



Social structure and abundance of coastal bottlenose dolphins, *Tursiops truncatus*, in the Normano-Breton Gulf, English Channel

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A large, but poorly studied, bottlenose dolphin community, *Tursiops truncatus*, inhabits coastal waters of Normandy (Normano-Breton Gulf, English Channel, France). In this study, the social structure and abundance of this community were assessed using photo-identification techniques. Like other bottlenose dolphin communities worldwide, this resident community has a fission–fusion social structure with fluid associations among individuals (half-weight index = 0.10). Association patterns were highly variable as indicated by a high social differentiation ($S = 0.95 \pm 0.03$). The majority of associations were casual, lasting days to months. However, individuals exhibited also a smaller proportion of long-term relationships. A mean group size of 26 was large compared with other resident coastal communities, and variable, ranging from 1 to 100, which could be the results of ecological conditions, in particular resource predictability and availability. Analyses also showed that the community was organized in 3 social clusters that were not completely isolated from each other. Abundance was estimated at 420 dolphins (95% confidence interval: 331–521), making this coastal community one of the largest identified along European coastlines. Because human activities in the Gulf are expected to increase in the upcoming years, long-term demographic monitoring of this dolphin community will be critical for its management.

Key words: abundance, bottlenose dolphins *Tursiops truncatus*, fission–fusion, mark-recapture, Normano-Breton Gulf, photo-identification, social structure

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The estimation of spatio-temporal variations of demographic parameters in top predator populations is critical to assess their health and the potential impact of anthropogenic activities and to take appropriate management measures (Frederiksen et al. 2004; Votier et al. 2005; Bejder et al. 2006). In addition, for social species, studying the social structure and differences in habitat use among social clusters (i.e., sets of individuals so that the majority of social associations occurs within, rather than between these sets of individuals) is also important to ensure their conservation (Sutherland 1998; Whitehead et al. 2004). For example, according to their spatial distribution or diet specializations, distinct social clusters may respond differently to human activities or environmental changes (McComb et al. 2001; Whitehead and Rendell 2004; Whitehead et al. 2004; Ansmann et al. 2012). Studying social structure can also shed light on the factors that are driving population processes. Sociality develops as a trade-off between the selective forces

conferring benefits to group-living (such as cooperation, protection from predators, transfer of information) and the costs incurred in a group (e.g., increased competition, parasite load, see review in Krause and Ruxton 2002). Social groups are likely to be maintained when the fitness gains of sociality outweigh the costs (Alexander 1974). Ecological factors, in particular variations in local resources, can affect the size and persistence of social groups (Wrangham 1980; Rubenstein and Wrangham 1986; Lusseau et al. 2004). For instance, in fission–fusion societies, associations between individuals are highly dynamic and temporary, lasting from several hours to a few months, and may be adjusted in response to fluctuations in resource availability (Connor et al. 2000; Wittemyer et al. 2005; Smith et al. 2008).

Bottlenose dolphins (*Tursiops* sp.), which are found from temperate to tropical waters, live in fission–fusion societies (Connor et al. 2000). They associate in small groups whose composition quickly changes (possibly several times per day).

Associations tend to be determined by sex and age (Connor et al. 2000). However, in these dynamic societies, besides mother and calf associations that typically last for at least 3 years (Wells et al. 1987), individuals can also share strong relationships such as those among adult males (Connor et al. 1992). Social structure varies across communities (i.e., groups of individuals of the same species that co-occur in space and time and have an opportunity to interact) and seems to be shaped by ecological factors, such as prey availability or oceanographic conditions and intrinsic factors, in particular, shared knowledge and behavioral strategies (Lusseau et al. 2003; Daura-Jorge et al. 2012; Mann et al. 2012). Great variations in distribution and size of communities have also been reported worldwide, with communities exhibiting patterns of residency ranging from resident (Wilson et al. 1999) to migratory (i.e., showing seasonal site fidelity—Barco et al. 1999), or transient (i.e., showing no site fidelity—Defran and Weller 1999). Abundance also varies from very small communities of tens (Liret 2001) to very large communities of thousands of individuals (Read et al. 2003).

Tursiops truncatus is the only bottlenose dolphin species occurring within European coastal and pelagic waters (Hammond et al. 2012). They are protected under the European Union's Habitats Directive (92/43/22C) and are listed in Annex II as a species whose conservation requires the designation of Special Areas of Conservation and in Annex IV as in need of strict protection. Three resident communities are found in French coastal waters of the Atlantic and the English Channel: 2 small communities (tens of individuals) in the Iroise Sea (Liret 2001) and a community in Normandy coastal waters (the Normano-Breton Gulf, also known as the Gulf of Saint-Malo and named the Gulf hereafter; Fig. 1).

Bottlenose dolphins of the Normano-Breton Gulf were the focus of this study, a community which remains poorly known. They are the most commonly encountered cetacean species in the area (GECC 2011). They are genetically isolated from the neighboring communities in the United Kingdom and Ireland (Louis et al. 2014). Furthermore, they inhabit an area of "Special Interest." First, a Marine Park is under creation, which is a marine protected area (IUCN category V "protected seascape"), which promotes sustainable development of human activities together with monitoring of biodiversity and protection. Second, human activities are increasing in the area, several large-scale marine renewable energy constructions are planned in the upcoming years. The construction of wind farms in the North and Baltic Seas has impacted the distribution of harbor porpoises (*Phocoena phocoena*) and their displacement was linked to the loud sounds produced by pile-driving events (Carstensen et al. 2006; Tougaard et al. 2009). In this context, it is important to carry out studies on the bottlenose dolphin community in the Gulf several years prior to the beginning of the building of these extended wind farms to gather benchmark data on the community before any potential impacts are manifested.

