De Heij and Baayen (2005) wherein animals caught in winter were mostly adults, those from summer mostly juveniles, with the exception of a few specimens. This suggests a possible coexistence of two generations. Boyle and Pierce (1994) reported a spawning season of *L. forbesii* off Scotland from December to April and deduced that, in the two years of their study, there was a sharp annual pulse of recruitment to the fishery in April with a second, more extended phase of recruitment between July and October.

Collins et al. (1999) analyzed the *L. forbesii* population off the Scottish west coast and detected an extended spawning season from November until April. They found up to three cohorts present off the Scottish west coast caused by the extended spawning period and different growth rates.

The presence of four to eight length classes in our study suggests that it is possible that different populations (North Sea and Atlantic population) occur in the northern and central North Sea and variable growth rates exists (Tables 6–8 and Fig. 5). The flexibility of breeding strategies in *L. forbesii* around Scotland with a variety of life-cycle patterns has been well described by Boyle et al. (1995). The maturity stages of *L. forbesii* indicate a protracted spawning period in the North Sea (Table 5), which also suggests the existence of various length classes (Fig. 5).

4.3. *L. vulgaris*

L. vulgaris is rare in the central North Sea. In contrast to *L. forbesii*, it was only caught in the southern parts of the North Sea, which is reflected in our winter 2008 samples, when high numbers were trawled in the English Channel and at one station in the Central part of the North Sea. It is assumed that *L. vulgaris* enters the North Sea from the south and migrates northwards in spring arriving first at the Dutch coast and in late summer off the Danish coast for spawning (Grimpe, 1925; Tinbergen and Verwey, 1945). Spawning occurs from April to August (Tinbergen and Verwey, 1945), our results suggest a main spawning period in spring. The high abundance of small *L. vulgaris* in winter in the central part of the North Sea could be a school of animals that had hatched in summer. In general the occurrence of *L. vulgaris* was not as constant as that of other loliginid species such as *A. subulata* and *L. forbesii*.

4.4. Ommastrephidae

I. coindetii was mostly common in winter 2009 at the central part of the North Sea. In summer 2007 and winter 2008 only three specimens were caught. It is known that the spawning period ranges from a few days to several weeks. In the North East Atlantic a summer peak of maturity has been observed (González and Guerra, 1996). According to Hernández-García (2002), water temperature is the main factor influencing the timing of reproduction in *I. coindetii*. Our data are too sparse to suggest any information on spawning or reproduction of this species in the North Sea or nearby waters.

There are no migration patterns known for *T. eblanae* in the North Sea. In general there were more *T. eblanae* found in winter than in summer. In winter 2008 *T. eblanae* was concentrated in the central part of the North Sea while in winter 2009 *T. eblanae* was common in the central and northern parts of the North Sea. The length distribution frequency and maturation stages suggest an autumn spawning season. Hastie et al. (1994) describes a spawning season from June to November for Scottish Waters. Zumholz and Piatkowski (2005) found maturing males and females in winter and summer in the central to northern North Sea, with fully mature animals only occurring in summer.

The European flying squid *T. sagittatus* is a neritic to oceanic species which explains its rare occurrence in the North Sea. *T. sagittatus* was only trawled in winter in the northern part of the North Sea. From June onwards, large schools appear off the south and southwest coast and in the northwestern fjords of Iceland, the Faroe Islands, Norway and, in some years, Scotland, where they stay until about December. Spawning is supposed to take place on the continental slope in late winter or early spring off northern Europe. In certain years, however, huge aggregations of this species have been observed in the North Sea, around Shetland and just off the Scottish coast (Joy, 1990). Our data are too sparse to suggest any significant information on distribution patterns, spawning or reproduction of this species in the North Sea or nearby waters.

4.5. Sepiolidae

Only Sepiolidae caught by FRV Walther Herwig III were identified to species level. Most were *S. atlantica* followed by *S. oweniana* and *R. macrosoma*.

S. atlantica is very common in UK waters. In Scottish waters a peak in maturity is observed in June, but mature specimens were found from March to August (Yau and Boyle, 1996). In this study 79 individuals were identified from the samples taken by FRV Walther Herwig III; 76 were caught in winter and only three were fished in summer. In winter the animals were trawled at the northwestern part of the North Sea. De Heij & Baayen (2005) described that they caught similar numbers of animals from August to September as in February in some years, while in other years very few animals were caught or none at all. The small numbers trawled in summer could be explained by the spawning season. Maturity stages suggest a spawning period in spring, consequently individuals might be too small to be sampled with the standard GOV net in summer.

S. oweniana individuals were trawled by FRV Walther Herwig III only in winter. De Heij and Baayen (2005) sampled in the central and southern North Sea and reported that this species was not encountered in February. Four females were caught in August–September 1999, close to the southern coast of Norway. In this study *S. oweniana* was trawled in the northern part of the North Sea between Scotland and Norway and additionally near the Danish coast. The reason why there were no *S. oweniana* in summer could be due to the timing of recruitment. In Scottish waters, spawning occurs from September to February and juvenile individuals (up to 9 mm DML) have been found in plankton samples between March and September (Yau, 1994). Again, the mesh size of the GOV may be too large to catch young *S. oweniana* in summer.

