



Evaluating the influence of ecology, sex and kinship on the social structure of resident coastal bottlenose dolphins

Marie Louis^{1,2,3,4} · Benoit Simon-Bouhet¹ · Amélia Viricel² · Tamara Lucas² · François Gally³ · Yves Cherel¹ · Christophe Guinet¹

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Abstract

Animal social structures are shaped by external environmental factors and individual intrinsic behavioral traits. They represent a balance between the costs and benefits of group-living to maximize individual fitness. Bottlenose dolphin, *Tursiops truncatus*, societies are fission–fusion with high variations in association strength, grouping patterns and influence of kinship on social bonds throughout the wide range of habitats where they occur. Here, the drivers of social structure in resident coastal bottlenose dolphins of the Normano-Breton Gulf (English Channel) were studied using a multidisciplinary approach combining individual monitoring (photo-identification) information, genetic and ecological data. First, the ecological segregation of the social clusters was tested. Then, the influence of kinship, sex and ecological specializations on association patterns was evaluated. Stable isotopes revealed that the social clusters had relatively distinct ecological niches. Resource partitioning among social clusters may reduce competition and may allow the area to sustain a larger resident bottlenose dolphin population. Individuals did not preferentially associate with related individuals or individuals of the same sex. However, sample size was relatively low for females and, therefore, a role of kinship in shaping association patterns could not be totally ruled out for those individuals. Instead, dolphins preferentially associated with individuals of similar ecology. The study also emphasizes that stable isotope analysis is a promising tool to investigate the link between social structure and ecological specializations, particularly in taxa that are difficult to observe in the wild.

Introduction

Animal social structures are shaped by the trade-off between the benefits and costs of group-living (see review in Krause and Ruxton 2002). While sociality can provide benefits such as increased foraging efficiency (e.g., Packer and Ruttan 1988), knowledge sharing (e.g., McComb et al. 2001; Safi and Kerth 2007) and reduced predation risk (e.g., Kelley et al. 2011), and therefore, can increase reproductive success (e.g., Silk et al. 2003; Frère et al. 2010a) and lifespan (Silk et al. 2010), it can also impose costs such as competition for food resources or mating, and disease transmission (Wrangham et al. 1993; Clutton-Brock et al. 1998; Altizer et al. 2003; Clutton-Brock 2007). Resource variability can modify the costs and benefits of living in groups, leading to intraspecific or intra-population variation in social organization. For instance, habitat availability can lead to intraspecific social behavior variation (e.g., Karczmarski et al. 2005; Chaverri 2010). Food availability can modify a given population's social structure through time (e.g., the loss of an anthropogenic food resource for bottlenose

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✉ Marie Louis
marielouis17@hotmail.com

¹ Centre d'Etudes Biologiques de Chizé, UMR 7372, CNRS, Université de La Rochelle, La Rochelle, France

² Littoral Environnement et Sociétés, UMR 7266, CNRS, Université de La Rochelle, La Rochelle, France

³ Groupe d'Etude des Cétacés du Cotentin, Cherbourg-Octeville, France

⁴ Scottish Ocean Institute, East Sands, St Andrews KY16 8LB, UK

dolphins, Ansmann et al. 2012; prey availability for spotted hyenas, Smith et al. 2008; seasonal changes in food resources for elephants, Wittemyer et al. 2005 or salmon abundance for killer whales, Foster et al. 2012). These extrinsic factors interact with intrinsic behavioral factors to alter social structure. For instance, individuals may prefer to associate with conspecifics with whom they share similar characters, a process referred to as homophily. Homophily has been documented based on age (e.g., Wey and Blumstein 2010), sex (see review in Ruckstuhl 2007), kinship (Hamilton 1964; Holekamp et al. 1997; Wiszniewski et al. 2010), reproductive condition (e.g., Möller and Harcourt 2008) and or on behavioral phenotypes (e.g., Croft et al. 2009; Mann et al. 2012). Fission–fusion societies, where associations are mainly temporary and show hourly or daily turn-overs, are particularly influenced by ecological factors (Couzin 2006; Lehmann et al. 2007; Smith et al. 2008). Bottlenose dolphin (*Tursiops* sp.) societies are fission–fusion (Connor et al. 2000). They can show strong genetic divisions and are found in a wide range of environments from tropical to temperate areas, and shallow inshore enclosed estuaries to deep pelagic waters (Natoli et al. 2004; Louis et al. 2014a; Lowther-Thieleking et al. 2015). Hence, large behavioral variation conditioned by phylogenetics and different environments may be expected. Associations among individuals are usually fluid and highly dynamic (Connor et al. 2000) although a few communities with a stable social structure have been reported (e.g., Doubtful Sound, New Zealand, Lusseau et al. 2003, Sein Island, France, Louis et al. 2017). Male mating strategies and social behavior vary both between and within populations. In inshore *Tursiops* sp. and *Tursiops aduncus* populations of Australia and inshore *Tursiops truncatus* populations of the North-West Atlantic (NWA), males form alliances of varying degree of complexity, both between related and unrelated individuals, to compete for females (Krützen et al. 2003; Parsons et al. 2003; Connor et al. 2011; Wiszniewski et al. 2012). In contrast, male bottlenose dolphins do not seem to form alliances in the North-East Atlantic (NEA) coastal population of the Moray Firth (Wilson 1995). Females tend to form “bands” and share moderate bonds with related and unrelated females (Wells 1991; Frère et al. 2010b; Wiszniewski et al. 2010) or with females in the same reproductive state (Möller and Harcourt 2008). In some *Tursiops* sp. populations, individuals associate preferentially with individuals of the same sex (Wells et al. 1987; Smolker et al. 1992; Fury and Harrison 2008) and male and female associations seem to be mainly linked to reproduction (Smolker et al. 1992; Owen 2003). Shared behavioral strategies such as foraging techniques can also influence social organization (Ansmann et al. 2012; Mann et al. 2012).

