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Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations

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ABSTRACT

Social and network analyses that incorporate information on individuals within a population enhance our knowledge of complex species. In this study, the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland, was analyzed by examining the dynamics of the whole population and then of individuals classed by sex, age, and area. 121 dolphins were identified during 522 sightings between 2012 and 2015. The mean half-weight association index (HWI) of the population was 0.07±0.02. The highest HWIs for individuals of known sex were for female-male pairs. Mean within-class HWI was significantly higher than mean between-class HWI for both age and area classes. Ordinations and sociograms were used to visualize social networks. Permutation tests revealed nonrandom associations for the population overall and both between and within classes. Temporal analyses showed associations persisting for >1,000 d. The whole population's best fit model was for two levels of casual acquaintances. Movement analyses demonstrated the use of the inner estuary by only 25% of the population revealing a potential community division by area. The difference between mean HWI when socializing (0.09±0.03) compared to foraging (0.06±0.03) was significant. These results highlight the importance of localized research, reflecting the complexity found in bottlenose dolphin societies globally.

Key words: bottlenose dolphin, social structure, photo-identification, associations, networks, *Tursiops truncatus*, individual classification

Introduction

Social structure, a concept that integrates the ethological interactions and ecological relationships between conspecifics, is a fundamental component of the biology of an animal population (Lusseau *et al.* 2006). For intelligent mammals with complex societies, the social structures of populations are integral to our overall knowledge of the species. Social structure can affect population growth, genetics, and animal movements, and represents an important factor in management and conservation (Whitehead 2008, 2009). Because not all individuals of a species are the same, it is important to explore population demographics and examine the interactions of different members within the social structure of a population. For example, sociality can be driven by individual classes such as sex (Connor *et al.* 2000) or age (Lusseau and Newman 2004, McHugh 2010), or other factors such as habitat use (Wiszniewski *et al.* 2009, Titcomb *et al.* 2015). It is therefore important to take such variables into account during the investigation of a population's social structure.

If nonrandom patterns of association are found in a population, this can suggest the patterning of social relationships that characterizes that society as a whole (Smolker *et al.* 1992). Because of the many spatiotemporal changes in associations in a society, assessing its structure can be difficult, but available quantitative techniques, such as association and network analyses (Whitehead 2008), help to define social structure more precisely and explain observed association patterns (Lusseau *et al.* 2006). Additionally, sophisticated studies of social structure based on identifiable individuals can provide detailed measures and examples of these social systems (Whitehead 2008).

Bottlenose dolphins (*Tursiops* spp.) are highly intelligent marine mammals known to live in extremely dynamic complex social systems referred to as fission-fusion societies (Connor *et al.* 2000). This is one of the most complex social organization systems seen in the animal kingdom (Smolker *et al.* 1992), where large numbers of individuals associate in small groups that change size and composition frequently, at different spatial and temporal scales (Connor *et al.* 2000). Social relationships exhibited by individual dolphins are maintained within a constantly changing social environment where individuals are drawn from a large social network (where they may be present in a wide range of different groups) but associate consistently with just a few other individuals (Smolker *et al.* 1992).

Well-studied bottlenose dolphin societies in Shark Bay, Australia, and Sarasota Bay, USA, exhibit strong long-term associations between adult individuals of the same sex (Smolker *et al.* 1992, Connor *et al.* 2000, Owen *et al.* 2002, Wells 2014, Connor and Krützen 2015). These associations are characterized by dramatic sex differences in association patterns comprising long-term bonds between males in alliances and looser network associations among female dolphins. In Doubtful Sound, New Zealand, sex-specific alliances were not observed amongst bottlenose dolphins, but some male-female associations were stable over the course of several years (Lusseau *et al.* 2003). However, in well-studied bottlenose dolphin populations in the Moray Firth, Scotland and Sado Estuary, Portugal, no strong sex-specific associations have been found (Wilson 1995, Augusto *et al.* 2011). In the Sado Estuary, associations are similar between all individuals, with no patterning according to sex or age class (Augusto *et al.* 2011). Thus, it would appear that the sex class of individuals plays a varying role in bottlenose dolphin societies globally.

For long-lived, slow-developing species like bottlenose dolphins, there is a prolonged juvenile period. Typically, most studies tend to focus only on adults because they are more easily identifiable; however, an understanding of juvenile association patterns and social structure is necessary to achieve a full understanding of the social dynamics of a population (McHugh 2010). In some studies that explored age effects, differences in patterns of association have been discovered in relation to age class (Samuels 1996). Exclusively juvenile groups are found in some populations (Wells 2014) and age-related homophily has been found in dolphin social networks (Lusseau and Newman 2004). In other studies where bottlenose dolphin groups do not seem to be segregated by sex or age class, some of these demographically mixed groups have formed socially distinct communities within populations (Lusseau *et al.* 2006).

The study of association patterns with respect to area use is important because differences in area use do not necessarily lead to differences in association patterns and *vice versa*. However, if the social structure of a population *is* related to area use, this has important implications for population management (Lusseau *et al.* 2006, Cantor *et al.* 2012). To answer these questions, sightings of individual dolphins may be classified by area within the study site. Then, association analyses can be used with classifiers to interrogate the data set for potential preferences or avoidances between the classes.

The bottlenose dolphin (*Tursiops truncatus*) population in the Shannon Estuary, Ireland, is stable and composed of *ca*. 120 individuals (Berrow *et al.* 2012) and is genetically discrete (Mirimin *et al.* 2011). Dolphins are present in the estuary year-round (Berrow *et al.* 1996, Ingram 2000, Berrow 2009) and have been observed exclusively in the Shannon Estuary and adjacent (<25 km) Tralee and Brandon Bays (Ryan and Berrow 2013, Levesque *et al.* 2016). This species also occurs around the entire Irish coast (O'Brien *et al.* 2009) and in offshore waters (Louis *et al.* 2014) but these are thought to constitute distinct populations (Mirimin *et al.* 2011). The Shannon Estuary is a Special Area of Conservation (SAC) for bottlenose dolphins (NPWS 2012), which are listed on Annex II of the EU Habitats Directive. Given the level of protection assigned to this population, information on the social structure of dolphins in the estuary is important for their long-term conservation and the development of a local management plan.

Only two studies to date have investigated the social structure of bottlenose dolphins in the Shannon Estuary (Ingram 2000, Foley *et al.* 2010); however, neither had access to data on individual sex or age, and although Ingram (2000) identified some spatial patterns, these were not based on classifying individuals by area of sighting locations. Our study marks a significant advance on previous work by operating with a much larger set of data and by considering within-population structure based on sex, age, and area.

In describing and analyzing the social structure of a unique population of bottlenose dolphins in Ireland, this paper makes data available for comparisons with similar studies. Studying bottlenose dolphins in varying social systems contributes to current knowledge of social structure and the evolutionary mechanisms that may have affected differences among populations. Knowledge of the social structure of a bottlenose dolphin population contributes to the conservation of the species, especially to population management within SACs and Marine Protected Areas, and helps to understand trends in long-term monitoring.

This paper aims to describe and analyze the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland using a 4-year data set. We begin by (1) examining the social attributes of the population as a whole, and then explore the social dynamics of the population further by classifying individual dolphins by (2) sex, (3) age, and (4) area. We hypothesized that the structure of the population would be similar to that of many other populations described worldwide in several ways, specifically that there would be (1) preferred and avoided associations between individuals; (2) a pattern of single-sex groups and strong within-sex-class associations; (3) a pattern of single-age-class groups and strong within-age-class associations; and (4) area-based social clustering of the population within the study area as a whole.

METHODS

Study Site

The study site is located in the Lower River Shannon Special Area of Conservation (SAC; Site Code 002165), a 684 km^2 Natura 2000 designated site (NPWS 2012) on Ireland's west coast between Co. Clare, Co. Kerry, and Co. Limerick (52°36'N, 9°38'W), in which bottlenose dolphins are a qualifying interest. Surveys occurred west of Aughinish and east of Loop Head and Kerry Head (Fig. 1).

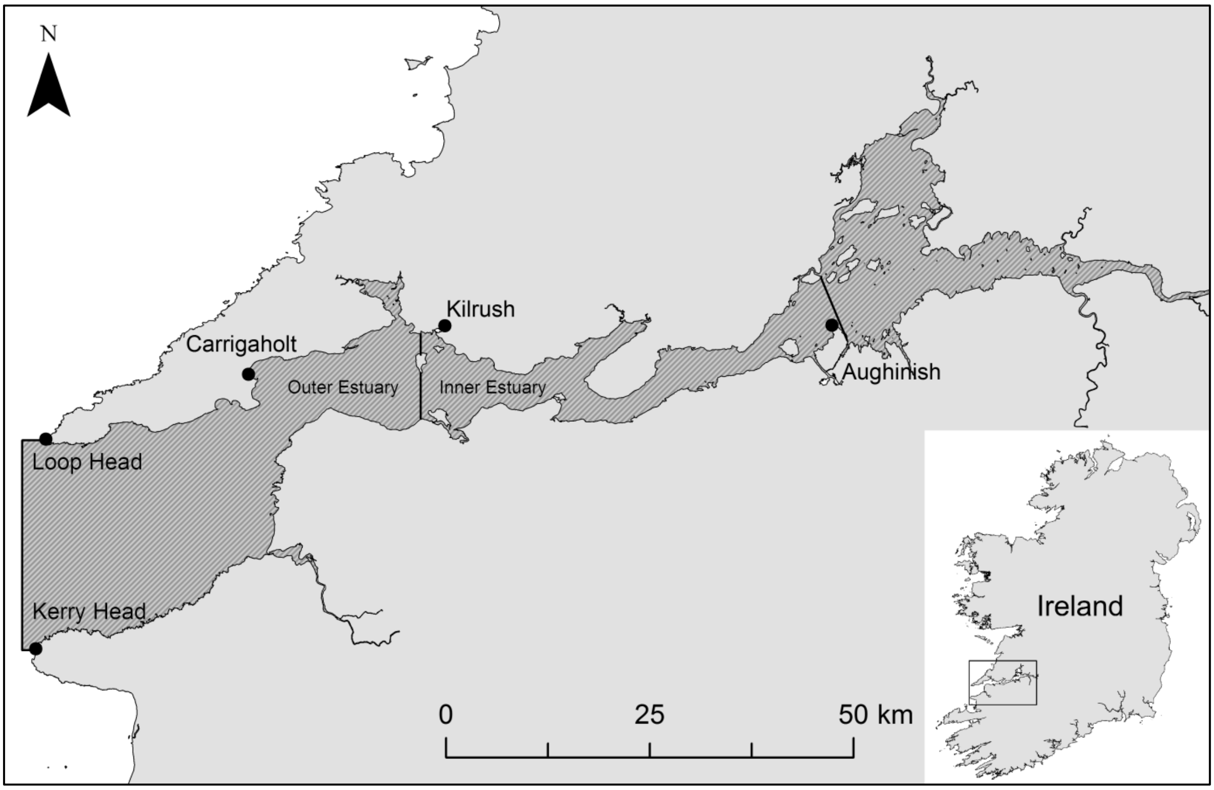


Figure 1. Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC; shaded dark gray area) while the line at Aughinish represents the boundary of the area within the SAC surveyed during this study. The study site is divided between the inner estuary and outer estuary areas by a north-south line drawn through Scattery Island, near Kilrush.

