Aquatic Mammals 2010, *36*(4), 372-381, DOI 10.1578/AM.36.4.2010.372

Social Structure Within the Bottlenose Dolphin (*Tursiops truncatus*) Population in the Shannon Estuary, Ireland

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Abstract

The Shannon Estuary is home to Ireland's only known resident population of bottlenose dolphins (*Tursiops truncatus*) and is designated as a candidate Special Area of Conservation (cSAC) for this species. Proper conservation management of these dolphins requires an understanding of the social structure of this population. Four years of photo-identification data (2005 to 2009, excluding 2007) were used to construct sociograms that complement a cluster analysis of individually marked dolphins and their associates. The results found little evidence of social stability or group fidelity for this study's dolphin population. Analysis of dolphins observed in consecutive years showed that the probability of group members encountering an individual dolphin in the second year did not depart from a random model. The social parameters for this resident population seem to be typical for this species. Bottlenose dolphins are found to exhibit a highly fluid, dynamic social structure within which individuals change their composition and associates regularly. These dolphins in the Shannon Estuary appear to live in a fission-fusion based society.

Key Words: Shannon Estuary, social structure, fission-fusion, inter-annual fidelity, bottlenose dolphins, *Tursiops truncatus*

Introduction

Bottlenose dolphins (*Tursiops truncatus* [Montagu, 1821]) are one of 24 species of cetaceans recorded in Irish waters (Berrow, 2001; O'Brien et al., 2009a). Bottlenose dolphins inhabit most warm, tropical, and temperate waters, adapting to a variety of marine and estuarine habitats (Perrin et al., 2009). In Ireland, bottlenose dolphins are protected under the Wildlife Act (1976 and Amendment 2000) and are listed under Annex II of the European Union Habitats Directive which entitles them, and their habitat, to strict protection. The Directive requires Member States to designate Special Areas of Conservation (SACs) for bottlenose dolphins that correspond to their ecological requirements.

Many marine mammal species are naturally divided into groups that occupy distinct geographical regions and habitat niches within each species' overall range (Kerosky et al., 2008). Cetaceans as a whole display a wide variety of complex groupings and social structures. Some species are largely solitary, living alone or in small groups, like humpback whales (*Megaptera novaeangliae*) (Clapham, 2008). Others, such as spinner dolphins (*Stenella longirostris*), appear to be dependent on large, socially cohesive groups for survival (Karczmarski et al., 2005). Sperm whales (*Physeter macrocephalus*) tend to live in extended family groups with long-term relationships between individuals (Whitehead et al., 1991).

A number of cetacean species live in social groups that vary in composition on an hourly or daily basis. This type of structure is known as a *fission-fusion* society (Mann et al., 2000). Fission-fusion societies are fluid and dynamic whereby groups of cetaceans change their associates regularly. This fission-fusion type of social structure facilitates important life learning abilities such as feeding, reproduction, defence, and communication (Bräger et al., 1994). Social structure of this kind can be seen in the dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand (Pearson, 2009); bottlenose whales (*Hyperoodon ampullatus*) in Nova Scotia, Canada (Gowans et al., 2001); bottlenose dolphins in Shark Bay, Australia (Connor, 2007); and the bottlenose dolphin population in the Moray Firth, Scotland (Eisfield & Robinson, 2004). Lusseau et al. (2003) found that the resident group of bottlenose dolphins in the Doubtful Sound in New Zealand resided in a fission-fusion society but showed a high degree of social stability, which is largely unprecedented in comparison to other populations of this species.

Social structure can be assessed using photo-identification techniques (Würsig & Jefferson, 1990). Long-term photo-identification studies can be used as a tool to provide insight into population parameters such as life habitats, movements, and associations.

The Shannon Estuary is home to Ireland's only known group of resident bottlenose dolphins (Berrow et al., 1996), and it is the only designated candidate SAC (cSAC) for this species in Ireland. The group size is estimated at 120 to 140 individual dolphins in the estuary (Ingram, 2000; Englund et al., 2008), with ongoing research since 1993 suggesting that individuals are resident year-round and that the estuary is a calving area (Berrow et al., 1996; Ingram, 2000). In an unpublished report, Rogan et al. (2000) described the social structure of the Shannon dolphins as "fluid and gregarious, with numerous weak alliances between individuals." Little is known worldwide about the social organisation of this species which occupies open estuarine systems (Quintana-Rizzo & Wells, 2001) such as the Shannon. Photo-identification data have been collected by the Shannon Dolphin and Wildlife Foundation (SDWF) since 1993 (Berrow et al., 1996).