5. Conclusion

The cephalopod by-catch data of the IBTS samples from summer 2007 to winter 2009 provided new and meaningful information on the meso-scale distribution patterns of different cephalopod species occurring in the North Sea. The data identified typical distribution patterns of *A. subulata*, *L. forbesii* and, to some degree, *L. vulgaris* during winter and summer. Some information is given for other cephalopod species, but data of those species are too sparse for major conclusions. Additionally, our data suggest typical migration patterns throughout and into the North Sea for the loliginid species. Maturity stages and length frequency distributions give clues on possible spawning sites and seasons. Size and estimated growth seem to be strongly correlated to water temperature. The study points out the importance for the need of more detailed information on major cephalopod species in the central North Sea, particularly in light of rising sea temperatures and possible increases of cephalopod stocks in the North Sea.

Acknowledgements

This research was funded by the environmental foundation Deutsche Bundesstiftung Umwelt (DBU). We thank the chief scientists Gerd Wegner, Siegfried Ehrich and Anne Sell for supporting Daniel Oesterwind on board FRV Walther Herwig III. Thanks also to Ingo Wilhelms for help with ArcView, Annika Elsheimer for logistical support, and Christoph Noever for help in Kiel laboratory. Finally, special thanks to Louise Allcock for her comments and ideas during the editing process.

References

Anonymous, 2006. Manual for the International Bottom Trawl Surveys (IBTS), revision VII. Addendum to the Report of the International Bottom Trawl Survey Working Group (IBTSWG). Int. Counc. Explor. Sea C.M. 2002/D:03.

Anonymous, 2008. Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH). Int. Counc. Explor. Sea C.M. 2008/G:02.

Bellido, J.M., Pierce, G.J., Wang, J., 2001. Modelling intra annual variation of squid *Loligo forbesi* in Scottish waters using generalized additive models. Fish. Res. 52, 23–39.

Bhattacharya, C.G., 1967. A simple method of resolution of a distribution into Gaussian components. Biometrics 23, 115–135.

Boyle, P.R., Pierce, G.J., 1994. Fishery biology of northeast Atlantic squid: an overview. Fish. Res. 21, 1–15.

Boyle, P.R., Pierce, G.J., Hastie, L.C., 1995. Flexible reproductive strategies in the squid *Loligo forbesi*. Mar. Biol. 121, 501–508.

Caddy, J.F., Rodhouse, P.G., 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? Rev. Fish Biol. Fish. 8, 431–444.

Collins, M.A., Boyle, P.R., Pierce, G.J., Key, L.N., Hughes, S.E., Murphy, J., 1999. Resolution of multiple cohorts in the *Loligo forbesi* population from the west of Scotland. ICES J. Mar. Sci. 56, 500–509.

Collins, M.A., Yau, C., Boyle, P.R., Friese, D., Piatkowski, U., 2002. Distribution of cephalopods from plankton surveys around the British Isles. Bull. Mar. Sci. 71, 239–254.

De Heij, A., Baayen, R.P., 1999. Seasonal distribution of the cephalopod *Alloteuthis subulata* in the central and southern North Sea. Basteria 63, 129–138.

De Heij, A., Baayen, R.P., 2005. Seasonal distribution of cephalopod species living in the central and southern North Sea. Basteria 69, 91–119.

FAO, 2009. Fishery and Aquaculture Statistics. FAO Yearbook 2007. FAO, Rome, 72 pp.

Gayanilo, F.C., Sparre, P., Pauly, D. (Eds.), 2006. FiSAT II: FAO ICLARM Fish Stock Assessment Tools (Version 1.1.2). FAO, Rome, Available at: www.fao.org/fi/statist/fisoft/fisat/index.htm.

González, A.F., Guerra, A., 1996. Reproductive biology of the short-finned squid *Illex coindetii* (Cephalopoda: Ommastrephidae) of the Northeastern Atlantic. Sarsia 81, 107–118.

Grimpe, G., 1925. Zur Kenntnis der Cephalopodenfauna der Nordsee. Wiss. Meeresunters. Helgol. 16, 1–122.

Hastie, L.C., Joy, J.B., Pierce, G.J., Yau, C., 1994. Reproductive biology of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Scottish waters. J. Mar. Biol. Assoc. U. K. 74, 367–382.

Hastie, L.C., Pierce, G.J., Wang, J., Bruno, I., Moreno, A., Piatkowski, U., Robin, J.P., 2009. Cephalopods in the north-eastern Atlantic: species, biogeography, ecology, exploitation and conservation. Oceanogr. Mar. Biol. Ann. Rev. 47, 111–190.

Hernández-García, V., 2002. Reproductive biology of *Illex coindetii* and *Tadaropsis eblanae* (Cephalopoda: Ommastrephidae) off Northwest Africa (4°N, 35°N). Bull. Mar. Sci. 71, 347–366.