Data Collection

Long-term photo-identification studies of bottlenose dolphins in the Shannon Estuary have been ongoing since the early 1990s (Berrow *et al.* 1996, 2012; Ingram 2000; O'Brien *et al.* 2014). Additionally, over this time period, a dolphin-watching tourism industry has been established in which two main companies operate dolphin-watching tour boats and provide opportunistic platforms for research (Berrow and Holmes 1999).

In this study, surveys were conducted between March and November each year from 2012 to 2015 on board three vessels – the two dolphin-watching tour boats and a dedicated research vessel. The dolphin-watching boats operated independently from the ports of Carrigaholt and Kilrush, Co. Clare, with the research vessel also based in Kilrush (Fig. 1). The Carrigaholt tour boat concentrated effort in the outer estuary exclusively while the Kilrush tour boat primarily concentrated effort in the inner estuary area with some outer estuary trips. Overall, the mean length of dolphin-watching trips was 2.3 h (Barker and Berrow 2016). The research vessel was a 6 m RIB (Rigid-hulled Inflatable Boat) with a 115 hp outboard motor, with which surveys were conducted throughout all areas of the estuary between Loop Head and Aughinish. Trained onboard observers (n = 19 over 4 yr) located dolphins visually by eye and with the use of binoculars (Minox 7x50 or 8x42). Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~5 m, while observations from the Kilrush tour boat and the research vessel were made from the bow of the boats at <2 m above sea level. The tour boats had a minimum of one observer and a maximum of six observers per survey while the research vessel had between three and five crew per survey.

A sighting began when at least one dolphin was within 100 m of the vessel and ended after ≤30 minutes due to national regulations (Maritime Safety Directorate 2005). During a sighting, all vessels maintained a position parallel to the animals and approximately 100 m from them unless the dolphins approached the boat themselves.

Sampling methods were based on Mann's (1999) survey protocol, with sightings including records of individual dolphin IDs, group estimates, environmental measures (including water temperature, depth, and sea state), location (Latitude and Longitude; Garmin GPS 72H), activity states (travel, social, forage, rest, other, or unknown) and behavioral events (*e.g.*, leap) (see definitions in Baker *et al. in press*). A group was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh *et al.* 2011).

Photographs were taken throughout sightings using digital SLR cameras (Nikon D300 or Canon EOS 20D with 70-300 mm lenses) in an attempt to photograph each individual in each group for individual recognition through the photo-identification of dorsal fins (Würsig and Würsig 1977, Würsig and Jefferson 1990).

Data Management

Photos from all surveys and sightings were maintained in a database using the photographic software environment IMatch 5.6 (https://photools.com/M. Westphal 2016). A digital photo-id catalogue housed the best images of each individual in the population and was used by researchers to compare with the dorsal fin photos taken during sightings. When a tentative match was made, based on the nicks and notches along the edge of the dorsal fin, researchers were required to match at least one additional secondary characteristic such as fin shape, scars, rake marks, deformities, and persistent skin lesions, by using the filter function in IMatch to search for additional images of the individual in question, before entering their match. Following the visual comparison and matching by the first researcher, each image was then checked by two other researchers independently of one another, wherein the match was verified, or rejected and then rematched. The final identifications of each individual dolphin in each sighting were verified by the lead researcher who had the most photo-id experience, as recommended by Pearson *et al.* (2016). The long-term monitoring of this relatively small population, coupled with the high encounter rate, knowledge of life history and well-maintained photo-id catalogue of 204 known individuals (recorded between 2008 and 2016) greatly enhanced the process and efficiency of individual dolphin identification.

Both written sighting records and individual dorsal fin photographs (one best photograph per individual per sighting) were entered into a specially adapted version of FinBase (*MS Access*), a relational sightings database for bottlenose dolphin research (Adams *et al.* 2006). Each dorsal fin photo's quality was graded using the FinBase Photographic Quality form and assigned to its specific sighting and survey using the FinBase Match/Catalog form, wherein the dolphin class, degree of obstruction and distinctiveness were also graded to defined scales within the program. Activity state data originated from the FinBase database, where each sighting was assigned a single predominant activity state (travel, social, forage, rest, other, or unknown) by the observer during data collection.

Data Classification

(i) Sex classification

Information on the sex of individual dolphins was obtained in three ways, using (1) genetic sex determination from biopsy tissue samples (*n* = 27), collected under NPWS permits (Berrow *et al.* 2002, Mirimin *et al.* 2011); (2) photographs of the genital area (*n* = 1); and (3) consistent observations with a dependent calf multiple times over multiple years (*n* = 30; Smith *et al.* 2016). As a result, 47% of known sexes were determined through biopsy sampling and 53% from observational data. For females identified through association with a calf, the number of mother-calf pair sightings ranged from 6 to 92. Overall, 48% of individuals available for analysis were of known sex.

(ii) Age classification

Age class was determined by observations of individual size, reproductive state and/or knowledge of long-term life history (unpublished data). Adults were larger and darker in color than juveniles, and sometimes with a dependent calf. Juveniles were less than two-thirds the size of adults and were not observed to be dependent calves. In some cases, individual juveniles were of known age due to knowledge of their association with their mother as a calf in the previous years before weaning.

(iii) Area classification

The study site was divided between the inner estuary and outer estuary areas by a north-south line drawn through Scattery Island, near Kilrush. This line divided the estuary roughly in half, was a reference point for the center of the study area and divided research surveys east and west of the port of Kilrush. A classifier for area was created based on the sighting records of individuals by location, because preliminary evidence suggested differences in the use of the inner and outer survey areas by individuals in the population. If an individual had *ever* been observed in the inner estuary, it was classified as ‘inner’. If an individual had *never* been observed in the inner estuary, it was classified as ‘outer’ (Table S1). This provided a basic classification from which individual area use within the study site could be explored (see map in Fig. 1; Fig. S1).

Data Analysis

(i) Analytical definitions

Data were queried in FinBase and input into SOCPROG 2.7 (compiled version), a dedicated software package that uses data on the associations of identified individual animals for the analysis of their social structure (Whitehead 2009), in group mode, with a supplemental file detailing individual sex, age, and area classifiers. The sampling period was defined as one day, based on the natural break between daylight sampling sessions and because the proportion of individuals sampled within a one day timeframe was appropriate for data analysis. Associations between individuals were defined by shared group membership, with each record/sighting constituting one group. The half-weight association index (HWI) was used as the coefficient of association. This measure represents the strength of social bonds among individuals (with a range of possible values between 0 (never seen together) and 1 (always seen together)), while also accounting for the possibility of missing individuals during sighting encounters (which is a possibility when opportunistic research platforms like dolphin-watching tour boats are used). The HWI is defined as $HWI = 2N_T/(N_a+N_b)$ where N_T represents the number of times two individuals are seen in the same sighting and N_a and N_b represent the total number of times each individual is sighted, respectively (Cairns and Schwager 1987). Thus, this association index indicates the proportion of time that each pair of individuals is seen in a group together. For all analyses other than the temporal analyses and movement analyses (where all data were used), restrictions were set within SOCPROG to include only individuals with >5 sighting records.

Dependent calves were excluded from analyses because their presence was a result of their mothers' presence in groups. Excluding dependent calves from the dataset left adults and juveniles, but for analyses using sex class, only adults were available as sex had not been determined for any of the juveniles. Both adults and juveniles were included in the analyses using area class.

SOCPROG was used to generate basic population data, quantify the number of individuals in defined classes, produce descriptive statistics and examine association patterns between individuals in the population. A discovery curve was plotted to assess photographic coverage of identified population members using cumulative number of identifications and year of sampling.

(ii) Group composition, associations and clusters

Group composition was explored by examining the identities of individuals in every group, classifying them by sex and age and calculating overall proportions. Associations between and within sex classes were quantified and compared using a Mantel test and a histogram of proportional HWIs (Whitehead 2009).

Average linkage hierarchical cluster analysis was used to investigate relationships within the inner area class wherein individuals were assigned to clusters (clusters may be semipermanent social units, communities, or other social entities). A Cophenetic Correlation Coefficient (CCC) value greater than 0.8 (where 1.0 = perfect fit and 0.0 = no relationship) and a modularity greater than 0.30 indicate that a dendrogram is an acceptable representation of input distances and its division into clusters is appropriate (Whitehead 2009).

(iii) Social networks

Association matrices were visualized as social networks (or sociograms) for all associations with HWI ≥ 0.20 with individual nodes shaded, first by age and then by area class, and weighted links representing strength of association between individuals at three levels. A further sociogram was constructed using cluster analysis results to visualize the clustering of individuals in the inner estuary network.

Weighted social network measures were calculated for all individuals and for age, area, and sex classes separately using the network analysis statistics module in SOCPROG and standard errors were calculated using the bootstrap method with 1,000 replicates. ‘Strength’ was calculated as the sum of association indices of any individual with all other individuals; thus, high strength values indicate strong associations with other individuals in the population. ‘Reach’ was measured as the overall strength of network neighbors.

(iv) Behaviorally specific associations and preferences

We used methods similar to Gero *et al.* (2005) to determine whether behaviorally specific preferred associations existed within the population, as it is important to assess the effect of activity state on associations in fission-fusion networks (Gazda *et al.* 2015, Moreno and Acevedo-Gutiérrez 2016). Restrictions were implemented in SOCPROG for each of four main activity states – rest, travel, social, and forage. The data were restricted by each activity state in turn and the HWI matrix was saved as a SOCPROG association measure. Then, SOCPROG’s analyses of multiple association measures module was used to view dyadic plots and different dyadic outputs of the association measures. A Mantel test was run to test for correlation between social and foraging HWIs.

(v) Association preferences/avoidances

Permutation tests (Bejder *et al.* 1998, Whitehead *et al.* 2005) were used to test for preferred/avoided associations across the whole population, the null hypothesis being that there were no bottlenose dolphin dyads in the Shannon Estuary population that preferred or avoided to associate. Then, permutations were run to test for preferred/avoided associations within and between classes (age, area, and sex) as well as for each year of data separately (and sex-specific associations within each year) and for activity states (social, forage, rest, and travel). The null hypothesis in each case was that individuals would associate randomly with one another. The real HWI matrix was permuted 40,000 times with 100 trials per permutation for each analysis. Associations were permuted within sampling periods (*i.e.*, days). The test calculates a statistic for the real data and for many permutations of random data (with constraints). The null hypothesis that only random associations exist is rejected if the statistic for real data is greater than the statistic for 95% of the random data ($P < 0.05$) (Bejder *et al.* 1998).