The goal of this study was therefore to provide baseline knowledge on social structure and abundance of this bottlenose dolphin community, both for its monitoring and management

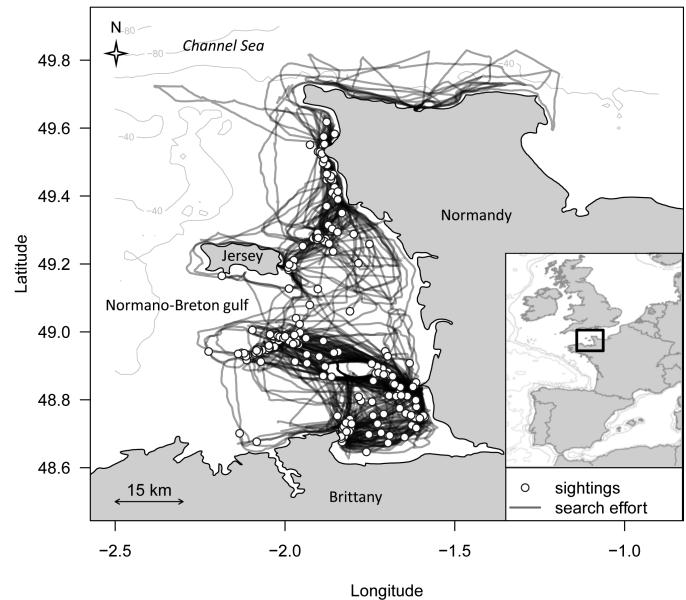


Fig. 1.—Map of the study area in the Normano-Breton Gulf of the English Channel, distribution of photo-identification survey effort for bottlenose dolphins (*Tursiops truncatus*; i.e., boat Global Positioning System tracks when searching for dolphins), and location of sightings of bottlenose dolphins from 2007 to 2010.

and for research on the factors that affect their social structure. Despite being extensively studied, research projects across the broad range of bottlenose dolphins can contribute towards a better understanding of the factors shaping sociality in the species. First, group patterns were examined and the social structure of the community was investigated using association and lagged association rate analyses. It is essential to identify whether there were any completely discrete social clusters before estimating abundance. It is key to determine if population estimates are appropriate for the whole community or should be based on different social clusters. The 2nd objective of this study was to estimate the size of the community frequenting the Gulf using photo-identification and mark-recapture models.

MATERIALS AND METHODS

Surveys and photo-identification.—The Normano-Breton Gulf is characterized by shallow waters (depth ranges from 0 to 40 m). Seabed is dominated by coarse sediments and a smaller proportion of rocks, sand, and mud. From 2006 to 2010, year-round boat surveys were performed in the Gulf, by the GECC (Groupe d'Etude des Cétacés du Cotentin). Surveys were run at an approximate speed of 15 knots using a 6-m rigid inflatable boat with 2–6 observers aboard, generally including 2 photographers. They were conducted whenever sea state was favorable (i.e., sea state < 3 Beaufort). The aim of these surveys was to photo-identify bottlenose dolphins in the Gulf waters. From 2007 to 2010, Global Positioning System (GPS) tracks of the surveys (in decimal degrees) were recorded together with observation effort and dolphin group encounter data. The search effort (i.e., the GPS track records of the boat when dolphins were not followed) was represented in R version 3.0.0

(R Development Core Team 2013) using the *marmap* package (Pante and Simon-Bouhet 2013; Fig. 1). The 1st contact point was reported on the map for each group encounter. The study area was not homogeneously surveyed during the study period because of a lack of logistical support. At first, surveys were initiated within the southern part of the Gulf. Then, the survey area was extended to the central part of the Gulf from 2007 onwards. A single survey week was conducted in the northern part in 2007 and the surveys were extended to the northern area in 2008. In 2008 and 2009, the whole Gulf was surveyed, but the spatio-temporal coverage was not homogenous. In 2010, the whole area was surveyed regularly.

During surveys, dorsal fins and upper backs of encountered bottlenose dolphin individuals were photographed using Canon EOS 20 D and 40 D digital SLR cameras with Canon 100–400- and 70–300-mm zoom lens (Canon, Courbevoie, France). Individuals were identified using natural marks: scars, nicks, and scratches on their dorsal fins (Würsig and Würsig 1977; Würsig and Jefferson 1990). A catalog was created and used to re-identify individuals. When available, both sides of the dorsal fin were included in the catalog. A marking level (M), according to the number and size of the nicks, was attributed to each individual. It varied from M1 for individuals with a smooth dorsal fin with scratches to M4 for strongly marked individuals (numerous and large nicks; see Supporting Information S1). Individuals with a smooth dorsal fin and without any or few slight scratches were considered as unmarked and were not entered in the catalog. Quality of the fin photographs was assessed using 3 grades (excellent, good, or poor), which depended on several criteria, i.e., the focus, angle of the animal, presence of water splashes, proportion of the fin out of the water, and the distance to the photographer (see Supporting Information S2). Only good and excellent fin photographs, taken on either side of the fin, were used for photo-identification. If there was any doubt in the identification, dolphins were not classified. Several people worked on photo-identification data and to minimize errors, 1 person double-checked all the identifications over the whole study period. The cumulative number of identified dolphins for each year was calculated. The protocol followed guidelines for research on live animals of the American Society of Mammalogists (Sikes et al. 2011).

Social structure.—Social structure was investigated using data collected between 2006 and 2010. Individuals were considered associated if they were observed in the same group. A “group” was defined as all dolphins within an area of 100-m radius involved in similar behavioral activities (Wells et al. 1987). A “sighting” refers to the encounter of a group or the encounter of an individual within a group. Group size was estimated visually by at least 2 observers. Photo-identification work started when the 1st dolphin was spotted, it lasted as long as the dolphins were in the sight of the observers and ended usually when the surveyors decided that they had enough photographs of the animals or when dolphins showed boat avoidance behaviors. Attempts were made to photograph all the animals, whatever their levels of markings.

The statistical analyses conducted here were robust to the non-identification of some members of a sampling unit (see below). Thus, we did not exclude any group from the analyses (e.g., based on the proportion of individuals photographed). Social structure analyses were run using the SOCPROG 2.4 program (Whitehead 2009) implemented in Matlab version 7.6.0. (Mathworks Inc. 2008). A daily sampling period was used to avoid demographic effects (such as death, emigration, or immigration) and we excluded the individuals that were identified on < 5 occasions to minimize the bias due to these infrequently sighted individuals. However, the choice of an appropriate cut-off was not straightforward and various values have been used in the literature (e.g., Lusseau et al. 2006; de Stephanis et al. 2008; Wiszniewski et al. 2009; Ansmann et al. 2012). Whitehead (2008a) recommended a minimum of 5 identifications. We performed analyses on individuals identified in at least 5–12 sampling periods. Since results with 6–12 identifications were similar to those with 5 identifications, but included far less individuals and were therefore less representative of the field data, we only present here the results that included animals identified in at least 5 sampling periods. Individuals with a smooth dorsal fin (M1) were excluded from analyses because their scratches or pigment spots could change quickly. Moreover, as their scratches and pigment spots are only visible on 1 side, it is difficult to identify them on both sides and this could lead to misidentifications. Therefore, only marked adults and subadults were considered in these analyses; newborn and young animals were generally difficult to identify due to their low level of marking.