The influence of foraging ecology on social structure has been studied through direct observations of feeding

behavior (Ansmann et al. 2012; Mann et al. 2012). However, foraging specializations cannot always be observed visually, especially in temperate seas where water is generally not clear enough to monitor underwater behavior from the boat. In that context, stable isotope ratios such as carbon ($\delta^{13}\text{C}$), sulfur ($\delta^{34}\text{S}$) and nitrogen ($\delta^{15}\text{N}$) can provide indirect information of a consumer foraging resources. Carbon and sulfur stable isotopes are indicators of feeding habitats and can separate pelagic vs. benthic and inshore vs. offshore food resources (Peterson and Fry 1987; Kelly 2000; Connolly et al. 2004). $\delta^{34}\text{S}$ values varies from 2 to 6‰ in terrestrial habitats to 21‰ in marine habitats (Peterson and Fry 1987). Stable isotopes of nitrogen are enriched in tissues of consumers relative to their food resources, and they can, therefore, provide information on consumer trophic position (Kelly 2000). They can also be used to discriminate between different habitats (e.g., offshore vs. inshore, Chauvelon et al. 2012).

In coastal waters of the Normano-Breton (NB) Gulf (English Channel), a recent study showed that resident bottlenose dolphins formed three social clusters which were using different areas of the gulf although their ranges overlapped (Louis et al. 2015, see summary of the social structure analyses from the latter study in “Social structure”). In addition, abundance estimation was 421 individuals (95% CI 333–520) in 2010 (Louis et al. 2015). In the present study, we investigated the drivers of social structure in this bottlenose dolphin community. We first assessed whether the three social clusters were ecologically distinct using the isotopic niche (skin $\delta^{13}\text{C}$, $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values) as a proxy of the ecological niche and hence of ecology (i.e., resource use) homophily. Then, the relative influence of sex, genetic relatedness and ecological similarity (i.e., similarity in stable isotope signatures) on association patterns was investigated. Additionally, we tested whether preferred associates were more related and shared more similar ecology than expected by chance. Given the above literature, we predicted no or weak influence of relatedness, but possibly an influence of sex and likely an influence of ecological specializations on associations patterns. Finally, we discussed the ecology and evolutionary processes that are likely to drive sociality.

Materials and methods

Boat surveys, biopsy sampling and photo-identification

Ninety-eight biopsy samples were collected during boat surveys from September 2010 to August 2012 using a crossbow (Panzer Barnett 5) and arrows and tips (length = 30 mm and diameter = 8 mm) with three internal barbs for sample retention made by Finn Larsen (Danish

Institute for Fisheries Research, see Fig. 1 for sampling locations). Individuals were photo-identified (i.e., using the natural marks on their dorsal fins) at the time of sampling. Prior to sampling, they were also identified visually to avoid double sampling as much as possible. Eight samples were found to be duplicates (the same individual was biopsied twice). 90 different individuals were sampled including 28 females and 62 males and samples were collected all-year round, weather permitting (spring = 26, summer = 30, fall = 31 and winter = 3). We only sampled adults and biopsy samples were collected under the permit 09/115/DEROG from the French ministry. Samples contained both skin and blubber tissues and were generally 6 mm in diameter and 1.5 cm long. The skin was separated from the blubber and cut into two samples. Then, skin samples were frozen at $-20\text{ }^{\circ}\text{C}$.

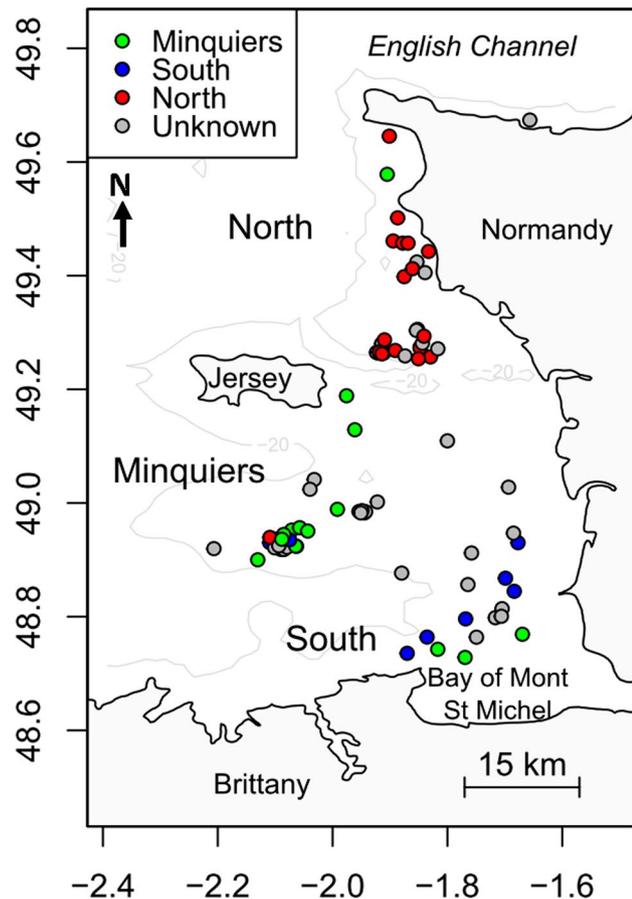


Fig. 1 Biopsy sample locations of individual bottlenose dolphins in the Normano-Breton gulf ($N=90$). Social cluster memberships of the sampled individuals are indicated, i.e., South ($N=8$), Minquiers ($N=27$) and North ($N=19$). Some individuals could not be assigned to any social cluster as they were sighted in less than 5 different days or were unmarked ($N=36$)