(vi) Stability of associations over time

Temporal analyses were used to determine the stability and persistence of associations over time. The lagged association rates were standardized as we could not be certain that all individuals had been identified in every sighting. These standardized lagged association rates (SLARs) were plotted against time lag with moving averages and standard errors calculated using the temporal jackknife method. The null association rate was added to the plots; this represents the theoretical SLAR if individuals associated randomly (Whitehead 2008). Four exponential models were fitted and the model with the lowest Quasi Akaike Information Criterion (QAIC) was determined the best fit, with the ΔQAIC (difference between QAIC and that of the best model) indicating the degree of support for the other models (>10 difference = no support; Whitehead 2008). To determine if sex-specific patterns of association persisted over time, SLARs were plotted for female-male associations using the same methods.

(vii) Movements throughout study area

To investigate movements between the two defined areas of the study site, sighting records were filtered and categorized as either Area 1 (inner estuary) or Area 2 (outer estuary). We used movement analyses in SOCPROG to examine how individuals moved among the inner and outer estuary areas of the study site. The lagged identification rate (LIR), the probability that if an individual is identified in the area at any time it is identified during any single identification made in the area some time lag later (Whitehead 2001), was used to assess movements among the two areas. LIRs were calculated for each single area and then between the two areas. We then used overall LIRs to assess movements within and between areas which indicated the general probabilities that individuals would be in the same study area or in a different one after particular time lags (Whitehead 2009). The number of bootstrap replications was set to 1,000 to calculate bootstrap-estimated standard errors of the LIRs. Again, selection of the best fitting models was determined using the lowest Quasi Akaike Information Criterion (QAIC) value. The QAIC was used (rather than the AIC) to compensate for overdispersed data (Whitehead 2007).

RESULTS

(i) Survey effort and photo-identification

Of the 353 surveys (607 sightings) carried out between 2012 and 2015, 312 (522 sightings) contained photos of individually identifiable adult and/or juvenile bottlenose dolphins (Table 1). A total of 136,486 photographs were taken and 45,371 of these were used for photographic analysis of dolphin sightings. A total of 2,948 identifications were made of 121 distinct individual dolphins. On average, 106 individuals (88%) of the 121 identified were sighted each year. Ninety-eight percent of individuals (119) were sighted in multiple years, with 64% of individuals (77) seen in all four study years from 2012 to 2015.

Table 1. Summary of survey effort by sampling variable, for sightings containing photos of individually identifiable bottlenose dolphins, in the Shannon Estuary, Ireland. Named vessels are *Muc Mhara* (the research RIB), *Draíocht* (the Carrigaholt tour boat), and *DD (Dolphin Discovery*, the Kilrush tour boat).

Survey Effort	2012	2013	2014	2015	Total
No. days	29	50	65	53	197
No. surveys	57	78	100	77	312

No. sightings		95	119	180	128	522
No. sightings by vessel	Muc Mhara	1	7	59	15	82
	Draíocht	66	78	52	70	266
	DD	28	30	65	39	162
No. sightings by survey area	Outer estuary	76	96	89	95	356
	Inner estuary	13	17	66	29	125
	Whole estuary	6	6	25	4	41

On average, surveys (from all boats collectively) yielded 2.7 sightings of bottlenose dolphins per day, with a mean of 12.2 individual dolphins identified per day (*n* = 121, range = 1-60), thus about 10% of the adult/juvenile population in this study was identified each day. The mean number of sightings per individual was 24.4±21.7 (*n* = 121, range = 1-101).

A discovery curve plotting number of individuals identified against cumulative number of identifications reached a clear plateau suggesting good coverage of the population after about 1,000 identifications and that almost all the individuals recorded in 2014 and 2015 were resighted from records in 2012 and/or 2013 (Fig. 2). In fact, no new (adult/juvenile) individuals were recorded during the 2015 field season.

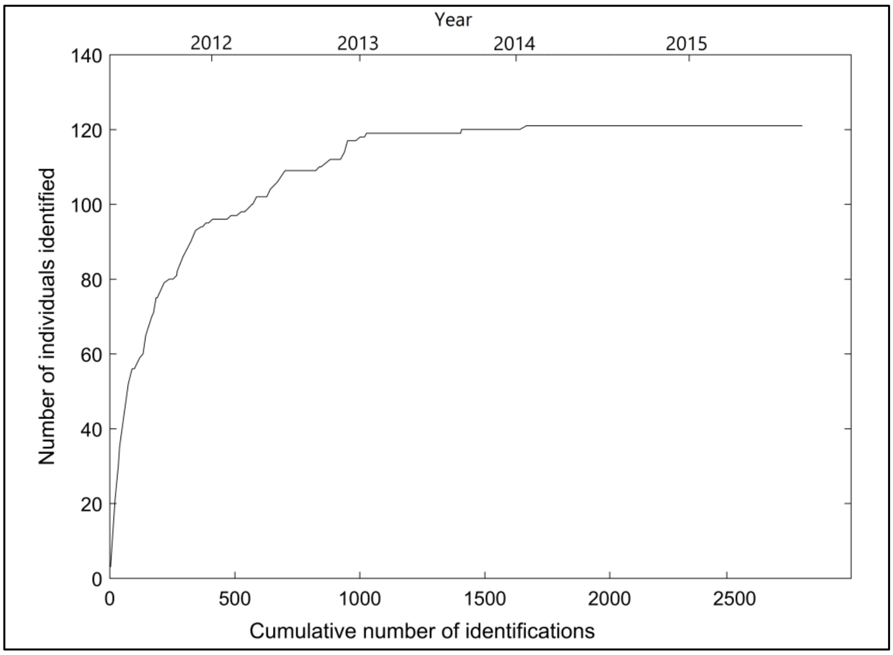


Figure 2. Discovery curve of number of individual bottlenose dolphins identified *vs.* cumulative number of identifications, with year of sampling between 2012 and 2015 (*n* = 121).

Of the 121 individuals sighted, 58 were of known sex (46 female, 12 male) and 63 were of unknown sex. Age class was divided into 93 adults and 28 juveniles. The area classifier consisted of 33 ‘inner’ and 88 ‘outer’ estuary individuals. Within this, the inner class consisted of 27 adults and 6 juveniles; the outer class of 66 adults and 22 juveniles.

(ii) Group composition, associations and clusters

Of 268 group sightings in which at least one individual was identified as male, 241 (90%) had females present. While, of 450 group sightings in which at least one individual was identified as female, 241 (54%) had known males present. Of the 522 sightings analyzed, 225 groups contained juveniles; only 7% (16) of these groups contained no other age class. The overall proportion of single sex groups *vs.* mixed sex groups could not be determined because 80% of the sightings analyzed contained at least one individual of unknown sex. When restrictions were set within SOCPROG to include only individuals with >5 sighting records, 106 distinct individual dolphins and 519 sightings were available for association and network analyses.

The overall mean HWI of the Shannon Estuary population was 0.07±0.02. The maximum HWI that any individual had with any other individual ranged from 0.16 to 0.72 (mean = 0.41, SD = 0.11; n = 106).

When sex was selected as the class variable, and analyses included only individuals of known sex, the HWIs over 0.4 were for female-female and female-male pairs only, with female-male association indices higher than all others (>0.6; Fig. 3). The mean HWI for male-male associations was the highest (mean = 0.1191, SD = 0.0313), and mean female-female (mean = 0.0872, SD = 0.0259) and female-male (mean = 0.0913, SD = 0.0427) association indices were almost equal. However, this may have been due to the much larger sample size for females (*n* = 45) compared to males (*n* = 10). Overall, associations between different sex classes were roughly the same (mean = 0.0913, SD = 0.0402) as those within same sex classes (mean = 0.0930, SD = 0.0294) and the difference between them was not statistically significant (two-sided Mantel test, *t* = -0.30, *r* = -0.01, *P* = 0.81).

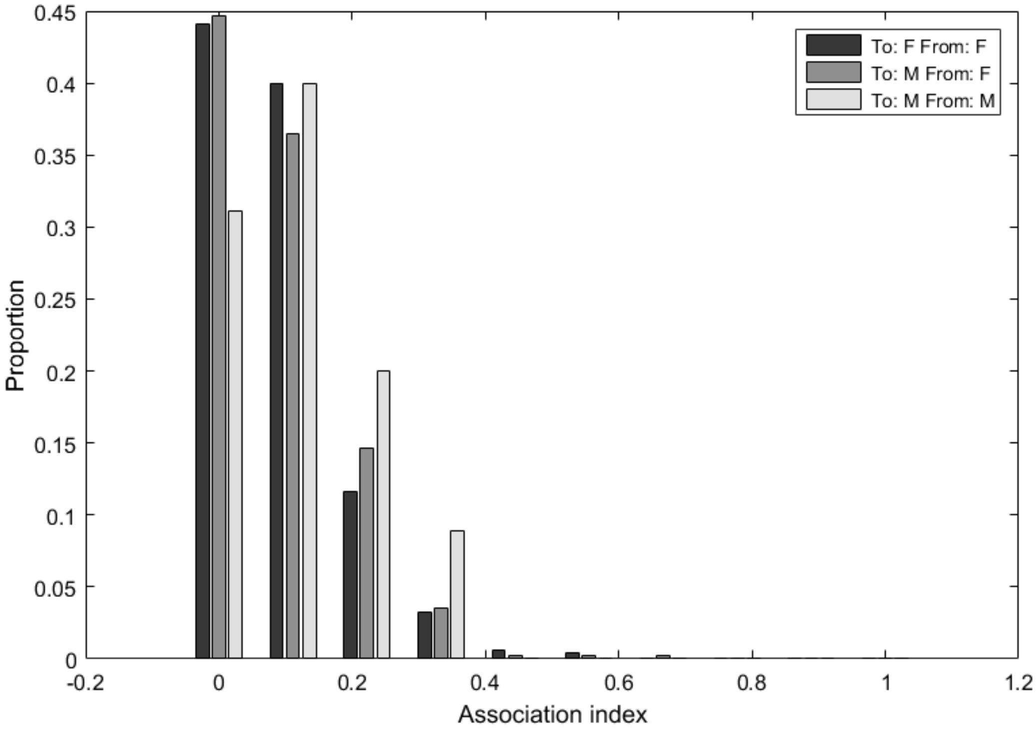


Figure 3. Histogram of half-weight association indices (HWIs) between female-female, female-male and male-male pairs in the Shannon Estuary (*n* = 55).

In age classes, juvenile-juvenile associations were the strongest (mean = 0.13, SD = 0.04), followed by adult-adult associations (mean = 0.09, SD = 0.02). Adult-juvenile associations were the weakest (mean = 0.05, SD = 0.02). The strongest association recorded in the population was between two juveniles (HWI = 0.72). Generally, associations within same age classes (mean = 0.10, SD = 0.03) were stronger than those between different age classes (mean = 0.05, SD = 0.02) and this difference was statistically significant (two-sided Mantel test, *t* = 10.72, *r* = 0.22, *P* = 0.00).