The aim of this study was to examine photo-identification data to assess the social structure of the Shannon Estuary dolphins. In particular, this present study set out to investigate whether these dolphins resided in a typical fission-fusion society. Information on social structure is important for the conservation management of this species in the Lower River Shannon cSAC.

Materials and Methods

Study Area

The River Shannon is the longest waterway in Ireland at 240 km in length. The river rises in the "Shannon pot," a karst in County Cavan (Gunn, 1995) and reaches the Atlantic Ocean on Ireland's west coast at 52° N and 10° W. This 75-km tidal salt wedge estuary has been long regarded as one of the most important Atlantic salmon (*Salmo salar)* rivers in Ireland. The Shannon Estuary is a major shipping route, with 10 million tonnes of traffic per year. The estuary is narrow and steep sided from Foynes to Kilrush, beyond which it broadens out and extensive mud flats are visible at low tide (Rogan et al., 2000).

Data Collection Protocols

Photo-identification (Photo ID) was conducted as part of an ongoing dolphin tour boat monitoring programme. Tour boats operated from two ports, Kilrush and Carrigaholt in County Clare, watching dolphins in different parts of the estuary. Kilrush-based vessels generally operate in the inner and middle estuary, while Carrigaholt vessels operate in the outer and middle estuary (Berrow & Holmes, 1999). Photo ID was also conducted during dedicated surveys along pre-determined track lines using a Rigid Inflatable Boat (RIB) (6 m). The use of tour boats and RIBs ensured that the data were not spatially constrained during each survey year. Data from 2005, 2006, 2008, and 2009 survey seasons (April to October in all years) followed protocols detailed in Berrow et al. (2005), Berrow & Atkinson (2006), and Berrow & Ryan (2008, 2009). These data were extracted from the *Shannon Dolphin Photo ID Catalogue* hosted by the SDWF, and photos were gathered by a variety of researchers over the 4 y with the same protocols used for data collection. In the years 2005, 2006, 2008, and 2009, there were 22, 63, 32, and 39 trips per year, respectively. Effort in hours was not recorded.

A Canon EOS D20 camera with a Canon EF 70-200 F USM lens × 2 converter was used for photo ID, and *Photoshop Elements 2000*© was used to crop and resize images. Photographs of each individual dolphin's dorsal fin were recorded and assigned a unique identification number. Resightings and photo matching of these marked individuals and their associates have been underway since 1993. The use of the word *marked* refers to individual dolphins that have identifiable markings on their body, mainly their dorsal fins. Gender was not determined for any individual sighted during this study.

The data were managed to suit the needs of the software programme, *SOCPROG 2.4* (Whitehead, 2009), for association analysis (i.e., the data had to be organised so that a location and all known associations for each dolphin in the catalogue were displayed on one spreadsheet). Locations were assigned based on the area in which the dolphins were observed during trips; a general location (outer, middle, or inner estuary) was assigned based on where individual dolphins were documented. Details were error checked to ensure no duplicate data were entered by referring to the original data sheets.

The data were then entered into the software programme for the association analysis. The Cophenetic Correlation Coefficient (CPCC) was used to determine what type of cluster analysis was most suited to these data. The CPCC is defined as the linear correlation between the cophenetic distances obtained from a dendrogram and the original distances (dissimilarities) used to construct the dendrogram. It is a measure of how faithfully the dendrogram represents the dissimilarities among observations or data (Romesburg, 2004). The highest P-values obtained for this coefficient were obtained from Hierarchical Cluster Analysis, which was used for this study as the majority of