Social structure

The social structure of this population was analyzed in a previous study using photo-identification data collected between 2006 and 2010 (Louis et al. 2015). Association coefficients (HWI: half-weight index) were calculated between pairs of individuals sighted in at least 5 different days using SOCPROG (Whitehead 2009). Three social clusters were identified and each individual was assigned to one of the social clusters (“South”, “Minquiers” and “North” corresponding to the areas where the individuals from each cluster were observed the majority of the time, see Fig. 1 for their locations, Louis et al. 2015). Fifty-four biopsy-sampled individuals were included in social structure analyses ($N=8$ for the “South”, $N=27$ for the “Minquiers” and $N=19$ for the “North” clusters, Fig. 1). The remaining sampled individuals were either sighted in less than 5 different days ($N=24$) or were not identified either because they were unmarked or because the quality of the photo taken was not good enough to recognize the individuals ($N=12$).

Genetic laboratory analyses and microsatellite marker quality

We used 92 samples that were genotyped at 25 microsatellites (Louis et al. 2014b, see microsatellite list and their characteristics in Supplementary Table S1, Dryad: <https://doi.org/10.5061/dryad.57rr4>). Two possible duplicates (based on photo-identification) were included in the analyses to genetically confirm their identity. Amplification and sequencing conditions are available in Louis et al. (2014b). Individuals were sexed using the SRY plus ZFX/ZFY fragments amplification method described in Rosel (2003).

To evaluate genotyping error rate, nine individuals were randomly selected for re-amplification and scoring at all loci. The two duplicates, which were confirmed using the program Excel Microsatellite Toolkit (Park 2001), were also included in error rate calculation. Ten percent of the dataset was thus re-analyzed. All individuals were successfully amplified for at least 23 loci and there was 0.56% of missing values in the dataset. We used Microchecker 2.2.3 to check for null alleles and scoring errors (Van Oosterhout et al. 2004). We tested for departures from Hardy–Weinberg equilibrium (HWE) and linkage equilibrium using 10,000 dememorizations, 1000 batches and 10,000 iterations per batch in GENEPOP on the web version 4.2 (Raymond and Rousset 1995; Rousset 2008). Significance levels were corrected for multiple comparisons using the sequential Bonferroni technique (Holm 1979). Fine-scale genetic structure was investigated to avoid misinterpreting the results because of population structure (please see Supplementary text S1).

Ecology and social structure

Skin $\delta^{13}\text{C}$, $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values were measured in 88 individuals (for two samples, there was not enough skin tissue for both genetic and stable isotope analyses). Prior to isotopic analyses, skin samples were cut in small pieces and dried at 45 °C in an incubator for 48 h. As lipids are depleted in ^{13}C relative to other tissue components (De Niro and Epstein 1977), they were extracted from skin samples prior to stable isotope analyses (SIA) of carbon and nitrogen, but not of sulfur. Lipid extraction had no effect on $\delta^{34}\text{S}$: differences between measurements with lipid extraction and without lipid extraction were less than 0.2‰, which is in the precision range of the measurements. The samples were agitated with 2 ml of cyclohexane for 1 h and centrifuged for 10 min at 3500 tours/min. Supernatants containing lipids were discarded. This protocol was repeated until the supernatant was transparent. Samples were dried in an incubator for 48 h. Subsamples were weighted (0.3–0.4 mg for carbon and nitrogen SIA and 1.0–1.3 mg for sulfur SIA) with a microbalance and packed into 5 × 8 mm tin cups. Carbon, sulfur and nitrogen isotope ratios were determined by a continuous flow mass spectrometer (Thermo Scientific, Delta V Advantage) coupled with an elemental analyzer (Thermo Scientific, Flash EA 1112). Stable isotope values are presented in the conventional δ notation (in ‰) relative to Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ values, IAEA-1 and IAEA-2 for $\delta^{34}\text{S}$ values, and atmospheric N_2 for $\delta^{15}\text{N}$ values. Isotopic measurement errors were less than 0.20‰. To ensure that the lipid extraction was effective, we checked that the C/N mass ratios of all the samples were below 4.

All stable isotope statistical analyses were carried out in R 3.0.0 (R Core Team 2013). Mean differences in $\delta^{13}\text{C}$, $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values among the three dolphin social groups, between males and females and among seasons were compared using ANOVA and Tukey's post hoc tests (implemented in the R package multcomp, Hothorn et al. 2008) or Kruskal–Wallis and Dunn-tests (implemented in the R package dunn.test, Dinno 2017), depending on whether the data satisfied the required assumptions: normality and homogeneity of variances.

Stable isotope niches of the three social groups were estimated using multivariate, ellipse-based metrics: SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011) implemented in the SIAR package version 4.2 (Parnell and Jackson 2011). Standard ellipse is to bivariate data what standard deviation is to univariate data. The standard ellipse area (SEA) is defined by a subsample (40%) of the bivariate data (i.e., $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and was calculated from the variance and covariance of the data. We corrected SEA for sample size (SEA_c). This approach is robust when comparing small and unbalanced sample sizes and is not biased by outliers (Jackson et al.