Similarly, associations within same area classes (mean = 0.11, SD = 0.05) were much stronger than those between different area classes (mean = 0.04, SD = 0.03) and this difference was also statistically significant (two-sided Mantel test, t = 16.75, r = 0.30, P = 0.00). Inner-outer class associations were the weakest (mean = 0.04, SD = 0.02), outer-outer associations were relatively stronger (mean = 0.08, SD = 0.02), but inner-inner associations were by far the strongest (mean = 0.17, SD = 0.06).

Average-linkage cluster analysis of the matrix of HWIs of individuals classified as inner in the bottlenose dolphin population resulted in three clusters, with a maximum modularity (Type 1; controlling for gregariousness) of 0.13 at a HWI of 0.10. IDs 244 and 150 were the most associated individuals with a HWI of 0.72 (Fig. 4). Although the modularity was low (indicating that the division into clusters may not be appropriate), the Cophenetic Correlation Coefficient (CCC) value of 0.88 indicates that the dendrogram is an acceptable representation of input distances. Thus, inner estuary individuals appear to be clustered into two major groups consisting of 21 individuals and 11 individuals, and a third ‘cluster’ with a single individual (ID 34). A similar cluster analysis of outer class individuals resulted in ten clusters but the CCC value of 0.67 was not high enough to accept the dendrogram as a true representation of individual clustering.

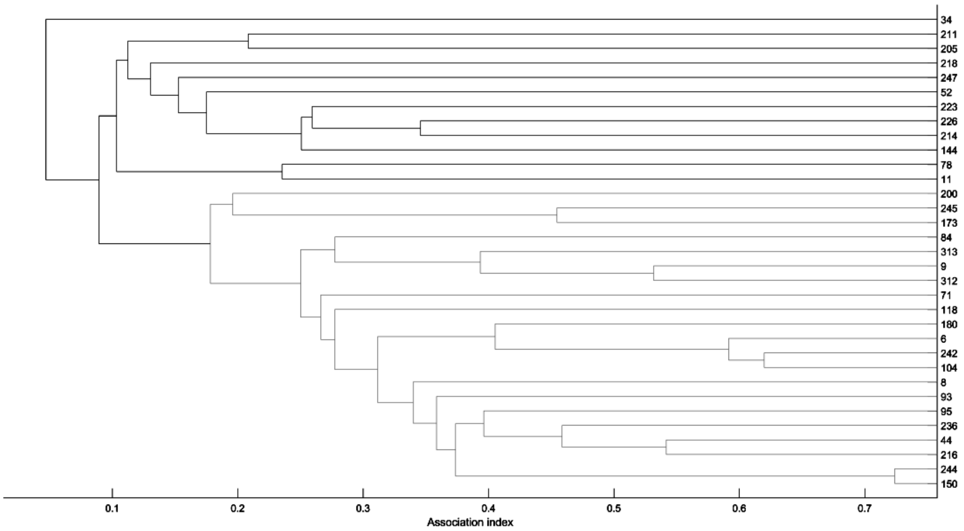


Figure 4. Average-linkage cluster analysis (CCC = 0.88) of the matrix of HWIs of individual bottlenose dolphins classified as inner (*n* = 33).

(iii) Social networks

A sociogram was constructed for all individuals analyzed (*n* = 106) with age classifiers (adult, juvenile), illustrating the social connections between individuals with HWI ≥0.25 and the strength of association at three levels (HWIs of 0.25, 0.50 and 0.75). The population appears to be somewhat aggregated according to associations by age class, with a major mass of adults associating with adults and two smaller collections of juveniles associating closely with other juveniles (Fig. 5).

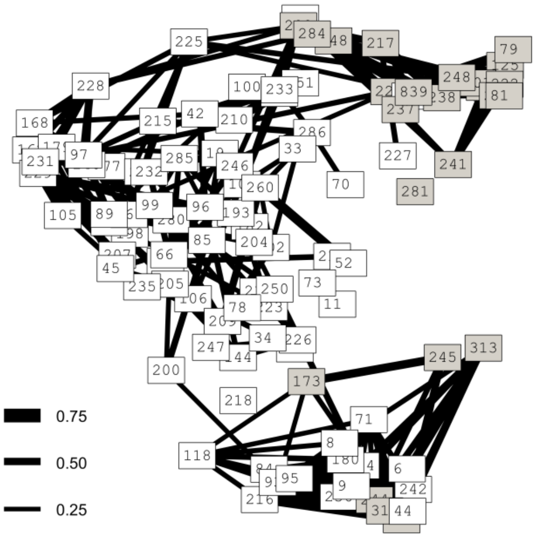


Figure 5. Sociogram of all individual bottlenose dolphins (n = 106) with node color for age (adult = white, juvenile = gray), illustrating the social connections between individuals with HWI ≥0.25. The thickness of lines represents the strength of association at three levels. Numbers within each node represent individual dolphin ID codes.

Next, a sociogram was constructed for all individuals analyzed (n = 106) with area classifiers for outer (n = 73) and inner (n = 33), with the inner class further divided (using the results of the previous cluster analysis) into three clusters (Fig. 6A). This diagram illustrates the social connections between individuals with HWI ≥0.25 and the strength of association at three levels (HWIs of 0.25, 0.50, and 0.75). Overall, the population appears to be roughly assembled by association into two groups or communities with a third group of key individuals forming connections between the two major groups, although their associations are weaker than those among the major group members themselves.

The strong associations between individuals within the inner class (n = 33) are apparent in a sociogram of only inner individuals (Fig. 6B) where the clustering of individuals from the cluster analysis is clearly depicted. The major inner cluster of 21 individuals and the other 12 individuals who sit between this major cluster and the outer estuary individuals are apparent.

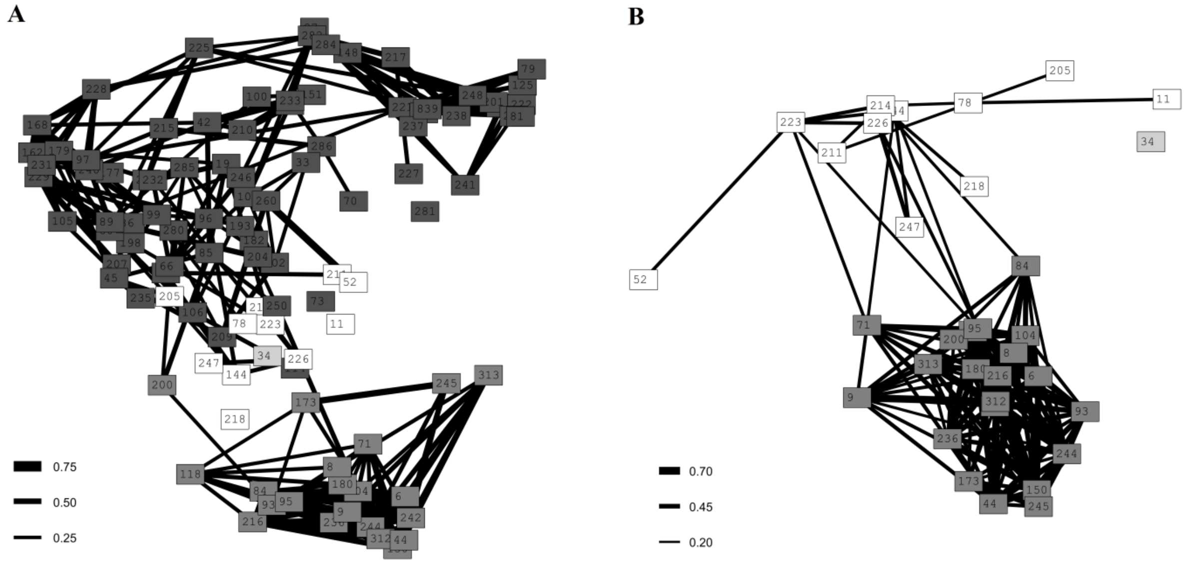


Figure 6. Sociograms of (A) all individual bottlenose dolphins (*n* = 106) with node color for area (outer = dark gray, inner = gray, light gray and white) and (B) individuals assigned to the inner class (*n* = 33) clustered using the hierarchical cluster analysis results into three clusters (gray, light gray and white). The diagrams illustrate the social connections between individuals with (A) HWI ≥0.25 and (B) HWI ≥0.20. Different scales were used to most clearly illustrate the structure of each network. The thickness of lines represents the strength of association at three levels. Numbers within each node represent individual dolphin ID codes.

With further exploration of age class division in the social network, not only do juveniles and adults have closer associations within classes than between, but if each age class is further classed by area, there are clear dissimilarities in association between inner and outer adults and inner and outer juveniles. Thus, individuals of each age group are divided from each other and are further divided within their age groups by their area class.

Social network metrics were calculated for the population overall and for each identified class (age, area and sex) separately (Table 2). For both direct (strength) and indirect (reach) connectedness, the average measures for adults were significantly higher than for juveniles ($P < 0.05$; determined because the difference in mean values between classes was greater than twice the sum of the bootstrapped standard errors). Similarly, the average measures of strength and reach for females (and unknown sex individuals) were significantly higher than for males ($P < 0.05$), although the small sample size for males may have affected the measures for that class.

Table 2. Social network measures calculated for the Shannon Estuary bottlenose dolphin population overall and by age, area and sex classes separately. Values are presented as Mean ± SD [bootstrapped standard error].

	n	**Strength**	**Reach**
Overall	106	7.77 ± 1.91 [0.52]	64.04 ± 17.30 [8.46]
Age			
Juveniles	25	3.21 ± 0.93 [0.37]	11.12 ± 4.06 [2.64]
Adults	81	6.83 ± 1.84 [0.43]	49.94 ± 14.09 [6.39]
Area			
Inner	33	5.28 ± 1.91 [0.31]	31.45 ± 12.97 [3.71]
Outer	73	6.08 ± 1.63 [0.55]	39.60 ± 11.36 [7.40]
Sex			
Female	45	3.84 ± 1.14 [0.30]	15.99 ± 4.95 [2.46]
Male	10	1.07 ± 0.28 [0.11]	1.22 ± 0.27 [0.26]
Unknown	51	3.65 ± 0.91 [0.30]	14.14 ± 4.12 [2.48]

(iv) Behaviorally specific associations and preferences

Restrictions on sightings based on predominant activity state produced four separate association matrices. The mean HWI for socializing groups was higher (0.09±0.03) than for foraging groups (0.06±0.03). HWIs for pairs of individuals in sightings where the activity state was foraging were significantly different to those in sightings where the activity state was socializing (n = 77, two-sided Mantel Z-test, matrix correlation of association matrices

= 0.28, $P < 0.05$). Permutation tests were carried out for sightings of the four main activity states (travel, forage, social, rest). The CVs of the real HWIs were significantly larger than those of the random data for travel ($P < 0.0001$), social ($P < 0.0001$) and foraging ($P < 0.05$) behavioral associations (Table 3). No significance was found for associations calculated for the activity state rest, although this may have been due to the small sample size in this case (only 13 sightings compared to more for other activity states, unpublished data). The significance found for the first three activity states indicated that behaviorally specific preferred associations exist in this population.