The half-weight index (HWI) was used to quantify the strength of associations between pairs of individual dolphins. This index minimizes bias if all the associates are not identified (Cairns and Schwager 1987). Since the HWI is commonly used in bottlenose dolphin social structure studies, this makes comparisons among studies easier.

The index is described by:

$$\text{HWI} = \frac{X}{X + 1/2(Ya + Yb)}$$

where X = number of groups including both dolphins a and b , Ya = number of groups including dolphin a but not dolphin b and Yb = number of groups including dolphin b but not dolphin a . It ranges between 0 (a and b never seen together) and 1 (a and b always observed together). Standard deviation and coefficient of variation (CV) of the HWI were also calculated.

A Monte Carlo permutation test was conducted to determine whether observed association patterns were significantly different from random association patterns using the recommendations of Bejder et al. (1998) with modifications included in Whitehead (1999, 2008a, 2009). The matrix of observed association indices was permuted within sampling periods until P stabilized at 10,000 permutations with 100 flips. The test was then run 3 additional times to ensure the stability of P . A higher SD of the observed association indices in comparison to the SD of permuted data indices shows that long-term preferred and/or avoided associations are present in the community (Whitehead 1999, 2008a).

Reliability of the social structure representation was assessed using Pearson's correlation coefficient (r) and social differentiation (S —Whitehead 2008a, 2008b). We estimated the accuracy of the social structure representation by correlating estimated HWI association indices with their true value using the maximum likelihood estimator ($r = 0$ for an inaccurate representation; $r = 1$ for an excellent representation). The social differentiation, which is the CV of association indices estimated using maximum likelihood, gives the variability of association indices in the community. A value of S close to 0 indicated that association indices were homogenous in the community and a value of $S \geq 1$ suggested the association indices were highly variable. Fewer data are needed to accurately reconstruct social structure when the social differentiation is moderate or high (i.e., > 0.5 —Whitehead 2008a, 2008b). Standard errors were calculated for r and S from bootstrap with 1,000 replications.

The social structure of the community was examined using a hierarchical cluster analysis with the average-linkage method on the HWI data matrix. We considered the average-linkage method as the most accurate method to display social structure in clusters because outlier distances have less impact on the results than with single- or complete-linkage methods (Milligan and Cooper 1987; Whitehead and Dufault 1999). It is therefore the most commonly used method in social structure analyses (e.g., Lusseau et al. 2003; Wiszniewski et al. 2009; Augusto et al. 2011). We assumed that a cluster with a cophenetic correlation coefficient (CCC—i.e., the correlation between the observed dyadic association indices and the indices represented in the dendrogram) higher than 0.8 indicated a reliable separation among clusters (Whitehead 2008a). The most parsimonious cut-off in the cluster was defined using the division that maximizes the modularity coefficient, Q (Newman 2004; Lusseau 2007; Whitehead 2008a), which was defined as the difference between the proportion of the total association measured within clusters versus the expected proportion if pairwise association indices were randomly distributed. Therefore, this method divides the individuals into clusters where association indices are higher among members of the same cluster than expected by chance. The analysis takes into account differences of gregariousness of individuals (i.e., mean number of associates of an individual). A modularity coefficient of 0 shows a random group structure. A modularity coefficient ≥ 0.3 indicates a good division among clusters (Newman 2004). To test if association indices were significantly higher inside each of the social clusters than between them, a Mantel test was conducted using the *ade4* package (Chessel et al. 2004; Dray and Dufour 2007; Dray et al. 2007) in R statistical software version 3.0.0. Using this test, the mean association indices of individuals within and between clusters were compared.

To visualize whether social clusters were spatially distributed, the median latitude/longitude of the sighting positions of each individual was calculated. Because individuals identified only a few times were included (minimum identifications set to 5), we used the median position because it is more robust to outlier positions than the mean. The median absolute deviation (MAD) was also calculated to account for the variability in the sighting positions (Venables and Ripley 2002). Median position

and MAD for each individual were then represented on a map that also indicated its social cluster to examine whether ranging differences accounted for the social structure of this community.

To determine the temporal stability of associations among individual dolphins, variations in standardized lagged association rates (SLAR—Whitehead 1995, 2008a) were calculated. SLAR is the probability, given that a and b are associated at time 0, that b will be randomly chosen as associate of a after a specified time lag. The probability was averaged over all individuals. This average standardized association rate was estimated by $g(\tau)$ as defined by Whitehead (1995) and plotted in relation to time lag in days. The SLAR is robust to the nonidentification of all the associates. All individuals (even rarely observed individuals) were considered for this analysis because poorly observed animals will have little impact on the SLAR estimation (Whitehead 2008a). SLAR was compared to the standardized null association rate (NAR), which represents the SLAR when there are no preferred associations, to determine whether the patterns of associations were nonrandom (Whitehead 1995, 2008a). Then, 4 exponential decay models of temporal stability were fitted to the data set (Whitehead 1995, 2008a). These models consider 2 types of associations: constant companionships (i.e., lifetime associations) and casual acquaintances (associations lasting from a few days to a few years). Each model was composed of a combination of these 2 types of associations (Table 1). The rapid dissociations (associations lasting only a few hours) were not incorporated directly into the models because they were confounded by gregariousness. Therefore, each of the 4 models may or may not have included rapid dissociations (Whitehead 2008a). The model that best described the temporal dynamics of the social structure was selected by the quasi-Akaike Information Criterion (QAIC—Whitehead 2007). The precision of the parameters was estimated using jackknife (Efron and Stein 1981; Whitehead 1995, 2008a).

Abundance.—Mark-recapture models were applied to photo-identification data to estimate the size of the community. For this analysis, only individuals of marking levels M3 and M4, unambiguously identifiable on both sides of the dorsal fin on good and excellent fin photographs, were included to minimize identification errors. The total community size was estimated using survey data collected from July to September 2010 over the whole study area of the Normano-Breton Gulf. For the 2006–2009, no particular effort was made to survey the whole Gulf as regularly as in 2010, which made it impossible to reliably estimate abundance without spatial bias.