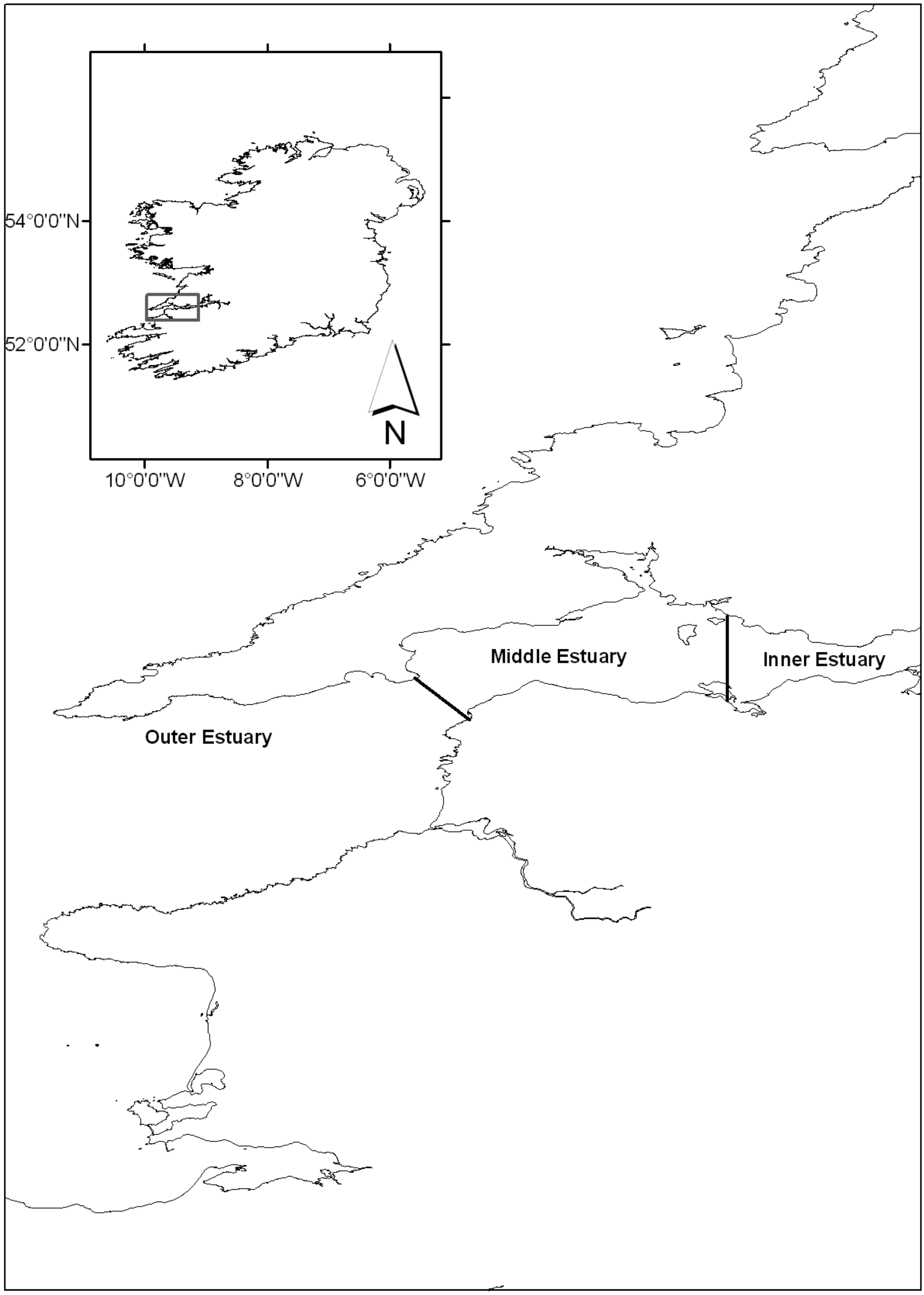

Figure 1. Map of the Shannon Estuary with key areas defined

the values were above 0.8 correlation, which is the recommended level of correlation for this type of analysis (Whitehead, 2009). The Half Weight Index (HWI) was chosen as the most appropriate for this data because it accounts for not every member of the group being identified. The HWI estimates the proportion of time that particular individuals are present in the same social group (Cairns & Schwager, 1987). Sociograms were used to assess the strength of association between individuals seen in any one year (McSweeney et al., 2008).