(v) Association preferences/avoidances

The overall significance for preferred/avoided associations in the population, using the coefficient of variation (CV) of association indices as a test statistic, was $P < 0.0001$ (CV = 1.24 for real data, compared with CV = 1.11 for mean of randomly permuted data). Thus, the null hypothesis that only random associations exist could be rejected.

When the HWIs within and between classes (age, sex and area) and years were investigated, the CVs of the real HWIs were significantly larger than those of the random data ($P < 0.0001$, Table 3) in most cases, although the strength of significance varied for juvenile-juvenile ($P < 0.01$) and male-male ($P < 0.05$) associations. The persistence of significant results for most variables provides further evidence for rejecting the null hypothesis that there are no bottlenose dolphin dyads in the Shannon Estuary population that prefer or avoid association.

Table 3. Real and random coefficients of variation (CV) of half-weight association indices (HWIs) across age, area and sex class, year (and within year female-male HWIs) and activity state, and pooled for all sightings.

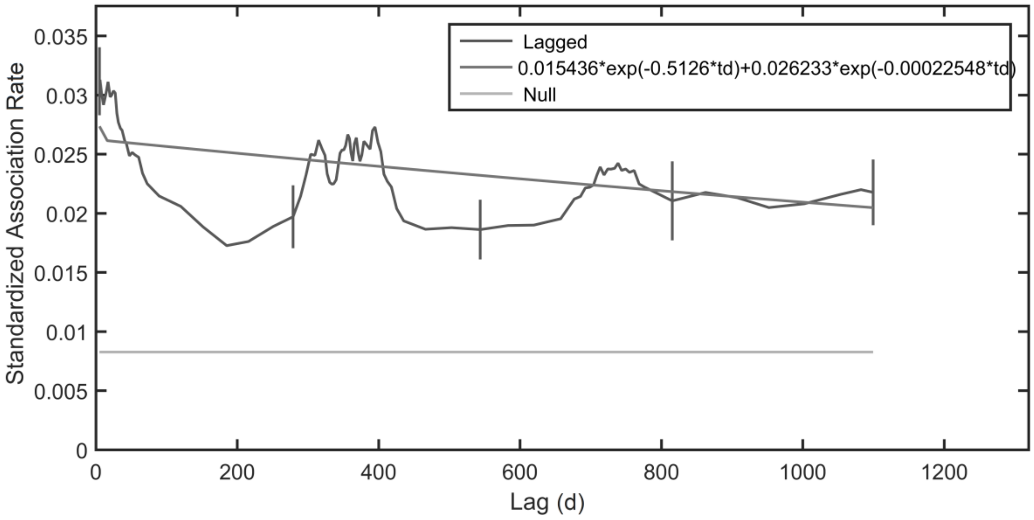
Variable	*n*	CV of real HWI mean	CV of random HWI mean	*P*	Variable	*n*	CV of real HWI mean	CV of random HWI mean	*P*
Age class					***Year***				
Adult	81	1.08	0.97	<0.0001	2012	88	1.88	1.80	<0.0001
Juvenile	25	1.04	1.01	<0.01	Female-male	37-9	1.55	1.51	<0.05
Adult-juvenile		1.53	1.49	<0.0001	2013	103	1.71	1.65	<0.0001
Area class					Female-male	43-10	1.32	1.31	<0.05
Inner	33	0.74	0.68	<0.0001	2014	101	1.75	1.63	<0.0001
Outer	73	1.14	1.07	<0.0001	Female-male	44-10	1.33	1.27	<0.0001
Inner-outer		1.31	1.27	<0.0001	2015	95	2.10	2.02	<0.0001
Sex class					Female-male	40-8	1.68	1.67	0.31
Female	45	1.06	0.95	<0.0001	***Activity State***				
Male	10	0.84	0.80	<0.05	Social	88	2.22	2.21	<0.0001
Female-male		1.03	0.98	<0.0001	Foraging	93	2.21	2.19	<0.05
					Rest	47	1.88	0.00005	1.00
					Travel	95	2.03	1.95	<0.0001
					Overall	106	1.24	1.11	<0.0001

(vi) Stability of associations over time

Standardized lagged association rates (SLARs) and null association rates were plotted against time lag (with moving averages and standard errors estimated using the temporal jackknife method) for all 121 bottlenose dolphins (Fig. 7A) and four exponential models for SLARs were fitted. The SLARs remain consistently higher than the null association rate; after 1,000 d, the stabilization is still well above the standardized null association rate. The fourth model – “two levels of casual acquaintances” – had the lowest QAIC and so fit best (Fig. 7A). There was no support for the other three models (ΔQAIC > 15).

Interestingly, when female-male association rates were plotted, the best fit model was for “preferred companions and casual acquaintances” (Fig. 7B). This indicates that sex-specific patterns of association may persist over time between females and males at two levels of association – one of “preferred companions” and one of “casual acquaintances”.

A



B

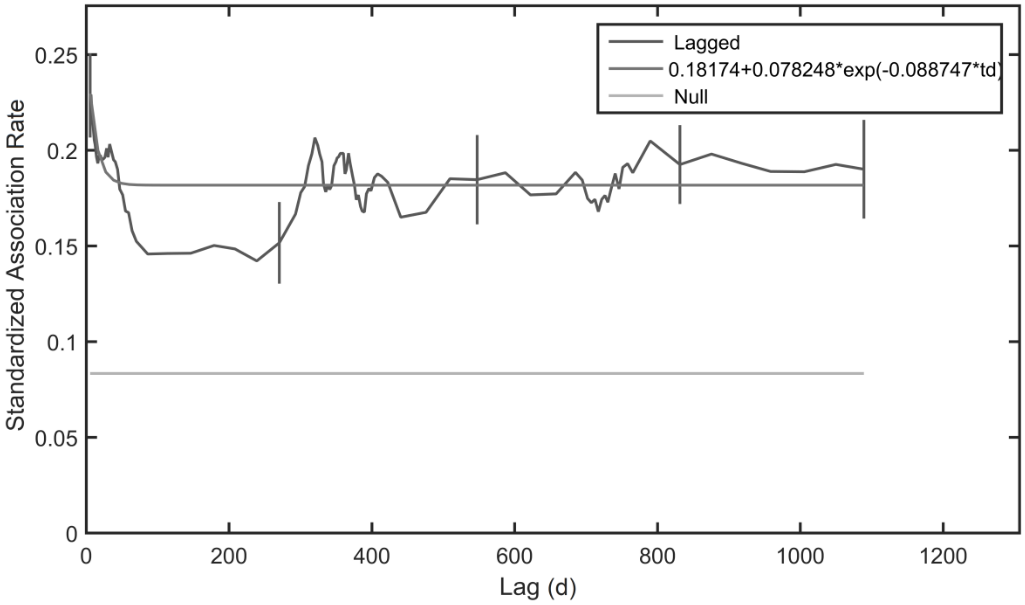


Figure 7. Standardized lagged association rates (SLARs) and null association rate plotted against time lag with best fit exponential model for (A) whole population (*n* = 121) and (B) female-male (*n* = 55) associations. Standard error bars (vertical lines) estimated using temporal jackknife method. SLAR curves were smoothed with moving averages of (A) 160,000 and (B) 2,000 associations.

(vii) Movements throughout study area

Lagged identification rates (LIRs) plotted against time lag, among the two areas of the study site, suggest that the probability of an individual being identified in either the inner or outer estuary and then being identified in either area some time later remains almost the same over time (LIRs for inner estuary to inner estuary were higher than all others, at ~0.045). The best fitting models for the probabilities of movements from one area to the other (either Area 1 to 2, or Area 2 to 1) were different for the two cases; for LIRs of individuals moving from the inner to the outer estuary, the first two models indicating a “fully mixed” population fit best, whereas for LIRs of individuals moving from the outer to the inner estuary, the last two models indicating a “migration/interchange” population fit best. The goodness of fit chi-squared value was significant (*P* = 0.00) for all models.

Overall LIRs plotted to assess movements within and between areas suggest that after 200 d, the probability that an individual is in the same study area is higher than the probability that an individual is in a different study area, but after 360 d (and up to 1,100 d) the probabilities are virtually the same for either scenario (Fig. 8).

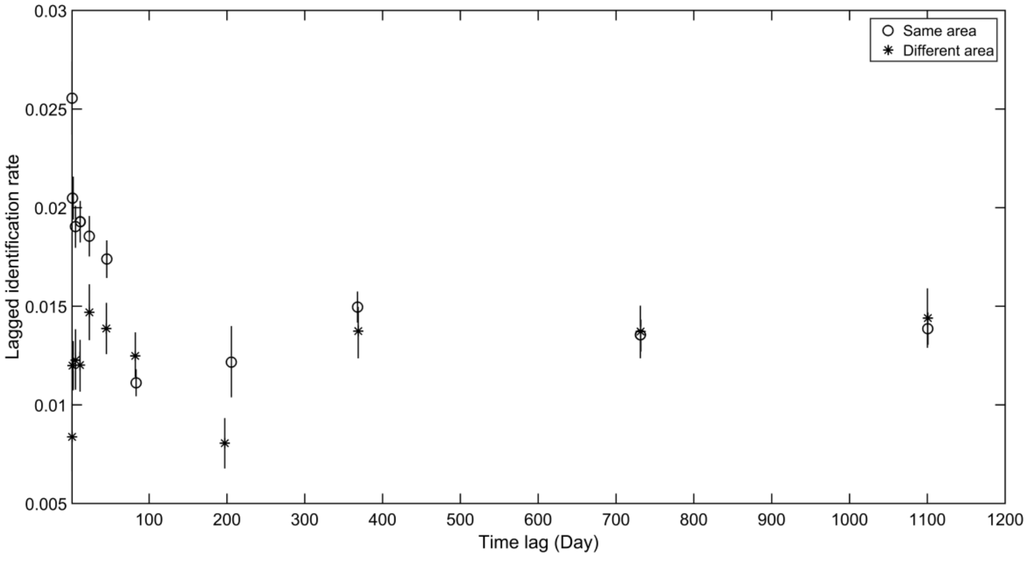


Figure 8. Plot of lagged identification rates against time lag (day) for individual movements within (circles) and between (asterisks) areas of the study site (bootstrap-estimated standard errors (bars) from 1,000 bootstrap replications) of individual bottlenose dolphins sighted in the Shannon Estuary.

DISCUSSION

Research on bottlenose dolphin social structure began in the 1980s (*e.g.*, Wells *et al.* 1987, Wells *et al.* 1991, Smolker *et al.* 1992) and continues today (*e.g*., Wells 2014, Connor and Krützen 2015, Louis *et al.* 2015). The structure of many resident populations has been described including in Sarasota Bay, USA (Wells 2014), Shark Bay, Australia (Connor *et al.* 2001), the St John's River, USA (Ermak 2014), the Aeolian Archipelago, Italy (Blasi and Boitani 2014), Laguna, Brazil (Daura-Jorge *et al.* 2012), Port Stephens, Australia (Wiszniewski *et al.* 2010) and the Sado Estuary, Portugal (Augusto *et al.* 2011). Recently, studies have illuminated the importance of social structure in relation to cetacean culture (Krutzen *et al.* 2005, Mann *et al.* 2012, Cantor and Whitehead 2013) and activity patterns (Gazda *et al.* 2015).