During the 2010 summer season, 7 capture occasions were conducted from 10 July to 18 September. Each capture occasion was composed by 2 whole survey days (1 survey in the northern part and another in the southern and central parts of the Gulf) to cover the whole area. Efforts were made to minimize the time between each of the 2 surveys during a capture occasion, but it varied with weather conditions, they were usually carried out 1–2 days apart. In 2 occasions, surveys were carried out simultaneously on the same day, using 2 boats. Summer was chosen for abundance estimation because good weather permitted more regular surveys than during other seasons.

Abundance of well-marked individuals (N) was estimated in *MARK* software (White and Burnham 1999). Among the standard sequential mark-recapture models for closed populations (Otis et al. 1978), models M_o , M_h , M_t , and M_{th} were compared. Capture probabilities could vary among individuals (h) and over time (t) because of a variety of factors such as avoidance or attraction to the boat (Hammond 1986), individual differences in home ranges, variations of survey effort and different photographers. The models assuming a behavioral response to capture (M_b , M_{tb} , M_{bh} , M_{tbh}) were not tested because photo-identification is a noninvasive method. It is therefore common to exclude models assuming a behavioral response in photo-identification studies (e.g., Wilson et al. 1999; Daura-Jorge et al. 2013). Heterogeneity among individuals (h) was modeled using 2 mixtures. Standard models (M_o and M_t) were built from finite mixture models (M_h and M_{th}), setting the mixture parameters to 1.

The following assumptions were made for the tested models:

- 1) The population was closed demographically (i.e., no deaths or births) and geographically (i.e., no emigration or immigration) during the time period considered.
- 2) All marked individuals were correctly identified and recorded on each capture occasion.
- 3) Marks were not lost and marked individuals were not preferentially photographed.

The sampling period was short (2 months), so there was a strong probability that the demographic closure assumption was respected. Dolphins are indeed long-lived animals with a low reproduction rate. Emigration and immigration could not be totally excluded, but could be considered minimal due to the short sampling period. The closure assumption was confirmed using the Close Test program (Otis et al. 1978; Stanley and Burnham 1999). Assumptions 2 and 3 were fulfilled because only well-marked and easily identified individuals with good to excellent fin photographs were included in analyses. Mark changes could occur, however because the sampling period was short and the surveys were regular, we assumed that any mark changes could be detected.

Abundance models were compared using AIC_c (which is adjusted to small sample size—Hurvich and Tsai 1989; Burnham and Anderson 2002). AIC_c weights were calculated, they measure the support of a given model relative to the others. Based on the AIC_c weights, we estimated the average

abundance across all models (Burnham and Anderson 2002). Log-normal confidence intervals were calculated following the formulas described in Lukacs (2013).

Abundance estimation (N) run in *MARK* was only based on well-marked individuals. Therefore, the mean proportion of well-marked individuals (M3 and M4) on the total number of fins (M1 to M4 and unmarked fins) was estimated. This was performed for each photograph showing at least 2 dorsal fins.

This mean proportion of well-marked individuals was calculated as follows:

$$\hat{\theta} = \frac{1}{n} \sum_{i=1}^n \frac{m_i}{t_i}$$

where, n is the number of photographs in the data set, m_i is the number of heavily marked individual fins on photograph i , and t_i is the total number of individual fins on photograph i .

To estimate the whole community size (N'), N was adjusted with the calculated proportion: $N' = \frac{N}{\hat{\theta}}$. Confidence intervals (CI) were corrected following Whitehead et al. (1997).

RESULTS

Survey effort and photo-identification.—Between 2006 and 2010, 201 bottlenose dolphin groups were recorded on 134 field-days. Photographs were taken during 199 group encounters. A mean of 171 photographs ($SD = 216$) per group were of sufficient quality to allow identification of at least 1 individual. A total of 336 marked individuals (M2, M3, and M4) and 361 M1 individuals were identified. Mean visually estimated encounter group size in the field was 26 ($SD = 18$, range: 1 to 100). Fifty-six percent of visually estimated individuals in the groups were of marking levels M2 to M4 and were photo-identified. Mean identified M2, M3, and M4 individuals per group were 14 ($SD = 13$, range: 1 to 87). Attempts were made to photograph all individuals, it is however difficult to disentangle the proportion of missed individuals from the proportion of M1 (only scratches) and unmarked individuals. Among the 336 marked individuals, 32% were seen only during 1 year, 18% during 2 years, and 50% during 3 or more years. The discovery rate of new well-marked (M3 and M4) individuals sharply

Table 1.—Models of temporal stability of associations fitted to the data set of photo-identified bottlenose dolphins (*Tursiops truncatus*) at Normano-Breton Gulf and ranked by quasi-Akaike Information Criterion (QAIC—Whitehead 1995, 2008a). CC: constant companionships, CA: casual acquaintances. Bold indicates the best-fitted model.

Models	Components	Parameter estimates and SE	QAIC	Δ QAIC
$a2 + a3 * e^{(-a1 * \tau)}$	CC + CA	$a1 = 0.012 \pm 0.012$ $a2 = 0.007 \pm 0.002$ $a3 = 0.010 \pm 0.003$	28,874	0
$a3 * e^{(-a1 * \tau)} + a4 * e^{(-a2 * \tau)}$	2 Levels of CA	$a1 = 1.525 \pm 3.860$ $a2 = 0.000 \pm 33.660$ $a3 = 0.059 \pm 0.352$ $a4 = 0.012 \pm 2.176$	28,883	7
$a2 * e^{(-a1 * \tau)}$	CA	$a1 = 0.001 \pm 0.000$ $a2 = 0.012 \pm 0.003$	28,907	33
$a1$	CC	$a1 = 0.009 \pm 0.002$	29,097	223

Table 2.—Closed population models for abundance estimations of photo-identified bottlenose dolphins (*Tursiops truncatus*) at Normano-Breton Gulf ranked by the lowest Akaike Information Criterion adjusted for small sample size (AIC_c). Model notation: p : probability of capture, c : probability of recapture, (\cdot) : constant parameter, (t) : time varying parameter, mixture parameter: π , A and B refer to the 2 mixtures, N : abundance estimation. SE refers to the standard error and var to the variance.