To assess inter-annual fidelity between individuals, each marked dolphin along with other identified dolphins with which it was sighted was tabulated by year. The number of dolphins with which each dolphin was sighted in two consecutive years was used to test the null hypothesis that they associate with other dolphins at random. If this were the case, the probability of a dolphin associating with the same dolphin in consecutive years was given by the hyper-geometric distribution (Zar, 1999):

$$P(X) = \frac{\binom{N_1}{X}\binom{N_T - N_1}{N_2 - X}}{\binom{N_T}{N_2}}$$

Where N_1 is the number of dolphins sighted with a certain dolphin in year 1, N_2 is the number in year 2, N_T is the total number of marked dolphins in the population, and X is the number sighted in both years. N_T was estimated to be 80 in all years (Ingram & Rogan, 2003; Englund et al., 2007, 2008). The expected number of dolphins sighted in both years is given by

$$\overline{X} = \frac{N_1 N_2}{N_T}$$

Results

The total number of individual dolphins recorded and identified in this study differed by year. This ranged from 37 to 50 identified individuals with an overall mean of 45 marked dolphins encountered each year. Sociograms are presented by year (Figure 2). The CPCC values represent the strength of the association analysis performed on the data (Table 1).

Sociograms and dendrograms facilitated a presentation of individual association data such that it was possible to assess the social structure of dolphins identified during each year of study (Figures 2 & 3). In the sociograms, individual dolphins are represented by numbers around the perimeter of the diagram. The thickness of the adjoining lines within the diagram represents the strength of associations between individuals in that year. In applying the variable stopping rule at 0.4 HWI in the dendrograms (Rogan et al., 2000; Dinneen, pers. comm., 23 May 2010), there is a rapid agglomeration of observed dyads and triads from which it becomes impossible to distinguish separate groups. The sociograms and dendrograms show only small groups, mainly dyads and triads. There is no evidence for the existence of large groups or clusters of individuals forming a significant level of organisation.

However, it is clear that some dolphins show association with many individuals (Figures 2 & 3)—for example, dolphin number 42 in 2005 was seen with dolphins 97, 18, 52, 59, 7, 96, 126 158, 166, 183, 181, 13, and 31. Also, dolphin 126 was seen with many individuals in 2008. Some dolphins were seen with just one other (e.g., dolphin numbers 84 and 148). Yet, some dolphins never met at all—dolphins 117 and 197 and dolphins 24 and 21 (Figure 2; sociogram for 2006). However, in the dendrogram for 2009, several dolphins are grouped at the base of the association index. This suggests that these dolphins where never seen apart in this year. It must be noted that the sociogram and dendrogram for 2006 have more associations than the other years due to the higher degree of sampling effort during this year.

This analysis of social structure indicates that fidelity and companionship between individual dolphins and other members of the population is low. The frequency of association of marked dolphins seen together in consecutive years is shown in Table 2 along with the expected frequency from the random model.