2011). The degree of SEA_c overlap between each social cluster was also estimated.

In addition, to test for an ecological subdivision in the dataset, a clustering analysis was performed based on probabilistic models with no a priori using the mclust package version 4.2 (Fraley and Raftery 2002; Fraley et al. 2012). It implements a maximum-likelihood clustering approach based on Gaussian mixture models. Model parameters are estimated using the expectation maximization (EM) algorithm initialized by hierarchical model-based clustering. We used the default settings where the optimal model (out of 10 models with different covariance structure) and number of clusters (set from 1 to 9) were selected by BIC (Bayesian Information Criterion). The analysis was performed both for the whole dataset and only for individuals whose social group was identified. Assignments obtained from stable isotope data were compared to the social cluster assignments.

Influence of relatedness, sex and ecology on association patterns

To test whether genetic relatedness, similar ecology, and sex were significant predictors of the strength of associations, a Double Dekker Semi-Partialling Multiple Regression Quadratic Assignment Procedure (MRQAP) was carried out using the sna package 2.3.1 in R 3.0.0. (Dekker et al. 2007; Butts 2013). The MRQAP is an extension of the Mantel test that allows a dependent matrix to be regressed simultaneously against multiple explanatory matrices that represent dyadic attribute relationships. Its interpretation is similar to multiple regression, but it takes non-independence of the pairwise data into account by randomly permuting the dependent matrix (see Mann et al. 2012 and Wey and Blumstein 2010 for further details). Association indices (HWI) were the response matrix. Relatedness, sex homophily and ecological similarity (i.e., similarity in stable isotope signatures) were the explanatory matrices.

Pairwise relatedness values were estimated using the Queller and Goodnight (1989) relatedness coefficient (R) in KINGROUP v.2 (Konovalov et al. 2004). All individuals were used to calculate allele frequencies ($N=90$), and then R was calculated between individuals used in social structure analyses ($N=54$). Male and female homophily matrices were created by assigning a value of 1 if dolphins were of the same sex and 0 otherwise. For the ecological similarity matrix, Euclidean distances of the values of $\delta^{13}\text{C}$, $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ (distISO) between individuals (i and j) were first calculated as follows:

$$\text{distISO} = \sqrt{(\delta^{13}\text{C}_i - \delta^{13}\text{C}_j)^2 + (\delta^{34}\text{S}_i - \delta^{34}\text{S}_j)^2 + (\delta^{15}\text{N}_i - \delta^{15}\text{N}_j)^2}.$$

Then the similarity matrix (simISO) was calculated by subtracting distISO from the maximum of distISO.

Mantel tests were conducted to evaluate the influence of each matrix on the association matrix using 10,000 permutations and the ade4 package 1.3.6. (Chessel et al. 2004; Dray and Dufour 2007; Dray et al. 2007). All analyses were carried out for the whole dataset and for males and females separately. Unless otherwise notified, results were similar to the ones obtained with both sexes.

To further test the role of kinship in shaping social structure, we tested whether relatedness was higher within social clusters than expected at random using a randomization test in R 3.0.0. Mean relatedness was calculated for each social cluster. Individuals were randomly permuted 10,000 times between groups and the number of individuals was kept identical as in the observed dataset. Significance was assessed by comparing the distribution of permuted mean relatedness for each cluster to the observed mean relatedness.

Finally, correlation between kinship and associations might be weak in fission–fusion societies when considering all the individuals. Kinship may mainly underlie preferred associations (Frère et al. 2010b; Wiszniewski et al. 2010; Carter et al. 2013). Hence, we tested whether preferred associates were more related and also if they shared more similar ecology than expected at random. Preferred associates were defined based on the strength of association indices as in Carter et al. (2013) and Frère et al. (2010b) (i.e., pairs that associate the most often and had HWI in the 95th percentile). This cut-off is conservative to avoid considering false positives. Other cut-offs were tested (97.5th and 90th percentiles) and gave similar results. The test was performed for the whole dataset and considering males and females separately. A randomisation approach was undertaken in R 3.0.0 to test whether the mean relatedness among preferred associates was higher than expected by chance. The random distribution was generated by randomly resampling 10,000 times (with replacement) a number of individuals corresponding to the number of preferred associates in the whole relatedness dataset and calculating the mean relatedness for each randomized sample. Significance was assessed by comparing the distribution of the permuted mean relatedness to the observed mean relatedness for preferred associates. The same approach was undertaken to investigate whether ecological similarity among preferred associates was higher than expected by chance.

Results

Biopsy sampling and quality-checking of the microsatellite data

Biopsy samples were obtained from 90 different individuals including 28 females and 62 males. Fifty-four individuals were included in social structure analyses and were

composed of 39 males and 15 females. The dataset was, therefore, clearly male biased. This bias could be linked to possible differential behavioral reactions towards the boat between males and females as suggested in Quéroutil et al. (2010). In addition, females with young calves were more difficult to sample as care was taken with those individuals to prevent harm to the calf.

No significant departure from HWE and no null alleles were detected in the microsatellite data. Linkage disequilibrium was significant for 0.7% of the pairwise comparisons and was therefore considered negligible. The genotyping error rate was 0.0036 (i.e., 1 incorrect genotype/275 genotypes reprocessed). No genetic structure was found within the sampling area (see Supplementary text S1 and Fig. S1 to S4 for details).