Models	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	Deviance	N	$SE(N)$	$var(N)$
$M_i(N, p(t) = c(t))$	49.24	0.00	0.67	1.00	118.35	123.10	5.53	30.58
$M_{ih}(N, \pi, p_A(t) = c_A(t), p_B(t) = c_B(t))$	50.63	1.38	0.33	0.50	103.18	127.06	6.60	43.56
$M_p(N, p(\cdot) = c(\cdot))$	77.45	20.21	0.00	0.00	158.73	124.77	5.87	34.46
$M_{ph}(N, \pi, p_A(\cdot) = c_A(\cdot), p_B(\cdot) = c_B(\cdot))$	81.08	31.84	0.00	0.00	158.33	129.25	11.23	126.11

increased between 2006 and 2007 (Fig. 2). This increase corresponded to the expansion of the study area. It then tended to stabilize, indicating that most of the individuals had been identified and that immigration could be considered low. However, when slightly marked (M2) individuals were included, the number of new individuals was still increasing in the recent years. These new individuals could either be previously smooth dorsal fin individuals (M1 or unmarked) that were already in the Gulf or immigrants.

Social structure.—Eight group encounters were removed from the analyses because no marked individuals (M2, M3, or M4) or no individual identified in at least 5 sampling periods were included. Therefore, 191 group encounters were used in the social structure analyses. A total of 206 marked dolphins (M2, M3, and M4) were identified in at least 5 sampling periods. They represented 88.92% ($SD = 15.32$) of all the marked dolphins identified in each group. Some dolphins (130) did not meet the minimum of 5 identifications criteria and were excluded from analyses. The mean number of observations of all marked dolphins (M2, M3, or M4) was 6.41 ($SD = 5.34$). When considering individuals identified at least 5 times, the mean number of observations of an individual was 10.12 ($SD = 5.42$) and the maximum was 29 observations.

The mean HWI was 0.097 ($SD = 0.136$, $CV = 1.396$). This SD was higher than the SD obtained from permuted data

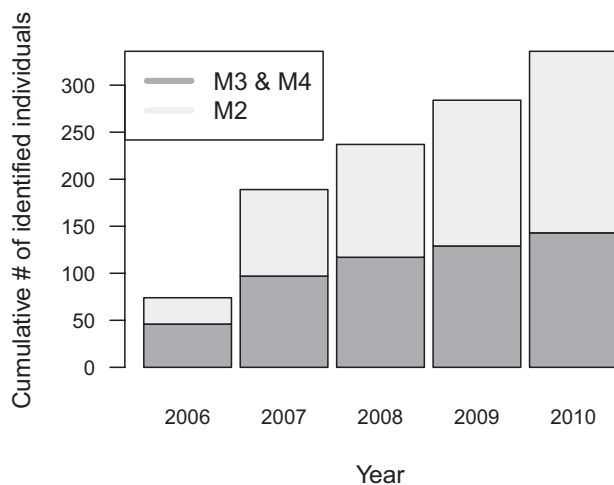


Fig. 2.—Cumulative number of photo-identified bottlenose dolphins (*Tursiops truncatus*) in the Normano-Breton Gulf from 2006 to 2010 according to their marking levels (M2 or M3 and M4).

($SD = 0.132$, $P < 0.001$), suggesting that individuals did not associate randomly and that there were long-term preferred or avoided companions in the community.

The correlation coefficient (r) between the true association indices and their estimates was 0.68 ($SE = 0.04$), indicating that the estimated association coefficients adequately represented social structure. Social differentiation was $S = 0.95$ ($SE = 0.03$), which indicated that relationship patterns were highly variable. $S^2 * H$ (H : mean number of associations per individual) = $0.95^2 * 211 = 190$, which is well above 5, indicating an excellent ability to reject the null hypothesis of no preferred/avoided associations (Whitehead 2008b). Therefore, these analyses had good power to detect the social system (Whitehead 2008a, 2008b).

The cluster CCC was 0.747, which is close to the 0.8 threshold indicating an effective social structure representation (Fig. 3; Whitehead 2008a). Maximum modularity ($Q = 0.320$) at $HWI = 0.085$ provided a reliable separation in 3 different clusters (Fig. 3; Newman 2004). One individual (represented by a black line in the Fig. 3) was not assigned to any of the 3 clusters. However, this individual was mostly seen with individuals of the cluster “North” (83% of its identifications). A Mantel test confirmed that there were significantly more associations among individuals within the same cluster than among individuals of different clusters ($r = 0.55$, $P < 0.001$). Mean HWI among individuals of the same clusters was about twice that of the HWI averaged on all individuals. Moreover, the mean association index between individuals of clusters “North” and “South” was very low ($HWI = 0.007$, $SD = 0.029$; Fig. 4). The dendrogram (Fig. 3) also showed that there were strong associations ($HWI \geq 0.5$) among a few individuals (1.93 % of the total possible associations).

The map showing the median geographical position of each dolphin’s sightings as a function of their social cluster indicated that the clusters showed a degree of spatial segregation (Fig. 5). Dolphins from cluster “North” were mainly observed in the northern part of the Gulf, dolphins from cluster “Minquiers” in the center part, and individuals from cluster “South” were mainly observed in the southern part of the Gulf. However, error bars (MAD) showed spatial overlaps between the locations of individuals of different clusters.

The SLAR (calculated based on the data; Fig. 6) remained higher than the NAR (Fig. 6), thus showing nonrandom temporal association patterns. The SLAR curve and error bars (that were

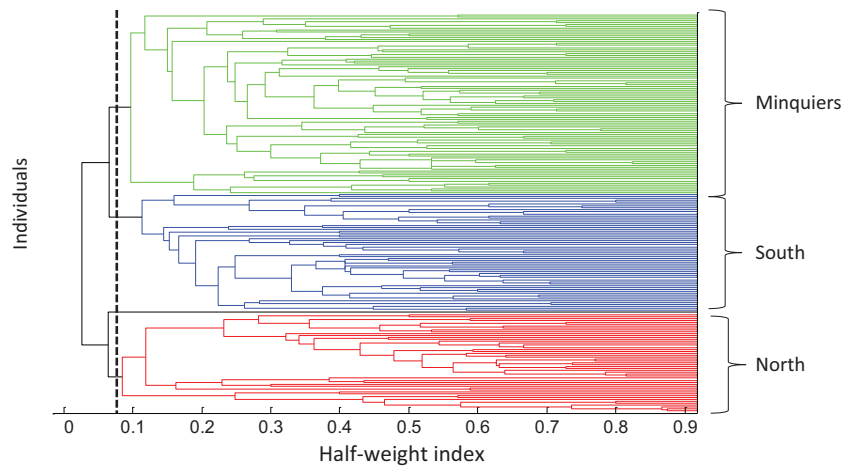


Fig. 3.—Hierarchical cluster diagram of the half-weight index coefficients between photo-identified bottlenose dolphins (*Tursiops truncatus*) at Normano-Breton Gulf. Cluster division was obtained using maximum modularity controlling for gregariousness (modularity value was 0.320 and was maximized at HWI = 0.085 as indicated by the dashed line). Cluster cophenetic correlation coefficient was 0.747. (Online version in color.)