Table 1. The number of trips that took place during each year of study

Year	Number of trips
2005	22
2006	63
2008	32
2009	39

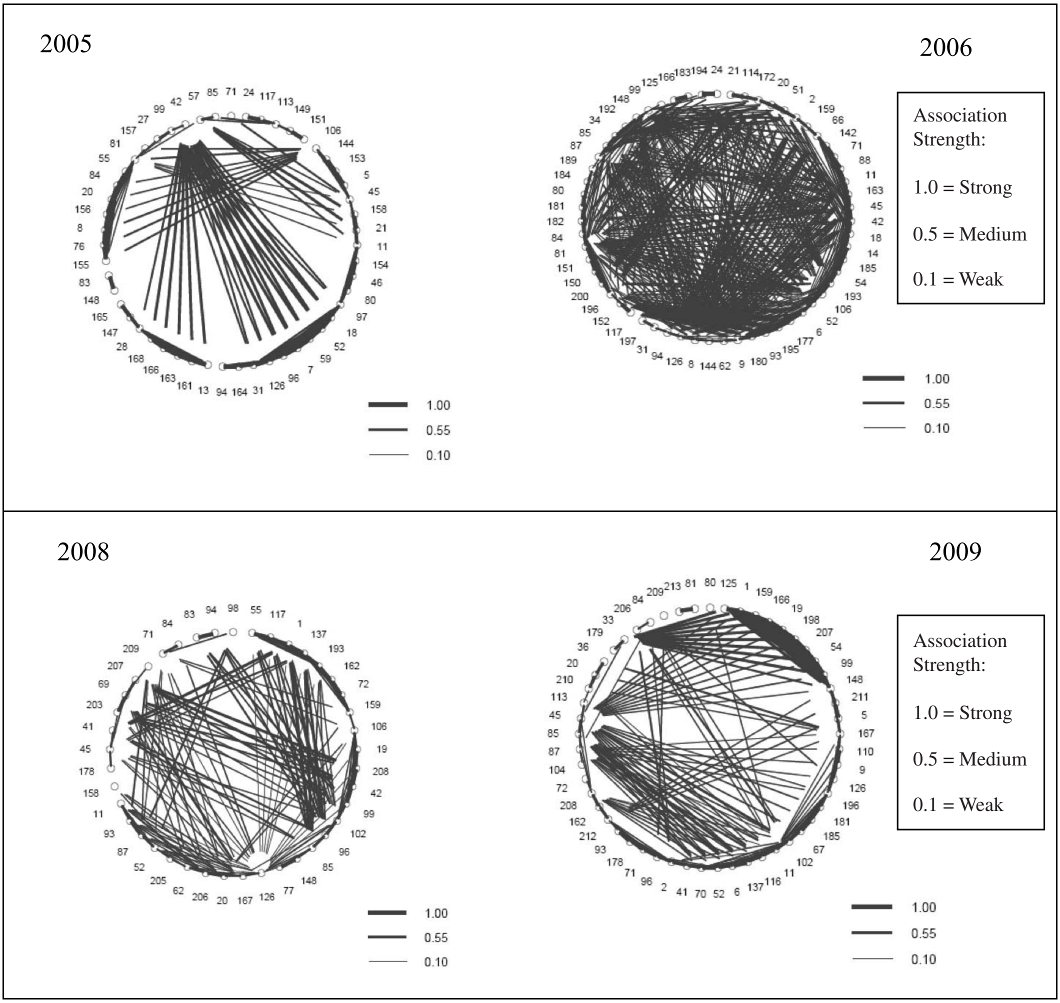

Figure 2. Sociograms for associations between bottlenose dolphins in the Shannon Estuary in each year of the study

The mean number of dolphins with which each dolphin was sighted varied between years from less than six (2005) to 19 (2006). This may reflect differences in sampling intensity. The numbers of identified dolphins that were present in the same social groups between consecutive years varied between 0 and 3, which agreed well with the number that was expected if they associate at random (Table 2). The probability of each outcome is also given in Table 2. Only one of the 30 P-values given in this table was less than 0.05, which may be expected by chance. The average number shared between consecutive years was 1.1 for 2005-2006 and 0.7 for 2008-2009, which was slightly lower than the average expected numbers: 1.4 for 2005-2006 and 0.9 for 2008-2009. This indicates fewer dolphins associated in consecutive years than expected by chance.