Studies of bottlenose dolphins have shown that the species generally lives in a fission-fusion social system (Connor *et al.* 2000) in which societies encompass both extremely fluid *and* stable associations between individuals (Smolker *et al.* 1992). Individuals within a population associate in temporary groups of variable size and composition, but there can be long-term associations among identified individuals within these fluid groups (Wells *et al.* 1991, Lusseau *et al.* 2003).

This study shows that bottlenose dolphins in the Shannon Estuary fit the general pattern of a fission-fusion society structured by age and area class, but perhaps also characterized by unusual female-male associations. Although individuals in the population associate with many others in a complex social network, significantly strong, persistent and preferred associations exist between individual dolphins. In Sarasota Bay, Florida, dolphin group composition is generally based on within-age and -sex class associations, including groups of females and calves, exclusively juvenile groups, and adult males, typically as strongly bonded pairs (Wells 2014). Our initial hypothesis was that the Shannon Estuary population would contain similar groups; however, this does not appear to be the case. In contrast, groups of dolphins in the Shannon Estuary appear to be composed of mixed sex and age classes although the associations between specific individuals indicate certain between- and within-class social preferences. Similarly, in Shark Bay, although Smolker *et al.* (1992) found groups often contained both sexes, there were consistent long-term associations between individuals of the same sex. This illustrates the difference between group composition and individual association preferences. Additionally, there is little evidence in the Shannon Estuary population for adult male groups, female-calf groups or exclusively juvenile groups.

The mean HWI of the Shannon Estuary population was 0.07±0.02. Several other bottlenose dolphin populations have reported mean HWIs including the Indian River Lagoon (0.010±0.006; Titcomb *et al.* 2015), Cedar Key (0.03±0.08; Gazda *et al.* 2015), St John's River, Florida (0.05±0.02; Ermak 2014), Sicily, Italy (0.06±0.02; Papale *et al.* 2017) and the Sado Estuary, Portugal (0.45±0.15; Augusto *et al.* 2011). The lowest of these mean HWIs is reported from the Indian River Lagoon where the dolphin population is spatially segregated into six distinct communities in which members of the furthest apart communities have the lowest association indices (Titcomb *et al.* 2015). By contrast, the highest example given here of mean HWI is reported for a very small ($n = 24$) bottlenose dolphin population in the Sado Estuary with strong stable community-wide associations (Augusto *et al.* 2011). These examples show that there is much variation in the observed mean HWI of a dolphin population. The presence of male alliances (with high HWIs) has been linked to population density (Ermak 2014) and this could be a possible factor in the differences found between the mean HWI values of different populations. The insular nature of small, localized or isolated populations may also lead to overall high mean HWIs regardless of within-population social structure.

Associations were not random in the Shannon Estuary dolphin population and this result was significant when applied to sex, age and area classes tested separately. The preference/avoidance of particular associates was also apparent for each year of data tested separately which further indicates the strength of this result as a representation of nonrandom population level associations.

The temporal stability of bottlenose dolphin social structure globally varies drastically, from being driven by constant companionship (Lusseau *et al.* 2003) to featuring casual acquaintances that last just a few days (Lusseau *et al.* 2006). Preferred associations in the Shannon Estuary dolphin population persisted over 1,000 days. The peaks in associations for all individuals after approximately 365 d and 730 d are most likely an effect of cyclical summer sampling periods. The best fitting model was for “two levels of casual acquaintances” associating and dissociating at two different time scales. The two time scales may simply be explained by the periods within and between field seasons. However, the two different levels of disassociation might also relate to the associating and dissociating of individuals within two separate classes; for example, age class and area class. Whitehead (2008) also similarly suggests that this type of SLAR might indicate the fission/fusion of nearly permanent social units into and out of subgroups on the short time scale and transfers between units on the longer one.

Although, as explained above, the line between the inner and outer estuary was based simply on dividing the study area into two roughly equal parts and reflecting operational issues, it turned out to be a useful reference point for tracking the movement and associations of individuals. The probability of identifying an individual in the inner estuary and then identifying it again in the inner estuary sometime later remained high over time. The same was true of outer estuary to outer estuary, although to a lesser extent. These results may represent some long-term site fidelity of individuals to certain parts of the estuary. The best fitting models for individuals moving from the inner to the outer estuary were for a “fully mixed” population. As all individuals who have been sighted in the inner estuary have also been sighted in the outer estuary, it follows that the population mixes in this area. The opposite was true of the best fitting models for individuals moving from the outer to the inner estuary which were for a “migration/interchange” population. Perhaps this can be explained by the fact that only a small number of individuals (~25% of the population) use the inner estuary, and thus would be returning to that area from the outer estuary over time. Overall rates suggest that individuals are more likely to be identified in the same study area after 200 d, but either the same or a different study area after longer periods. Perhaps this is suggestive of within-season site fidelity to either the inner or outer estuary. The use of the inner estuary by only a small percentage of the population seasonally has strong implications for management of the population as a whole, especially if other individuals are likely to go from the inner to outer but not likely to enter the inner area from the outer area during one season. For example, the degree of exposure to anthropogenic threats would be different for individuals of the inner and outer area classes.

There was good evidence for behaviorally specific preferred associations in the population with the mean HWI for socializing groups significantly higher than for foraging groups. The presence of preferred/avoided associations in sightings where individuals were engaged in either social or traveling behavior was highly significant, compared to slightly less significance during foraging activity. The low sample size for sightings of resting behavior may have had an effect on the lack of significance for this activity state. The difference in the level of significance for associations during foraging behavior *vs.* social or traveling behavior is interesting as Gero *et al.* (2005) similarly found that bottlenose dolphins have lower level "acquaintance"-type HWIs when foraging compared to socializing. This evidence for behaviorally specific preferred associations points to the behavioral flexibility of these dolphins and their ability to adjust their social patterns to optimally fit each of various behavioral situations.

Sex class associations

For adult individuals of known sex, the highest HWIs were for female-male pairs. Contrastingly, Smolker *et al.* (1992) found that female-male associations were generally inconsistent and primarily within the lowest HWI class in their study. In our study, the mean HWI of male-male associations was higher than the others; however, the much larger sample size for females may have affected this due to the incorporation of some female-female associations with low HWIs into the calculation of the overall mean for that sex class. Similarly, the very small sample size for males may have obscured association patterns for that sex class. Associations between different sex classes were similar to same-sex associations, and their difference was not statistically significant. Even so, the high mean HWI for male-male associations provides a good justification for further research with an increase in sample size of known males in the population. In the reporting of the societal attributes of cetacean social structure, one of the most frequently assessed aspects is sex-specific differences in patterns of association, and contrastingly, in other bottlenose dolphin studies, these associations are often stronger between members of the same sex (*i.e.*, within-class; *e.g.*, in Shark Bay, Smolker *et al.* 1992). In Sarasota Bay, adult females interact extensively with other females and adult males typically form strong male associations or alliances (Wells *et al.* 1987, Owen 2003) – features that do not seem to be present in the social characteristics of the Shannon Estuary bottlenose dolphin population.

When permutation tests were used to test for preferred/avoided associations between females and males, significance for nonrandom associations was apparent in the overall analysis. Thus, female and male bottlenose dolphins in the Shannon Estuary do not associate at random. However, when each year of data was tested separately, one year (2015, with 48 individuals of known sex) did not result in significant preferred/avoided female-male associations ($P = 0.31$). This year had the lowest number of males at eight individuals and it may be that significance could not be found within the small sample size.

Stable long-term female-male associations have been recorded in bottlenose dolphin populations in Doubtful Sound, New Zealand (Lusseau *et al.* 2003) and in Port Stephens, Australia, where constant companionships occur between females and males (Wiszniewski *et al.* 2010). Associations between female and male dolphins in the Shannon Estuary continued steadily over long time scales (>1,000 d), indicating that female-male associations are more long-lasting than the general associations of individuals in the population as a whole. The best fit model was, again, for two levels of disassociation, but this time for "preferred companions and casual acquaintances", indicating that sex-specific patterns of association may persist over time between females and males at both strong and weaker levels of association. As with the general lagged association rates, this result may simply reflect the gaps between field seasons, but it is possible that the stronger associations (the "preferred companions" level) might hold interesting information with respect to the mating system of this population.

Although only 52% of individuals in the current study were of known sex, there were no apparent divisions in the social network explained by the sex of individuals. In the Shark Bay social network, females tended to form longer chains of associates than males and almost every female was connected to all other females by a chain of consistent associates (Smolker *et al.* 1992). The significantly higher measures of strength (direct connectedness) and reach (indirect connectedness) found in our study substantiate the idea that female dolphins in the Shannon Estuary are also better connected than males.

More information on the life history of the Shannon Estuary bottlenose dolphin population will provide necessary data to assess the influence of female reproductive state on female-male relationships which has been shown to have a strong effect on differences in the consistency of female-male associations in other populations (Smolker *et al.* 1992). In Sarasota Bay, sexual segregation of males and females is common outside of the breeding season (McHugh 2010). It would be pertinent to gather more winter data on the Shannon dolphins to assess potential differences in their social structure, particularly with this in mind, as it is known that dolphins are present in the estuary during winter months (Berrow 2009). If additional winter data could be collected, analyses of year-round social associations could point to seasonality-related changes in the social structure of the population.

When combining the social analysis and group composition investigations, there was no evidence of all-male groups or the presence of male alliances that occur in other populations such as Shark Bay (Connor and Krützen 2015), Sarasota Bay (Owen *et al.* 2002), the Bahamas (Parsons *et al.* 2003, Rogers *et al.* 2004), and Port Stephens, Australia (Moller *et al.* 2001). There was similarly no evidence for long-term male-male associations such as those in Bunbury, Australia (Smith 2012), or the Moray Firth and Cardigan Bay (Sim 2015). Additionally, it is unusual to find relatively strong female-male associations in bottlenose dolphins, such as we have in this present study, so this warrants further research. There are various reasons why significant female-male associations might exist in a population, such as increased reproductive success (through increased mating opportunities, female mate choice, mate guarding, or increased access to food resources), reduced risk of infanticide or reduced harassment by other group members (Owen *et al.* 2002, Haunhorst *et al.* 2017).

Associations by age

Juveniles and adults had stronger within-class associations than those between age classes. The strongest association recorded in the population was between two juveniles, suggesting that the formation of strong associations early in life may be important in this population or might perhaps be related to maturing in the same age cohort, similarities in habitat use or kinship. Some other bottlenose dolphin populations typically contain exclusively juvenile groups (*e.g.*, Shark Bay, Smolker *et al.* 1992; Sarasota Bay, Wells 2014). Gero *et al.* (2005) observed a higher frequency of behavioral associations between juveniles than among any other relative age category in Shark Bay, while Smolker *et al.* (1992) noted that the most consistent preferential associations tended to be between subadults. In Sarasota Bay, young animals typically socialized at higher rates than adults, and juveniles preferred to interact with other juveniles and calves, and avoided adults (relative to their availability in the Sarasota Bay community) (McHugh 2010).