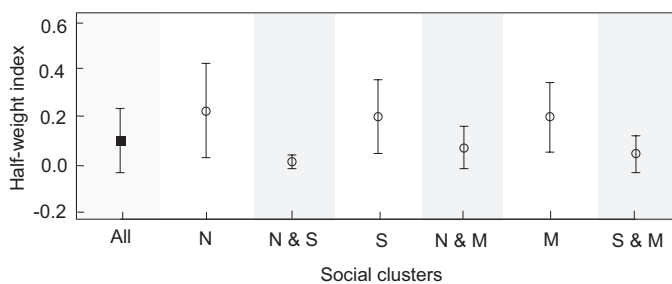


Fig. 4.—Plot of the mean half-weight index \pm SD calculated between all photo-identified bottlenose dolphins (*Tursiops truncatus*) at Normano-Breton Gulf (ALL, light gray shading and filled square), between individuals of the same social cluster (no shading) and between individuals of 2 distinct social clusters (gray shading). M = Minquiers, N = North, and S = South.

generated by the jack-knife technique) indicated high variability in the association durations. The model that best described the temporal stability of associations included 2 levels of associates, casual (short-term) acquaintances, and constant (long-term) companions (Table 1; Fig. 6). The fitted values from this model suggested a great decrease of SLAR from a few days to 100–200 days after 1st association of individuals. Past 200 days, the predicted SLAR stabilized around 0.007, which remained higher than values predicted by the NAR (0.003) suggesting the existence of a small proportion of long-term companions. From the best SLAR fitting model, the duration of the casual acquaintances, which was given by $1/a1$ was estimated at 80.6 ($SE = 77.3$) days (Whitehead 1995, 2008a; Table 1). Because of the high SE and the variability in the SLAR curve, one needs to be cautious when interpreting the results.

Community size.—Because social clusters were not completely discrete, abundance was estimated for the whole community. The closure assumption was verified according to the closure test of Stanley and Burnham (1999— $P = 0.68$) and the closure test by Otis et al. (1978— $P = 0.98$). Model M_i and M_{th} had the smallest AIC_c ($\Delta AIC_c < 2$) and accounted for all the AIC_c weights (Table 2). After model averaging, the estimated number of well-marked individuals (M3 and M4) was $N = 124$

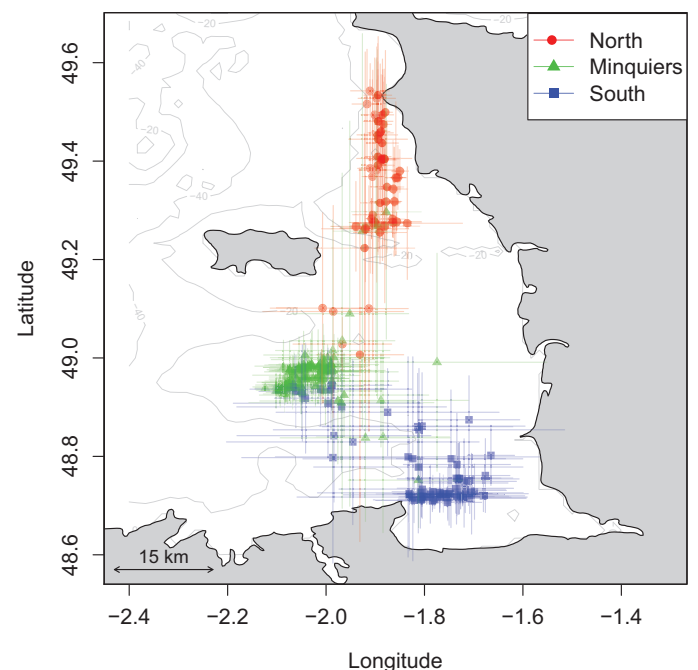


Fig. 5.—Map of the median latitude/longitude (points) and median absolute deviation (arrows) of the sightings of each photo-identified bottlenose dolphin (*Tursiops truncatus*) at Normano-Breton Gulf. Color and symbol codes indicate the social cluster of each individual. (Online version in color.)

(95% CI: 116–141). The mean proportion of well-marked animals on the total number of fins was $\theta = 0.29$ ($CV = 0.10$) giving an estimated total number of $N' = 420$ dolphins (95% CI: 331–521, $CV = 0.11$ and $SE = 46.92$) in 2010.

DISCUSSION

A fission–fusion social structure.—As described in other bottlenose dolphin communities studied so far, the Normano-Breton Gulf community lives in a fission–fusion society (Wells et al. 1987; Connor et al. 2000; Lusseau et al. 2006). At this study site, associations between individuals were in majority

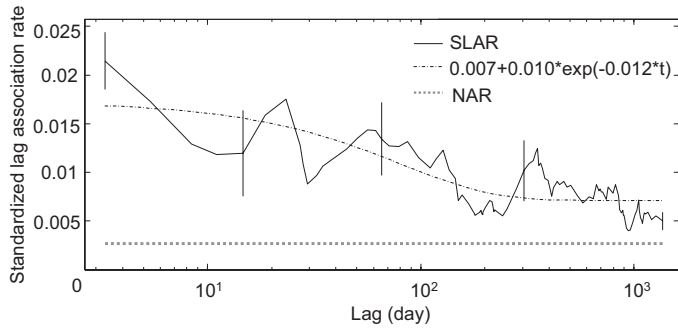


Fig. 6.—Graph of the standardized lag association rate (SLAR, solid curve) plotted against time lag (in days) for all the identified bottlenose dolphins (*Tursiops truncatus*) at Normano-Breton Gulf. The null association rate (NAR, thick dotted curve) was calculated to represent the expected LAR if individuals were associating randomly. The best fitting model (casual acquaintances and constant companions given by $a_2 + a_3 * e^{(-a_1 * t)}$; Table 1—Whitehead 1995, 2008a) is displayed (thin dotted curve).