Holme, N.A., 1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. J. Mar. Biol. Assoc. U.K. 54, 481–503.

Howard, F.G., 1979. Recent trends in the Scottish fishery for *Loligo forbesi*, together with some notes on the biology of the species. Int. Counc. Explor. Sea C.M. 1979/K:36.

Howard, F.G., Ngoile, M.A., Mason, J., 1987. *Loligo forbesi*: Its present status in Scottish fisheries. Int. Counc. Explor. Sea C.M. 1987/K:05.

Joy, J.B., 1990. The fishery biology of *Todarodes sagittatus* in Shetland waters. J. Cephalopod Biol. 1, 1–19.

Kristensen, I., 1966. De inktvissen langs de Nederlandse kust. Correspondentieblad van de Nederlandse Malacologiosche Vereniging 118, 1240–1243.

Lum-Kong, A., Pierce, G.J., Yau, C., 1992. Timing of spawning and recruitment in *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. J. Mar. Biol. Assoc. U.K. 72, 301–311.

Pauly, D., Caddy, J.F., 1985. A modification of Bhattacharya's method for the analysis of mixtures of normal distributions. FAO Fish. Circ. 781, 1–16.

Piatkowski, U., Pierce, G.J., Morais da Cunha, M., 2001. Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. Fish. Res. 52, 5–10.

Pierce, G.J., Boyle, P.R., Hastie, L.C., Key, L., 1994. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. Fish. Res. 21, 17–41.

Pierce, G.J., Bailey, N., Stratoudakis, Y., Newton, A., 1998. Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. ICES J. Mar. Sci. 55, 14–33.

Pierce, G.J., Boyle, P.R., 2003. Empirical modeling of interannual trends in abundance of squid (*Loligo forbesi*) in Scottish waters. Fish. Res. 59, 305–326.

Pierce, G.J., Valavanis, V.D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J.M., Katara, I., Piatkowski, U., Pereira, J., Balguerias, E., Sobrino, I., Lefkaditou, E., Wang, J., Santurtun, M., Boyle, P.R., Hastie, L.C., MacLeod, C.D., Smith, J.M., Viana, M., Gonzalez, A.F., Zuur, A.F., 2008. A review of cephalopod—environment interactions in European Seas. Hydrobiologia 612, 49–70.

Robin, J.P., Denis, V., 1999. Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. J. Appl. Ecol. 36, 101–110.

Rodhouse, P.G., Swinfen, R.C., Murray, A.W.A., 1988. Life cycle, demography and reproductive investment in the myopsid squid *Alloteuthis subulata*. Mar. Ecol. Prog. Ser. 45, 245–253.

Thomas, H.J., 1969. Some observations on the exploitation and distribution of squid around Scotland. Int. Counc. Explor. Sea C.M. 1969/K:29.

Thomas, H.J., Davidson, C., 1972. Further observations on the Scottish squid fishery. Int. Counc. Explor. Sea C.M. 1972/K:31.

Tinbergen, L., Verwey, J., 1945. The Biology of *Loligo vulgaris* Lam., vol. 2733. Transl. Ser. Fish. Res. Board Can, p. 35.

Viana, M., Pierce, G.J., Illian, J., MacLeod, C.D., Bailey, N., Wang, J.J., Hastie, L.C., 2009. Seasonal movements of veined squid *Loligo forbesi* in Scottish (UK) waters. Aquat. Living Resour. 22, 291–305.

Waluda, C.M., Pierce, G.J., 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. S. Afr. J. Mar. Sci. 20, 323–336.

Yau, C. 1994. The ecology and ontogeny of cephalopod juveniles in Scottish waters. Unpublished Ph.D. Thesis, University of Aberdeen.

Yau, C., Boyle, P.R., 1996. Ecology of *Sepiola atlantica* (Mollusca: Cephalopoda) in the shallow sub-littoral zone. J. Mar. Biol. Assoc. U. K. 76, 733–748.

Young, I.A.G., Pierce, G.J., Daly, H.I., Santos, M.B., Key, L.N., Bailey, N., Robin, J.P., Bishop, A.J., Stowasser, G., Nyegaard, M., Cho, S.K., Rasero, M., Pereira, J.M.F., 2004. Application of depletion methods to estimate stock size in the squid *Loligo forbesi* in Scottish waters (UK). Fish. Res. 69, 211–227.

Young, I.A.G., Pierce, G.J., Murphy, J., Daly, H.I., Bailey, N., 2006. Application of the Gómez-Muñoz model to estimate catch and effort in squid fisheries in Scotland. Fish. Res. 78, 26–38.

Zumholz, K., Piatkowski, U., 2005. Research cruise data on the biology of the lesser flying squid, *Todaropsis eblanae*, in the North Sea. Aquat. Living Resour. 18, 373–376.

Zuur, A.F., Pierce, G.J., 2004. Common trends in northeast Atlantic squid time series. J. Sea Res. 52, 57–72.