Samuels (1996) found that female juvenile dolphins in Shark Bay had stronger associations with adult females (their mothers) and other juvenile females than with male juveniles, while the top-ranked associates of juvenile males were other juvenile males and not adults or juvenile females. Similarly, juveniles in Sarasota Bay showed a marked preference for associating with other juveniles, especially of their own sex (McHugh 2010) – juvenile females interacted with more adult females and calves than males, while males interacted with more juvenile males than females did. McHugh (2010) suggested that differences between the association patterns of male *vs.* female juvenile dolphins might relate to their future reproductive roles in relation to calf-rearing and male mating strategies.

Unfortunately, it was not possible to test sex-based differences in juvenile associations in the current study due to lack of data on the sexes of juvenile animals.

There are various potentially beneficial reasons why juveniles might form preferential groups with other juveniles. While the formation of groups is often to reduce predation risk in other populations, the lack of any known predators of bottlenose dolphins in the Shannon Estuary suggests this is an unlikely cause. It is possible that juvenile dolphins might benefit from associating in groups to increase foraging efficiency, perhaps via increased efficiency of prey detection or capture (McHugh 2010). A third potential reason for juvenile-juvenile associations is socialization, wherein social interactions may be particularly important for young bottlenose dolphins due to the complex nature and fluidity of fission-fusion social systems and the long time period over which many relationships may develop (Kaplan and Connor 2007, McHugh 2010). Indeed, Stanton and Mann (2012) found that the survival of juvenile male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, could be predicted by the social bonds they formed as calves earlier in their lives.

In Doubtful Sound, New Zealand, evidence suggests that age-related homophily in bottlenose dolphin networks can influence the formation of clusters of preferred companionship (Lusseau and Newman 2004). Although somewhat mixed, there were clusters in the social network of the population for juveniles and adults. Adults had stronger social network measures for strength and reach than juveniles, meaning they had more direct and indirect connections to the rest of the network. Lusseau (2003) found that the social network of bottlenose dolphins in Doubtful Sound was held together by key individuals creating hubs for associations between other individuals and that these individuals were often older adults. In our network diagrams, the 12 inner estuary individuals who are not part of the core inner estuary cluster were located between that core group and the rest of the individuals in the overall population network diagram and were all adults, suggesting that they might play a similar role in linking the connections of associated individuals in this population.

Associations by area

The classification of individuals by sighting area revealed an interesting social division in the population. Inner individuals, that is, individuals who had been observed at least once in the inner estuary, had strong associations with inner individuals and, overall, within-area-class associations were stronger than between-area-class associations. Inner and outer estuary individuals had the lowest association indices; a similar result was found by Titcomb *et al.* (2015), where the lowest association indices were among individuals at the study site's northern and southern boundaries.

Dolphins in different habitats experience different environmental pressures which may influence individual association patterns (Smolker *et al.* 1992). Ecological factors, such as resource availability and distribution, might cause a population to split into two social units related to differences in habitat use or foraging specializations. If there were two key foraging areas, as suggested by the differences in habitat utilization described by Ingram and Rogan (2002), this could lead to niche partitioning in the Shannon Estuary. In some populations, bottlenose dolphins have formed communities defined as "associated individuals with long-term site fidelity to a specific area" (Wells 1986, Urian *et al.* 2009). Chabanne *et al.* (2017) suggest that a dolphin community might constitute a relevant local population comprising a total number of animals that could be affected by a proposed development and representing a population unit of some biological significance. Although all of the bottlenose dolphins in the Shannon Estuary use the outer estuary area of the study site, the differences in association between and within individuals in the inner and outer classes fits Croft *et al*.'s (2008) definition of a community as a group of individuals that are more associated amongst each other than with the rest of the society, and it might be appropriate to employ the term 'community' to describe these two social units.

The cluster analysis of inner individuals divided them into two main clusters. The largest cluster was a core group of 21 individuals who most frequently used the inner estuary area. Twelve other inner estuary individuals in the other major cluster appear to form a connection between this core inner group and the outer estuary individuals. These 12 individuals were all adults and had some of the highest betweenness centrality measures (*i.e.,* the number of shortest paths between other nodes/individuals that pass through that node/individual; Whitehead 2008) of the population further indicating the importance of their place in the overall network as individuals connecting other individuals. (A third 'cluster' was assigned to a single individual who did not have any HWIs > 0.2 with any other individual in the inner estuary network.) Similarly, Lusseau and Newman (2004) found some individuals that they described as "playing the role of broker" in their dolphins' social network and highlighted the importance of individuals that have preferred companionships in two communities, thus linking them together in a larger social context.

Additionally, when the age of individuals classified by area was taken into account, the social network divisions between inner and outer adults were apparent but especially clear were the divisions between inner and outer estuary juvenile dolphins. These six inner estuary juveniles (21% of all juveniles and 18% of inner estuary individuals) represented a key cohort within the inner estuary social unit.

It is important to emphasize that the clustering of these groups does not follow from the classification of the population by area: there is no reason in principle why the associations between individuals only observed in the outer estuary should be higher than those between these individuals and individuals who are sometimes observed in the inner estuary. The data presented here are necessary to substantiate the connection between area class and association. Similarly, Lusseau *et al.* (2006) found that their identification of two separate social units which mainly used two different areas was the result of genuine social affiliation and not an artefact of spatial distribution. Cantor’s (2012) work on spatiotemporal dynamics in a dolphin society found that spatial distribution did not influence the probability of individuals associating with one another.

‘Spatiosocial’ divisions in bottlenose dolphin networks can be related to many factors, including the geography of the study site (Wells 2014, Titcomb *et al.* 2015), individual ranging patterns (Lusseau *et al.* 2006), habitat preferences (Wiszniewski *et al.* 2009) or differences in cultural behavior (Mann *et al.* 2012). Overall, this apparent division of the population into two social units which correspond to area use within the study site is an important finding for management of the population as a whole.

Conclusions

The purpose of this study was to describe and analyze the social structure of wild bottlenose dolphins in the Shannon Estuary, Ireland, with the inclusion of additional data on sex, age, and area class for individual dolphins. Social analysis of the whole population revealed groups of mixed composition and variation in association measures across individuals. There is strong evidence that associations between bottlenose dolphins in the Shannon Estuary are not random and that they persist over time. There is also evidence that association measures are related to behavioral state.

Through the classification of individuals by sex, age, and area, important class-determined associations that were somewhat apparent between sex classes were found, but especially strong for within-age and within-area class relationships. Although the strength of female-male associations could not be absolutely determined, the results suggest that female-male associations persist without decline over periods of more than three years. Social network analyses illustrated the preferences of juveniles to associate with juveniles and adults with adults.

Movements between the inner and outer estuary areas of the study site were quite stable over time but use of the inner estuary was limited to a quarter of the population's individuals exclusively. This inner estuary social unit was further divided into a core group of individuals and another group with associations linking core group members and outer estuary individuals. This division in the social structure with respect to area use has important implications for management. This dolphin population has traditionally been managed as one unit, however this study, mirroring others such as in the Moray Firth, Scotland (Wilson *et al.* 2004, Lusseau *et al.* 2006), shows that it may be appropriate to consider the dynamics of the population's social structure in terms of area use when defining management guidelines, especially when the inner estuary is used by such a small (and therefore potentially vulnerable) number of individuals.

This study increases our knowledge of bottlenose dolphin social structure and could be used for comparative studies, to explore similarities and differences in bottlenose dolphin population dynamics. It is unique in its coverage of a moderately sized bottlenose dolphin population in Europe with considerable data on individual sex and age. The results presented have demonstrated the importance of investigating local social behavior in a species known to show a high degree of behavioral plasticity, and provide additional material for cetacean scientists to better understand bottlenose dolphin societies in all their variety. Furthermore, an understanding of the social structure of this population, especially because of its presence within a Special Area of Conservation designated for the species (NPWS 2012), is critical. The findings of this research will contribute to the management and conservation of this important dolphin population in Irish waters.

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Conflicts of Interest

The authors wish to declare that there are no conflicts of interest.

LITERATURE CITED

Adams, J. D., T. Speakman, E. Zolman and L. H. Schwacke. 2006. Automating image matching, cataloging, and analysis for photo-identification research. Aquatic Mammals 32:374-384.

Augusto, J. F., P. Rachinas-Lopes and M. E. dos Santos. 2011. Social structure of the declining resident community of common bottlenose dolphins in the Sado Estuary, Portugal. Journal of the Marine Biological Association of the United Kingdom 92:1773-1782.

Baker, I., J. O’Brien, K. McHugh and S. Berrow. *in press*. An ethogram for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. Aquatic Mammals 43.

Barker, J. and S. Berrow. 2016. Temporal and spatial variation in group size of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. Biology and Environment: Proceedings of the Royal Irish Academy 116B:63-70.

Bejder, L., D. Fletcher and S. Bräger. 1998. A method for testing association patterns of social animals. Animal Behaviour 56:719–725.

Berrow, S. and B. Holmes. 1999. Tour boats and dolphins: A note on quantifying the activities of whalewatching boats in the Shannon estuary, Ireland. Journal of Cetacean Research and Management 1:199-204.

Berrow, S., J. O'Brien, L. Groth, A. Foley and K. Voigt. 2012. Abundance estimate of bottlenose dolphins (*Tursiops truncatus*) in the Lower River Shannon candidate Special Area of Conservation, Ireland. Aquatic Mammals 38:136-144.

Berrow, S. D. 2009. Winter distribution of bottle-nosed dolphins (*Tursiops truncatus* (Montagu)) in the inner Shannon Estuary. Irish Naturalists' Journal 30:35-39.

Berrow, S. D., B. Holmes and O. R. Kiely. 1996. Distribution and abundance of bottle-nosed dolphins *Tursiops truncatus* (Montagu) in the Shannon Estuary. Biology and Environment: Proceedings of the Royal Irish Academy 96B:1-9.

Berrow, S. D., B. McHugh, D. Glynn, E. McGovern, K. M. Parsons, R. W. Baird and S. K. Hooker. 2002. Organochlorine concentrations in resident bottlenose dolphins (*Tursiops truncatus*) in the Shannon estuary, Ireland. Marine Pollution Bulletin 44:1296-1313.

Blasi, M. F. and L. Boitani. 2014. Complex social structure of an endangered population of bottlenose dolphins (*Tursiops truncatus*) in the Aeolian Archipelago (Italy). PLoS One 9:e114849.

Cairns, S. J. and S. J. Schwager. 1987. A comparison of association indices. Animal Behaviour 35:1454-1469.

Cantor, M., L. L. Wedekin, P. R. Guimarães, F. G. Daura-Jorge, M. R. Rossi-Santos and P. C. Simões-Lopes. 2012. Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society. Animal Behaviour 84:641-651.

Cantor, M. and H. Whitehead. 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philosophical Transactions of the Royal Society London B Biological Sciences 368:20120340.