fluid and weak, and in the range of the association indices observed in other fission–fusion communities (i.e., from 0.06 to 0.20—Wells et al. 1987; Smolker et al. 1992; Connor et al. 2000; Chilvers and Corkeron 2002; Wiszniewski et al. 2009). The temporal patterns of associations were also typical of a fission–fusion society where individuals have mainly short-term associates and a smaller proportion of constant companions. These results also indicated a gradient in the strength of associations as well as a high variability in relationship durations in the Normano-Breton Gulf community. Individuals may therefore adjust group patterns according to ecological conditions to maximize fitness gains as observed in other fission–fusion species (e.g., in spotted hyenas, *Crocuta crocuta*—Smith et al. 2008). Under the general pattern of fission–fusion societies, bottlenose dolphin communities show high variations in relationships among males, females, and between males and females at both an inter- and intra-population level (Connor et al. 2000, 2011; Lusseau et al. 2003; Wiszniewski et al. 2010, 2012a). It is likely that differences observed among communities are related to local ecological, breeding, antipredator constraints, and possibly anthropogenic activities, which can be highly variable throughout the wide geographical range of the bottlenose dolphin (Lusseau et al. 2003; Möller and Harcourt 2008; Augusto et al. 2011; Ansmann et al. 2012; Wiszniewski et al. 2012b). As found in other communities, stable and high association indices in the Normano-Breton Gulf community could indicate male alliances (e.g., Connor et al. 1992, 1999, 2011; Möller et al. 2001; Krützen et al. 2003). To date, however, alliances have not yet been reported in North-Eastern Atlantic communities (Moray Firth, Scotland and Sado estuary, Portugal—Wilson 1995; Augusto et al. 2011). Because individuals with a smooth dorsal fin (M1), which is typical for juveniles, were excluded from the analyses, the constant companions likely do not reflect mother and calf bonds in their 1st years of life. Moderate HWI could indicate female bands (Wells et al. 1987; Connor et al. 2000; Möller and Harcourt 2008). Associations between males and females are not stable in most communities and tend to be related to reproduction (Connor et al. 1992; Smolker et al.

1992; Owen et al. 2002). In some communities, kin selection (Hamilton 1964) might promote preferential associations with relatives (Krützen et al. 2003; Wiszniewski et al. 2010). On-going genetic analyses will identify the sex and genetic relatedness of the individuals to better understand the forces driving association patterns in the Normano-Breton Gulf.

Possible ecological drivers of large group sizes.—Encountered group size ($\bar{X} = 26$) was particularly high and variable (range: 1 to 100) for a resident coastal community. Similar group sizes were observed in highly mobile communities along coastal open habitats (e.g., a mean of 20 individuals along the California coastline—Defran and Weller 1999). However, in contrast to these mobile and wide-ranging communities, photo-identification work indicated interannual site fidelity in the Normano-Breton Gulf. Site fidelity is supported by stable isotope data performed on biopsy samples, which did not indicate seasonal trends (Louis 2014). In most studied resident coastal communities of bottlenose dolphins (*Tursiops* sp.), the group size ranged from 5 to 8 when groups were defined similarly as in our work (Wells et al. 1987; Wiszniewski et al. 2009; Bouveroux and Mallefet 2010; Ansmann et al. 2012; Fury et al. 2013). Caution should however be taken when comparing group sizes because group definitions can differ among studies (Connor et al. 2000). Predation risk could not explain these large group sizes because killer whales (*Orcinus orca*) or possibly “dolphin-attacking” shark species are not observed in this area and no bite marks were ever recorded in contrast with communities exposed to shark attacks (Heithaus 2001). Delphinid group patterns have also been related to prey availability and/or resource predictability (Lusseau et al. 2003, 2004). In Doubtful Sound (New Zealand), a large mean group size ($\bar{X} = 17$) together with a high proportion of stable associations may have allowed a high level of cooperation and efficient information transfer in a habitat with scarce resources (Lusseau et al. 2003). However, larger group sizes can also be the results of predictable resources. In Moreton Bay (Australia), dolphin groups composed by individuals feeding on trawler discards, a predictable food source, were larger than dolphin groups composed by individuals that did not interact with fisheries (Chilvers and Corkeron 2001; Ansmann et al. 2012). In addition, killer whale (British Columbia) and bottlenose dolphin (Moray Firth, Scotland) groups were smaller in years where less salmon was available (Lusseau et al. 2004). We could therefore state 2 hypotheses for the group sizes in the Normano-Breton Gulf. First, resources could be scarce and patchy, requiring a high level of cooperation among individuals. However, we would predict more stable and stronger relationships than the ones we recorded. The alternative hypothesis is that benefits of living in groups (sharing of knowledge, information exchange, hunting cooperation) could outweigh the costs (feeding competition) as a result of resource availability and/or predictability. Individuals may also adjust group size according to ecological conditions and behavioral activities as in other fission–fusion species (Witemyer et al. 2005; Smith et al. 2008). This flexibility could explain the observed variability of group sizes in this study. Additional data, on habitat productivity, ecology,

and behavior of the dolphins are needed to investigate these hypotheses.