Ecology and social structure

Skin $\delta^{34}\text{S}$ values were significantly different among social clusters ($N=54$, Kruskal–Wallis test, $H_2=20.8$, $P<0.01$). They were significantly higher in the Minquiers cluster than in the North and South clusters (Dunn-tests, $P<0.01$), but no differences were found between the Bay and North clusters (Dunn-test, $P=0.09$, Table 1, see Fig. 1 for area locations and Louis et al. 2015 for social structure analysis details). Skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied also significantly among social clusters [$N=54$, ANOVA, $F(2,51)=4.47$, $P=0.02$ for $\delta^{13}\text{C}$ and Kruskal–Wallis test, $H_2=12.79$, $P<0.01$ for $\delta^{15}\text{N}$] with only the Minquiers and the North clusters showing significant differences (Tukey HSD, $P=0.01$ for $\delta^{13}\text{C}$ and Dunn-test, $P<0.01$ for $\delta^{15}\text{N}$). The Minquiers dolphins' skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were lower than those of the North and South clusters (Table 1).

There were no significant differences between males and females in stable isotope values [$N=88$, Kruskal–Wallis test, $H_1=0.76$, $P=0.38$ for $\delta^{34}\text{S}$, ANOVA $F(1,86)=0.80$, $P=0.37$ for $\delta^{13}\text{C}$ and ANOVA $F(1,86)=0.004$, $P=0.95$ for $\delta^{15}\text{N}$, Supplementary Fig. S5a to S5c]. Skin $\delta^{34}\text{S}$ values did not show any seasonal variations ($N=88$, Kruskal–Wallis test, $H_3=3.53$, $P=0.32$, Supplementary Fig. S6a) while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ showed differences among seasons [$N=88$, ANOVA $F(3,84)=10.4$, $P<0.01$ and ANOVA $F(3,84)=4.68$, $P<0.01$, respectively,

Table 1 Skin stable isotope values for each social cluster of bottlenose dolphins in the Normano-Breton Gulf

Social cluster	<i>N</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{34}\text{S}$ (‰)	$\delta^{15}\text{N}$ (‰)
South	8	-17.2 ± 0.4	14.9 ± 1.0	14.9 ± 0.4
Minquiers	27	-17.3 ± 0.4	16.0 ± 0.4	14.6 ± 0.5
North	19	-16.9 ± 0.4	15.5 ± 0.6	15.2 ± 0.3

Values are mean \pm SD

Supplementary Figure S6b and S6c]. Skin $\delta^{13}\text{C}$ values were significantly lower in fall than in spring and summer (Tukey HSD, $P < 0.01$ for all comparisons). Skin $\delta^{15}\text{N}$ values were significantly lower in fall and summer than in spring (Tukey HSD, $P = 0.04$ and Tukey HSD, $P < 0.01$, respectively).

SEA_c for $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ overlapped between all social clusters (Table 2, Supplementary Fig. S7a and S7b), but SEA_c for $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ showed little overlap (Fig. 2, Table 2). Given the above results, we considered only $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values for the estimation of the most likely number of clusters with no a priori. The estimated number of clusters was 3, both when considering all the dataset and the data including only individuals that were used in social structure analyses. 70% of the individuals were assigned to the same stable isotope group as their social group when considering only individuals that were used in social structure analyses and 67% when considering all the dataset. It should be noted that the sample size for the South cluster ($N = 8$) was relatively limited.

Influence of relatedness, sex and ecology on association patterns

Ecological similarity was the only significant predictor of association strengths both when conducting MRQAP (Table 3) and Mantel tests. Only 4% of the variance in HWI was explained by ecological similarity in the

Table 2 Areas of overlap between SEA_c of different social cluster pairs of bottlenose dolphins in the Normano-Breton Gulf ($\% ^2$)

Pair of SEA_c	$\delta^{13}\text{C}$ and $\delta^{34}\text{S}$	$\delta^{34}\text{S}$ and $\delta^{15}\text{N}$	$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
South and Miquiers	0.08	0.04	0.29
South and North	0.40	0.01	0.09
North and Miquiers	0.07	0.09	0.11

Fig. 2 Skin $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values for each social cluster of bottlenose dolphins in the Normano-Breton Gulf. Solid lines indicate standard ellipses areas corrected for small sample sizes (SEA_c). Area values ($\% ^2$) are given in the legend

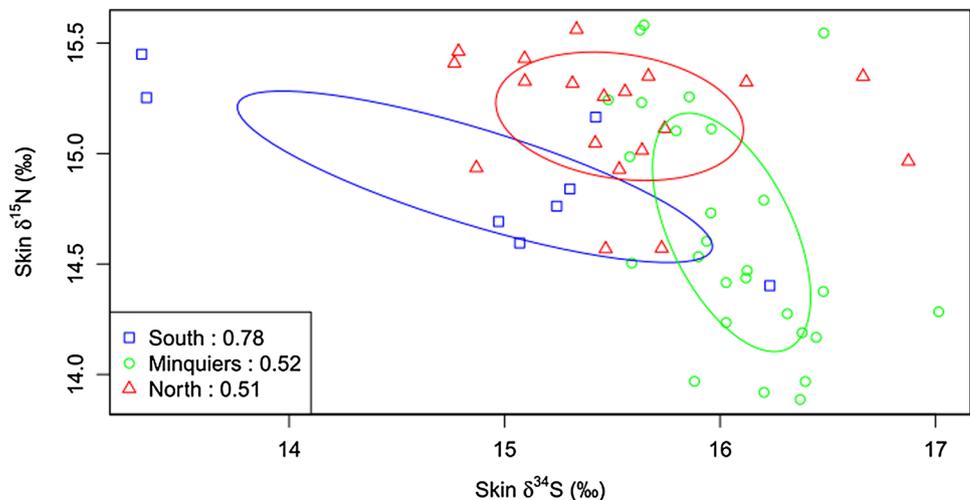


Table 3 Results from the MRQAP analysis to test the influence of ecological similarity, relatedness and sex on bottlenose dolphin associations in the Normano-Breton Gulf