Chabanne, D. B. H., H. Finn and L. Bejder. 2017. Identifying the relevant local population for Environmental Impact Assessments of mobile marine fauna. Frontiers in Marine Science 4:148.

Connor, R. C., M. R. Heithaus and L. M. Barre. 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. Proceedings of the Royal Society B Biological Sciences 268:263-267.

Connor, R. C. and M. Krützen. 2015. Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. Animal Behaviour 103:223-235.

Connor, R. C., R. S. Wells, J. Mann and A. J. Read. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. Pages 91-125 *in* J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead eds. *Cetacean Societies.* University of Chicago Press, Chicago.

Croft, D. P., R. James and J. Krause. 2008. Exploring animal social networks. Princeton University Press.

Daura-Jorge, F. G., M. Cantor, S. N. Ingram, D. Lusseau and P. C. Simoes-Lopes. 2012. The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biology Letters 8:702-705.

Ermak, J. 2014. The social structure and mating strategies of bottlenose dolphins (*Tursiops truncatus*) in the St. Johns River. MSc thesis, University of North Florida 82 pp.

Foley, A., D. McGrath, S. Berrow and H. Gerritsen. 2010. Social structure within the bottlenose dolphin (*Tursiops truncatus*) population in the Shannon Estuary, Ireland. Aquatic Mammals 36:372-381.

Gazda, S., S. Iyer, T. Killingback, R. Connor and S. Brault. 2015. The importance of delineating networks by activity type in bottlenose dolphins (*Tursiops truncatus*) in Cedar Key, Florida. Royal Society Open Science 2:140263.

Gero, S., L. Bejder, H. Whitehead, J. Mann and R. C. Connor. 2005. Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp. Canadian Journal of Zoology 83:1566-1573.

Haunhorst, C. B., M. Heesen, J. Ostner and O. Schülke. 2017. Social bonds with males lower the costs of competition for wild female Assamese macaques. Animal Behaviour 125:51-60.

Ingram, S. N. 2000. The ecology and conservation of bottlenose dolphins in the Shannon Estuary, Ireland. Doctoral dissertation, University College Cork, Cork, Ireland 213 pp.

Ingram, S. N. and E. Rogan. 2002. Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. Marine Ecology Progress Series 244:247-255.

Kaplan, J. D. and R. C. Connor. 2007. A preliminary examination of sex differences in tactile interactions among juvenile Atlantic spotted dolphins (*Stenella frontalis*). Marine Mammal Science 23:943-953.

Krutzen, M., J. Mann, M. R. Heithaus, R. C. Connor, L. Bejder and W. B. Sherwin. 2005. Cultural transmission of tool use in bottlenose dolphins. Proceedings of the National Academy of Sciences of the United States of America 102:8939-8943.

Levesque, S., K. Reusch, I. Baker, J. O'Brien and S. Berrow. 2016. Photo-identification of bottlenose dolphins (*Tursiops truncatus*) in Tralee Bay and Brandon Bay, Co. Kerry: A case for SAC boundary extension. Biology and Environment: Proceedings of the Royal Irish Academy 116B:1-10.

Louis, M., F. Gally, C. Barbraud, *et al.* 2015. Social structure and abundance of coastal bottlenose dolphins, *Tursiops truncatus*, in the Normano-Breton Gulf, English Channel. Journal of Mammalogy:1-13.

Louis, M., A. Viricel, T. Lucas, *et al.* 2014. Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. Molecular Ecology 23:857-874.

Lusseau, D. 2003. The emergent properties of a dolphin social network. Proceedings of the Royal Society of London, Series B: Biological Sciences 270 Suppl 2:S186-188.

Lusseau, D. and M. E. Newman. 2004. Identifying the role that animals play in their social networks. Proceedings of the Royal Society of London, Series B: Biological Sciences 271 Suppl 6:S477-481.

Lusseau, D., K. Schneider, O. J. Boisseau, P. Haase, E. Slooten and S. M. Dawson. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Behavioral Ecology and Sociobiology 54:396-405.

Lusseau, D., B. E. N. Wilson, P. S. Hammond, *et al.* 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 75:14-24.

Mann, J. 1999. Behavioral sampling methods for cetaceans: a review and critique. Marine Mammal Science 15:102-122.

Mann, J., M. A. Stanton, E. M. Patterson, E. J. Bienenstock and L. O. Singh. 2012. Social networks reveal cultural behaviour in tool-using dolphins. Nature Communications 3:980.

Maritime Safety Directorate. 2005. Marine Notice No. 15 of 2005. Department of Communications Marine and Natural Resources, Dublin 2 pp.

McHugh, K. A. 2010. Behavioral development of free-ranging juvenile bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Doctoral dissertation, University of California Davis, CA 169 pp.

McHugh, K. A., J. B. Allen, A. A. Barleycorn and R. S. Wells. 2011. Severe *Karenia brevis* red tides influence juvenile bottlenose dolphin (*Tursiops truncatus*) behavior in Sarasota Bay, Florida. Marine Mammal Science 27:622-643.

Mirimin, L., R. Miller, E. Dillane, S. D. Berrow, S. Ingram, T. F. Cross and E. Rogan. 2011. Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters. Animal Conservation 14:342-353.

Moller, L. M., L. B. Beheregaray, R. G. Harcourt and M. Krutzen. 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. Proceedings of the Royal Society of London, Series B: Biological Sciences 268:1941-1947.

Moreno, K. and A. Acevedo-Gutiérrez. 2016. The social structure of Golfo Dulce bottlenose dolphins (*Tursiops truncatus*) and the influence of behavioural state. Royal Society Open Science 3:160010.

NPWS. 2012. Conservation Objectives: Lower River Shannon SAC 002165. Version 1.0. 64 pp.

O’Brien, J., I. Baker, J. Barker, S. Berrow, C. Ryan, M. O’Connell and B. O’Donoghue. 2014. The first confirmed successful refloat of a stranded bottlenose dolphin (*Tursiops truncatus*) in Ireland and subsequent resighting with a neonate. Aquatic Mammals 40:191-194.

O’Brien, J. M., S. D. Berrow, C. Ryan, *et al.* 2009. A note on long-distance matches of bottlenose dolphins (*Tursiops truncatus*) around the Irish coast using photo-identification. Journal of Cetacean Research and Management 11:71-76.

Owen, E. 2003. The reproductive and ecological functions of the pair-bond between allied, adult male bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Doctoral dissertation, University Of California Santa Cruz, CA 326 pp.

Owen, E. C. G., R. S. Wells and S. Hofmann. 2002. Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. Canadian Journal of Zoology 80:2072-2089.

Papale, E., M. Ceraulo, G. Giardino, *et al.* 2017. Association patterns and population dynamics of bottlenose dolphins in the Strait of Sicily (Central Mediterranean Sea): implication for management. Population Ecology 59:55-64.

Parsons, K. M., J. W. Durban, D. E. Claridge, K. C. Balcomb, L. R. Noble and P. M. Thompson. 2003. Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. Animal Behaviour 66:185-194.

Pearson, H. C., T. M. Markowitz, J. S. Weir and B. Würsig. 2016. Dusky dolphin (*Lagenorhynchus obscurus*) social structure characterized by social fluidity and preferred companions. Marine Mammal Science 33:251-276.

Rogers, C. A., B. J. Brunnick, D. L. Herzing and J. D. Baldwin. 2004. The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. Marine Mammal Science 20:688-708.

Ryan, C. and S. Berrow. 2013. An extension to the known home range of Shannon Estuary bottlenose dolphins (*Tursiops truncatus* (Montagu 1821)). Irish Naturalists' Journal 32:77-78.

Samuels, A. 1996. A systematic approach to measuring the social behavior of bottlenose dolphins. Doctoral dissertation, Woods Hole Oceanographic Institution, MA 246 pp.

Sim, T. 2015. Associations or alliances? Comparisons of social relationships between male bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay and the Moray Firth. MSc thesis, Bangor University, Wales 102 pp.

Smith, H., C. Frère, H. Kobryn and L. Bejder. 2016. Dolphin sociality, distribution and calving as important behavioural patterns informing management. Animal Conservation 19:462–471.

Smith, H. C. 2012. Population dynamics and habitat use of bottlenose dolphins (*Tursiops aduncus*), Bunbury, Western Australia. Doctoral dissertation, Murdoch University, Perth, Australia 197 pp.

Smolker, R. A., A. F. Richards, R. C. Connor and J. W. Pepper. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38-69.

Stanton, M. A. and J. Mann. 2012. Early social networks predict survival in wild bottlenose dolphins. PLoS One 7:e47508.

Titcomb, E. M., G. O'Corry-Crowe, E. F. Hartel and M. S. Mazzoil. 2015. Social communities and spatiotemporal dynamics of association patterns in estuarine bottlenose dolphins. Marine Mammal Science 31:1314–1337.

Urian, K. W., S. Hofmann, R. S. Wells and A. J. Read. 2009. Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. Marine Mammal Science 25:619-638.

Wells, R. 1986. Structural aspects of dolphin societies. Doctoral dissertation, University of California Santa Cruz, CA 240 pp.

Wells, R. S. 2014. Social structure and life history of bottlenose dolphins near Sarasota Bay, Florida: insights from four decades and five generations. Pages 149-172 *Primates and Cetaceans.* Springer.

Wells, R. S., K. Pryor and K. S. Norris. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Dolphin societies: discoveries and puzzles:199-225.

Wells, R. S., M. D. Scott and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247-305 *in* H. H. Genoways ed. *Current Mammalogy.* Plenum Press, New York.

Whitehead, H. 2001. Analysis of animal movement using opportunistic individual identifications: application to sperm whales. Ecology 82:1417–1432.

Whitehead, H. 2007. Selection of models of Lagged Identification Rates and Lagged Association Rates using AIC and QAIC. Communications in Statistics - Simulation and Computation 36:1233-1246.

Whitehead, H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. The University of Chicago Press, Chicago and London.

Whitehead, H. 2009. SOCPROG programs: analysing animal social structures. Behavioral Ecology and Sociobiology 63:765-778.

Whitehead, H., L. Bejder and C. Andrea Ottensmeyer. 2005. Testing association patterns: issues arising and extensions. Animal Behaviour 69:e1.

Wilson, B., R. J. Reid, K. Grellier, P. M. Thompson and P. S. Hammond. 2004. Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. Animal Conservation 7:331-338.

Wilson, D. R. B. 1995. The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range. Doctoral dissertation, University of Aberdeen, Scotland 191 pp.

Wiszniewski, J., S. J. Allen and L. M. Möller. 2009. Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. Animal Behaviour 77:1449-1457.

Wiszniewski, J., D. Lusseau and L. M. Möller. 2010. Female bisexual kinship ties maintain social cohesion in a dolphin network. Animal Behaviour 80:895-904.

Würsig, B. and T. A. Jefferson. 1990. Methods of photo-identification for small cetaceans. Report of the International Whaling Commission:23-52.

Würsig, B. and M. Würsig. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science 198:755-756.