Table 2. Cophenetic Correlation Coefficient for years 2005, 2006, 2008, and 2009

Year	CPCC
2005	0.87
2006	0.74
2008	0.81
2009	0.88

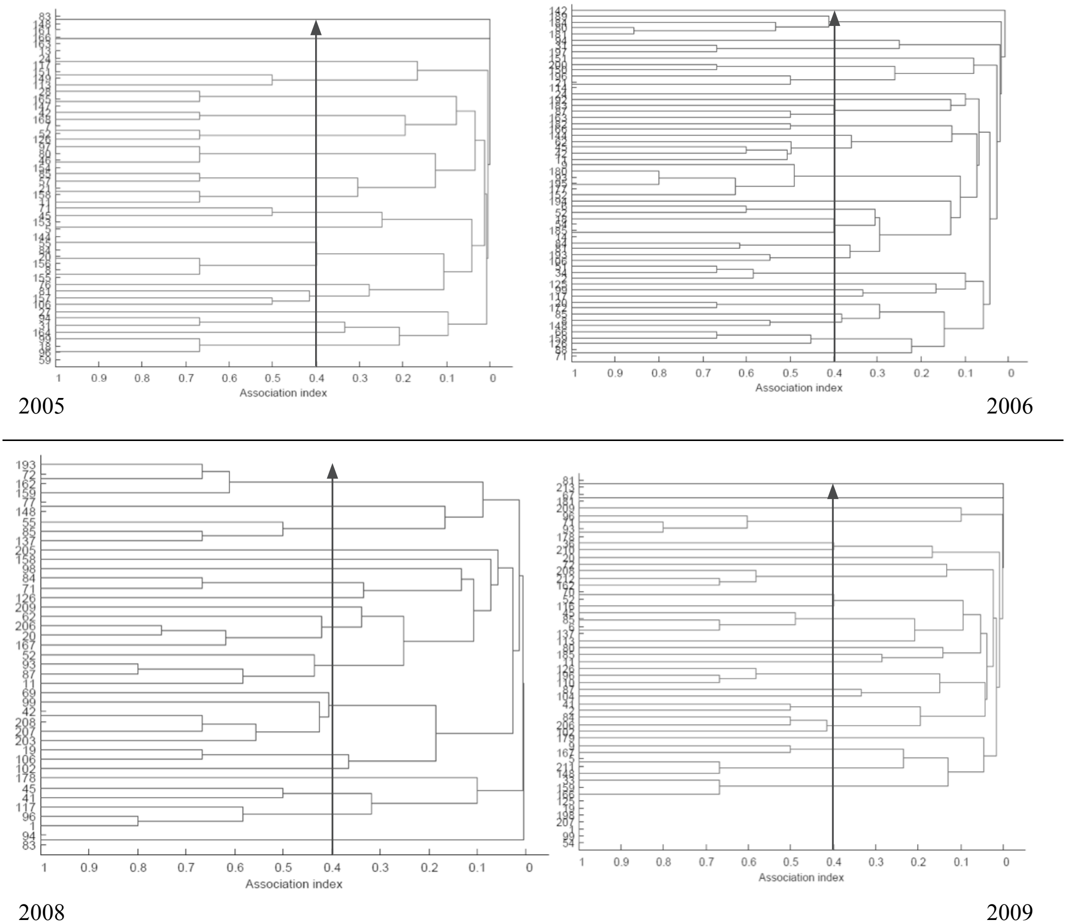

Figure 3. Dendrograms of bottlenose dolphins in the Shannon Estuary using hierarchical cluster analysis, with average linkage and the Half Weight Index for association of each year of study

In order to test the sensitivity of the results to the estimate of the total number of marked dolphins in the population (N_T), the expected average number shared between consecutive years was estimated for a range of N_T (Figure 4). The estimate of the average expected number of dolphins that meet in consecutive years depends on the estimate of the total number of marked dolphins. The average observed numbers are shown as horizontal lines; if these lines are above the curves, the observed number is higher than the expected, which indicates that no positive association exists. The figure suggests that N_T needs to be larger than around 100 before the observed number of dolphins shared between consecutive years is higher than the expected number, which would indicate that the dolphins do not associate at random but form long-term alliances.

Discussion

During the 4 y of study, survey work was not restricted to any one part of the estuary. Therefore, the results are not constrained spatially. There is strong evidence that the Shannon Estuary dolphin population is a closed population. O'Brien et al. (2009b) failed to match any dolphin from the Shannon Estuary to any other part of Ireland despite numerous matches of individual dolphins between coastal sites outside of the Shannon. There is also evidence of genetic discreteness in the Shannon Estuary population when compared to dolphins from other coastal sites (Mirimin et al., in press). This information suggests that this dolphin population may have been closed for some considerable period.

The estimated abundance of dolphins in the Shannon Estuary is thought to be 130 (120 to 140), with an estimated 60% of this population

Table 3. For each marked dolphin, the number of other marked dolphins that it associated with during 2005-2006 and 2008-2009 (N_1 and N_2) as well as the number shared between both years (X) and the expected number shared between both years if they mix at random ($\bar{X}$); $P(X)$ is the probability that the number shared occurred assuming a hyper-geometric distribution.

Dolphin ID	2005 (N_1)	2006 (N_2)	Shared (X)	Expected ($\bar{X}$)	$P(X)$
126	6	27	2	2.0	0.34
42	5	23	1	1.4	0.38
99	6	28	2	2.1	0.34
85	2	32	0	0.8	0.36
52	3	21	1	0.8	0.44
18	4	15	0	0.8	0.43
21	5	6	0	0.4	0.67
144	4	18	1	0.9	0.43
71	1	7	0	0.1	0.91
85	2	26	0	0.7	0.45
20	4	6	1	0.3	0.25
31	6	7	1	0.5	0.35
106	8	29	3	2.9	0.30
81	16	33	3	6.6	0.03
11	12	7	1	1.1	0.41
Mean	5.6	19.0	1.1	1.4	