Variable	Unstandardized coefficient	P value
Ecological similarity	0.05	0.00
Relatedness	0.03	0.21
Female homophily	0.03	0.10
Male homophily	-0.00	0.69

Significant P values ($P < 0.05$) are indicated in bold. Adjusted r^2 is 0.04

MRQAP analysis. The effect of ecological similarity was positive and the observed correlation using a Mantel test was $r = 0.19$ between ecological similarity and HWI matrices ($P < 0.01$, Fig. 3). Strongly associated individuals had similar ecology while weakly or never associated individuals may have similar or contrasted ecology (Fig. 3). Sex and relatedness had no influence on HWI (Table 3, Mantel tests $P = 0.45$ and $P = 0.09$, respectively, Fig. 4). There were strong associations both between males (number N of pairs showing a $\text{HWI} \geq 0.5 = 24$), females ($N = 7$) and between males and females ($N = 25$), although it should be noted that a limited number of females were sampled. In these strong association pairs, only two males were closely related ($R > 0.45$). Permutation tests indicated that mean relatedness observed within social clusters was not higher than expected at random (Table 4). Preferred associates were not more closely related than expected at random considering all individuals (mean $R = -0.002$, random mean $R = 0.001$, $P = 0.561$), females (mean $R = -0.034$, random $R = -0.007$, $P = 0.611$) and males (mean $R = 0.016$, random mean $R = 0.003$, $P = 0.230$). However, preferred associates showed significantly higher similar ecology than expected by chance considering all

Fig. 3 Relationship between ecological similarity and association index for each pair of bottlenose dolphins in the Normano-Breton Gulf ($N=54$ individuals; 1431 pairs)

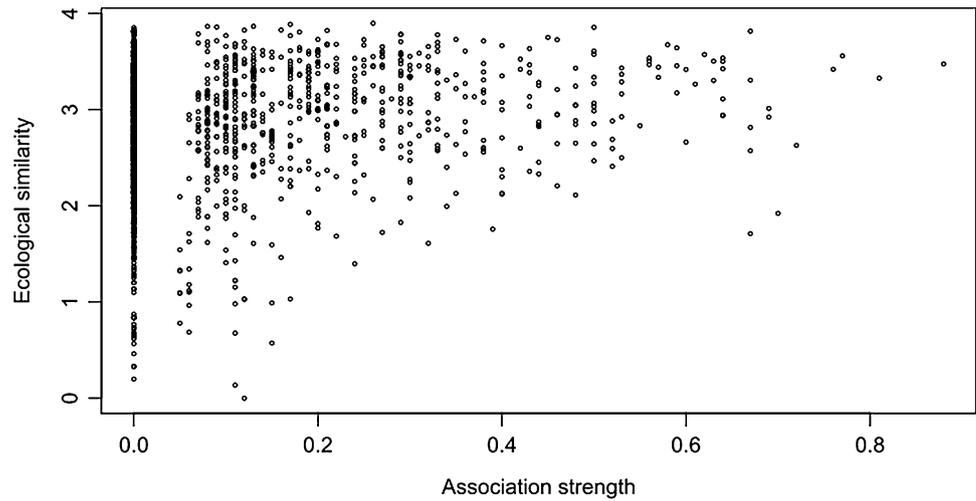


Fig. 4 Relationship between relatedness and association index for each pair of bottlenose dolphins in the Normano-Breton Gulf ($N=54$ individuals; 1431 pairs)

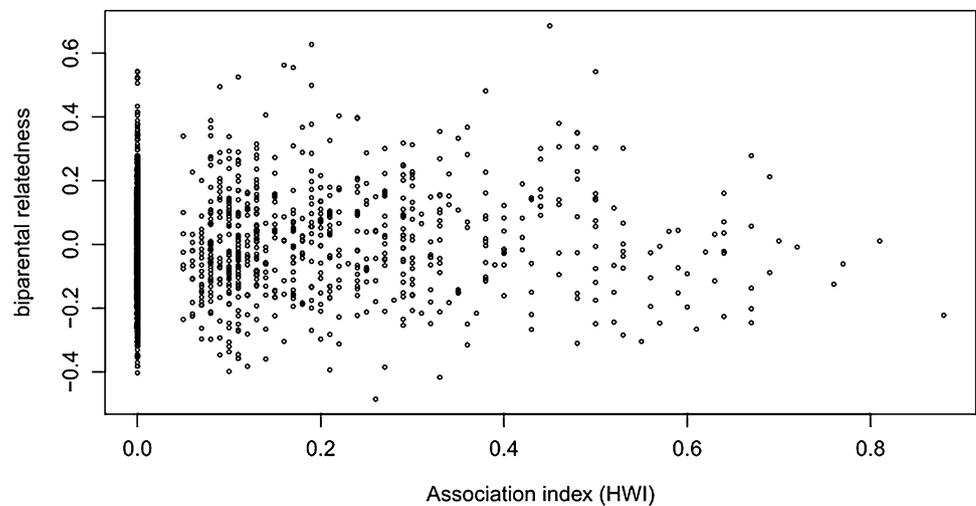


Table 4 Results of the permutation test to evaluate whether the mean observed relatedness (R observed) within each social cluster of bottlenose dolphins in the Normano-Breton Gulf is higher than the mean relatedness generated using permutations (R random) for each social cluster