Division in 3 social clusters.—Bottlenose dolphins in Normano-Breton Gulf were identified into 3 social clusters. It is important to evaluate whether nonsocial or indirect social factors could bias the results when conducting clustering analyses (Cantor et al. 2012). Uneven effort could have affected the sighting histories of individuals and separated individuals sighted in different years. However, because the whole area has been surveyed since 2008, we assumed that the partial coverage of the studied area of the 1st year, and to a lesser extent of the 2nd year of survey, did not greatly affect the clustering results. Moreover, individuals showed interannual site fidelity. Therefore, turnover population factors, as observed for Guiana dolphins, *Sotalia guianensis*, could not account for the division into 3 social clusters (Cantor et al. 2012). We investigated whether the clusters were spatially segregated to test if the observed social division could mainly be driven by shared use of space (Lusseau et al. 2006). Social clusters showed a degree of spatial segregation since individuals of each cluster were mainly observed in a specific area of the Normano-Breton Gulf (i.e., the northern, the central, or the southern part of the Gulf, depending on the cluster). Mean association indices between individuals of the southern cluster and the northern cluster were particularly low, which indicated a degree of separation (but not isolation) between these clusters. However, ranges of individuals from different clusters largely overlapped, which was expected given the high mobility of dolphins. The observed division into 3 clusters could therefore be linked to a combination of different habitat use and social preferences. These spatial results should be interpreted with great caution because a minimum of 5 identifications is low to draw conclusions on ranging patterns. Indeed, a minimum of 10–30 identifications was used in other studies (e.g., Frère et al. 2010; Wiszniewski et al. 2012b). The low number of identifications also prevented using more appropriate methods to estimate the home ranges of highly mobile individuals and core areas, in particular the fixed-kernel density method (Worton 1989), which has been used in social structure studies on delphinids or other mobile species (e.g., Wiszniewski et al. 2012b; Best et al. 2013; Carter et al. 2013). The approach used herein is exploratory. Spatial segregation should be further investigated once enough data per individual are gathered, which will allow the use of fixed-kernel home range analyses. Social division in different clusters is a common feature in bottlenose dolphin societies (Chilvers and Corkeron 2001; Lusseau et al. 2006; Wiszniewski et al. 2009). Division into social clusters was linked to ranging patterns in several communities (Lusseau et al. 2006; Wiszniewski et al. 2009). In the Moray Firth community (Scotland), division is maintained in areas where dolphins of both clusters are observed, indicating that social affiliations are not merely an artifact of habitat use (Lusseau et al. 2006). Moreover, even if individuals of different clusters have distinct ranging patterns, we could not rule-out social preferences within a cluster. Fine-scale site fidelity can create the opportunity for social preferences to develop, for example, as a result of shared behavioral

strategies (Ramos-Fernandez et al. 2006; Wiszniewski et al. 2009). In other areas, division in social structure may have arisen and may have been maintained in sympatry by different foraging strategies, such as interaction or not with fisheries (Chilvers and Corkeron 2001; Ansmann et al. 2012; Daura-Jorge et al. 2012) or hunting techniques (e.g., the use of sponges—Mann et al. 2012). Multiple other factors such as age, sex, and relatedness are also likely to contribute to bottlenose dolphin social affiliations (Möller and Harcourt 2008; Wiszniewski et al. 2010; Mann et al. 2012; Fury et al. 2013). Here, no interaction with fisheries has yet been reported (F. Gally, Groupe d'Etude des Cétacés du Cotentin, pers. comm.). Contrary to other communities (Ansmann et al. 2012; Daura-Jorge et al. 2012), it is therefore unlikely that variable interactions among bottlenose dolphin clusters and fisheries could explain the clustering observed herein. However, bottlenose dolphins are known to have various foraging strategies linked to both habitat type and learning during juvenile life (Sargeant and Mann 2009; Torres and Read 2009). More subtle ecological differences, such as targeting different prey or feeding habitats between social clusters in the Normano-Breton Gulf, are currently investigated using stable isotopes analyses on biopsy samples (Louis 2014).

Abundance.—During summer 2010, the estimated abundance over the whole area was 420 (95% CI: 331–521) individuals, making this community one of the largest observed along European coastal waters. In Europe, the size of most coastal communities of bottlenose dolphins ranges from around tens of individuals (Iroise Sea, Brittany, France—Liret 2001; Sound of Barra, Outer Hebrides, Scotland—Grellier and Wilson 2003; Sado Estuary, Portugal—Augusto et al. 2011), 100–250 individuals (Moray Firth, Scotland—Wilson et al. 1999; Cheney et al. 2012; Shannon estuary, Ireland—Berrow et al. 2012; Cardigan Bay, England—Pesante et al. 2008) to up to 300–350 individuals (Gibraltar, Spain—Chico Portillo et al. 2011). Because of uneven effort, abundance was not estimated for other years (i.e., 2006–2009). From now on, the sampling protocol of 2010 should thus be conducted in order to set a long-term demographic monitoring of these dolphins. Once sufficient years of photo-identification surveys in the whole Gulf are conducted, Pollocks' robust design (Pollock 1982; Kendall et al. 1997) could be an effective method to estimate abundance, survival, and temporary emigration (e.g., Verborgh et al. 2009; Daura-Jorge et al. 2013).

Monitoring and conservation.—This study is the first step of long-term monitoring of this population. It provides important baseline knowledge about the social dynamics and abundance of bottlenose dolphins within the Normano-Breton Gulf prior to important anthropogenic activities, such as the building of several large-scale marine renewable energy projects. Studies conducted during and after the implantation of wind and tide generator farms should enable researchers to assess the long-term consequences of these constructions on this community both in terms of social structure and demography. While the building phase can produce large acoustic disturbances, the sound produced by operating wind turbines is not expected to heavily impact

toothed whales (Madsen et al. 2006), although studies are lacking on cetaceans other than harbor porpoises (Carstensen et al. 2006; Tougaard et al. 2009). However, long-term disturbance and slow recovery has been reported in harbor porpoises (Teilmann and Carstensen 2012). Rigorous long-term monitoring of the temporal variations of abundance and distribution, along with demographic parameters, such as survival and calving rate, will be invaluable in detecting the effects of future human activities on this community. Moreover, the persistence of the social clusters and their ranging patterns should also carefully be monitored. As suggested by Lusseau et al. (2006), if social clusters show clear spatial or ecological segregation, models of population dynamics could take the social division into account as co-variables. In addition, as detailed in the Introduction, social structure is likely driven by environmental factors. Thus, changes in the environment, for instance on the distribution and abundance of resources, could impact social structure (Blumstein 2012). Evaluating long-term social dynamics in the future will therefore help to understand eventual population responses to changes in ecological conditions (Parsons et al. 2009; Blumstein 2012; Foster et al. 2012).

Given the high abundance and interannual site fidelity of bottlenose dolphins in the Gulf, we suggest that a Special Area of Conservation may be designated for these dolphins. Habitat use analyses would be needed to spatially delineate the conservation area. Moreover, bottlenose dolphins are one of the main year-round top predators in the Gulf along with harbor seals (*Phoca vitulina*), gray seals (*Halichoerus grypus*), and seabirds (GECC 2011). The monitoring of bottlenose dolphins could therefore be used as a bioindicator of the Normano-Breton Gulf ecosystem health (Hooker and Gerber 2004). Finally, pending investigations using genetic markers, stable isotopes, and eco-toxicological tools should help understanding the relative contribution of habitat use, relatedness, and sex composition shaping the social structure of this community.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Sample photos of bottlenose dolphin dorsal fin marking levels.

Supporting Information S2.—Sample photos of bottlenose dolphin dorsal fin quality grading.

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