Social cluster	R observed	R random	P value
Minquiers	0.023	-0.001	0.05
South	0.039	-0.000	0.17
North	-0.016	-0.001	0.78

There are no significant P values after Bonferroni correction (significant values at the 5% threshold are those for which $P < 0.017$)

individuals (mean simISO = 3.101, random mean simISO = 2.814, $P < 0.001$), females (mean simISO = 1.607, random mean simISO = 1.167, $P = 0.047$) and males (mean simISO = 3.092, random mean simISO = 2.799, $P = 0.001$).

Discussion

This study uses a multidisciplinary approach to understand the social organization of a highly mobile top predator.

The three social clusters showed relatively distinct ecological niches

We found good consistency between social structure and stable isotope clustering analyses. The three previously described social clusters (Louis et al. 2015) were ecologically distinct and skin $\delta^{34}\text{S}$ values were particularly efficient at detecting ecological differences among social groups. A previous study showed that, the three social clusters were spatially segregated despite showing some overlap in range (Louis et al. 2015). $\delta^{34}\text{S}$ values were consistent with the main sighting areas of the individuals.

For instance, skin $\delta^{34}\text{S}$ values are known to increase from terrestrial (2–6‰) to marine habitats (21‰, Peterson and Fry 1987). Accordingly, individuals of the social cluster from the Minquiers, the most offshore cluster, showed higher values of $\delta^{34}\text{S}$ than the dolphins from the North and South clusters. In contrast, individuals of the South cluster that were mainly located in and near the Bay of Mont Saint Michel (a very large mudflat with an estuary), had the lowest $\delta^{34}\text{S}$ values. In addition, individuals from the Minquiers social cluster showed significantly lower skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the North social cluster. This is concordant with a decrease in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with increasing distance from shore for marine organisms (Chouvelon et al. 2012). The mean values of those isotopes were marginally lower in the Minquiers than in the South cluster, but differences were not significant. Without stable isotope data on prey and the basis of the food web, it is difficult to explain this lack of differences as several processes could explain variations in skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This absence of differences does not mean that the dolphins were feeding on the same prey as different resources may have similar isotopic values. Skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values showed some seasonal variations which could not be investigated at the social group level due to low sample size while skin $\delta^{34}\text{S}$ values did not vary among seasons. This study, therefore, highlights the usefulness of $\delta^{34}\text{S}$, in addition to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, to investigate the population structure and ecology of marine predators, as it was already shown for yellow-eyed gulls (Moreno et al. 2010) and bottlenose dolphins in Florida (Barros et al. 2010; Olin et al. 2012). Photo-identification and stable isotopes provide information about population processes at different time-scales. Social structure analyses resulted from photo-identification data collected over a few years (from 2006 to 2010), while skin stable isotope values should be representative of the diet of the individuals approximately 1–2 months preceding sampling (Hicks et al. 1985; Browning et al. 2014; Giménez et al. 2016). Biopsy sampling only partially overlapped in time with the photo-identification data. Nonetheless, stable isotope clustering results that are representative of the diet of individuals over the past few weeks were consistent with social structure results collected over several years. Therefore, these results indicated that ecological differences among social clusters were likely to last longer than 1–2 months and were likely to be long-lasting. This resource partitioning among bottlenose dolphin social clusters may reduce intraspecific competition within the gulf. It may, therefore, increase carrying capacity and may allow the area to support one of the largest coastal bottlenose dolphin population in Europe (Louis et al. 2015).

Ecology but possibly not kinship influenced social structure

Kin selection theory predicts that associating with kin can provide indirect fitness benefits and higher survival, reproductive output, and food intake (Hamilton 1964; Alexander 1974; Silk 2007; Frère et al. 2010a). In this study, we did not find any influence of relatedness on social structure. However, given the low sample size for females, a role of kinship in shaping association patterns could not be totally ruled out for those individuals. In inshore bottlenose dolphin societies as well as in other fission–fusion species such as giraffes, *Giraffa camelopardalis*, females that associated preferentially were found to be more related than expected by chance (Frère et al. 2010b; Wiszniewski et al. 2010; Carter et al. 2013). Thus, further sampling of females is needed to reliably test this hypothesis in the NB Gulf population. As expected, males did not preferentially associate with kin. The lack of influence of kinship on male associations is common in mammals and bottlenose dolphin societies except when considering very close associates displaying cooperative behavior (Packer et al. 1991; Krützen et al. 2003; Wiszniewski et al. 2010). Further work could involve taking behavioral data to test for male alliance formation in the gulf and look at the influence of relatedness on those particular pairs. In contrast to some populations, there was no segregation by sex and strong associations were detected between males and females, which may indicate low female harassment by males (Fury et al. 2013).

Strongly associated individuals had similar ecology while individuals that never associated could present either dissimilar or similar ecology. For the latter, it should be noted that individuals having the same isotopic niche did not necessarily feed in the same geographical place on the same prey (e.g., Chérel and Hobson 2007). Further work investigating stable isotope values in potential prey of bottlenose dolphins is needed to better understand their ecology. Individuals sharing feeding strategies preferentially associated in other populations, e.g., individuals using sponges (Mann et al. 2012) and interacting or cooperating with fisheries (Ansmann et al. 2012; Daura-Jorge et al. 2012; Pace et al. 2012). We do not know which feeding techniques were used in the NB Gulf. Large group sizes and the turbidity of the water made it impossible to observe underwater behavior. Nonetheless, the isotopic niche results suggested that a shared foraging resource use was likely a factor leading to preferential associations between individuals in the English Channel. It is, however, difficult to disentangle if dolphins associated because of similar foraging resource use, or if they showed similar ecology as a result of transmission and learning from their associates (Daura-Jorge et al. 2012; Cantor and Whitehead 2013). Deviance explained by ecological similarity was low (approximately 4%). When provided,

deviance values obtained in other studies on fission–fusion species ranged from 17 to 31% (Mann et al. 2012; Carter et al. 2013). As statistical methods are not yet available for matrix data to enable the interaction of variables to be tested, the deviance explained by MRQAP is usually smaller than in standard linear regression. In addition, as individuals were sampled over 2 years, temporal and seasonal variations in stable isotope values could reduce the correlation between ecological homophily and association strength.

Other possible drivers of social structure

Other factors were likely to contribute to bottlenose dolphin social structure. Shared reproductive state could influence female bottlenose dolphin associations (Möller and Harcourt 2008). Age and personalities were shown to affect association patterns in other species (e.g., Croft et al. 2009; Wey and Blumstein 2010; Aplin et al. 2013; Hauver et al. 2013). Previous familiarity, in particular during the first years of life (Connor et al. 2000; Stanton et al. 2011) could influence associations in adulthood. Finally, predation is another major force that can influence social structure (see review in Krause and Ruxton 2002). In the Normano-Breton Gulf, killer whales and shark species were not observed and no shark bites were ever recorded, in contrast to Australian and NWA inshore populations (Wells et al. 1987; Heithaus 2001). This lack of predation could have an important evolutionary impact and might contribute to the possible absence of effect of relatedness on social structure.

Non-social factors, such as habitat use, are increasingly included in social structure analyses to tease apart preferential associations and relationships resulting only from shared use of space (Frère et al. 2010b; Cantor et al. 2012; Carter et al. 2013). As this study included individuals with a relatively limited numbers of visual observations (range 5–25), home ranges could not be included in the regression analysis. However, as dolphins are highly mobile, associations may reflect social preferences, at least to some degree, even in the case of overlapping ranges. In addition, shared use of space and similar habitat preferences could be indirect social factors by creating opportunities for individuals to interact. Our results showed that shared foraging resource use influenced association patterns. As detailed earlier stable isotope values of sulfur were consistent with the expected values of the main sighting areas of the individuals. However, foraging habitat may only represent a portion of the habitat used by each dolphin. For instance, in Sarasota Bay, Florida, individual bottlenose dolphins with nearly identical ranging patterns had very different stable isotope signatures, indicating different foraging habitats (Rossman et al. 2015). We cannot therefore totally extrapolate our stable isotopes results informing on feeding habitats to home ranges, and we

cannot make conclusions on the influence of home ranges on association patterns.

Even if social structure can be highly plastic and evolve rapidly under different ecological conditions (Smith et al. 2008; Foster et al. 2012), for some species, social structure may be strongly constrained by phylogenetics rather than being influenced by ecological selection (Di Fiore and Rendall 1994; Chapman and Rothman 2009). Additionally, phylogenetic inertia and ecological conditions may both play a role in shaping social structure as suggested for killer whales (Beck et al. 2012). This hypothesis is worth considering in the present study. Recent genetic studies showed that coastal bottlenose dolphin populations in the NEA were founded by a pelagic population relatively recently in comparison to coastal and pelagic ecotype pairs in other areas of the world (Moura et al. 2013; Louis et al. 2014a). This different taxonomic unit may have different social structure characteristics.

Conclusion

The combination of approaches was useful to get a better understanding of the social structure of this population. The results showed that ecology, i.e., individual resource use specializations, likely had an influence on the association patterns of coastal bottlenose dolphins in the NB Gulf. Individuals did not preferentially associate according to sex or relatedness although further sampling of females is needed to completely rule out the lack of preferential association with relatives. The present work contributes to a growing number of studies showing that bottlenose dolphin societies, known to be fission–fusion, are highly variable within this form of social structure (Lusseau 2003; Wiszniewski et al. 2010; Connor et al. 2011; Ansmann et al. 2012; Daura-Jorge et al. 2012; Wiszniewski et al. 2012). This might be explained by the wide range and contrasted type of habitats where the species occurs where ecological forces driving social structure can differ as well as by phylogenetic differences. Fine-scale resource partitioning within the population may decrease competition and may allow the area to sustain a large resident bottlenose dolphin population. We also showed that stable isotopes are useful to evaluate the influence of ecology on social structure and are particularly relevant in areas where foraging behavior of bottlenose dolphins cannot be monitored visually. This approach could be used for a wide range of difficult to observe taxa. Further work on stable isotopes in potential prey could help to better understand foraging specializations within the population and their role in shaping social structure.

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Compliance with ethical standards

Conflict of interest We declare that we have no conflict of interest.

Research involving human participants and/or animals All applicable international, national and institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Biopsy samples were collected under the permit 09/115/DEROG from the French ministry.

Informed consent Not applicable.

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