Dolphin ID	2008 (N_1)	2009 (N_2)	Shared (X)	Expected ($\bar{X}$)	$P(X)$
52	11	4	0	0.6	0.55
45	7	22	1	1.9	0.28
102	11	10	1	1.4	0.38
1	4	11	1	0.6	0.36
19	4	11	0	0.6	0.55
11	7	14	1	1.2	0.40
20	13	2	1	0.3	0.28
206	10	3	0	0.4	0.67
167	15	7	1	1.3	0.39
126	19	6	2	1.4	0.30
99	7	12	1	1.1	0.41
85	7	12	2	1.1	0.22
93	9	3	0	0.3	0.70
208	9	9	0	1.0	0.32
159	6	9	0	0.7	0.48
Mean	9.3	9.0	0.7	0.9	

being marked (Englund et al., 2008). The 45 dolphins used on average per year during this present study represents 60% of the marked population of dolphins within the Shannon Estuary. However, this also assumes that the behaviour of marked animals is typical of the entire population.

Some dolphins were observed with many other identified dolphins during the study period. For example, dolphin number 85 encountered 33 other marked dolphins in 2006. The total number of marked dolphins seen in 2006 was 61 (Keana, 2010). Thus, dolphin number 85 met approximately 50% of the marked population seen during the survey season. The same can be said for dolphin 126. It also met approximately 50% of the marked population in 2008 (Keana, 2010). The level of encounters of marked individuals with other marked individuals, along with the lack of inter-annual fidelity, supports the hypothesis that the social structure of the Shannon Estuary dolphins is dynamic and fluid, with little or no long-term companionship or fidelity between individuals.

Results from the sociograms and dendrograms showed similar association patterns. None of the figures showed evidence of a clear structure in social organisation in any year. However, with this said, the 2009 dendrogram (Figure 3) did show several dolphins that were never seen apart in this particular year.

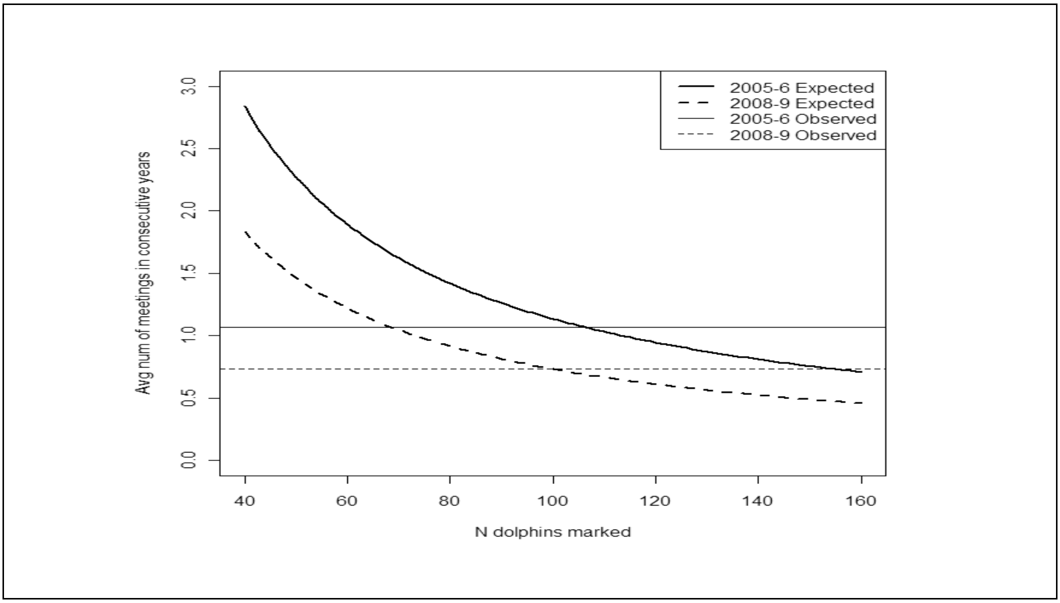

Figure 4. The observed and expected results for the average number of marked dolphin meetings in consecutive years in relation to the estimated population size of marked dolphins in the estuary

A study carried out on killer whales (*Orcinus orca*) (Tosh et al., 2008) using similar sociograms found that the social structure in the subantarctic Marion Island population was largely dominated by three females. Eisfield & Robinson (2004) used sociograms on the southern Outer Moray Firth (Scotland) bottlenose dolphin population and obtained similar results to this present study. Their results showed no clear division in the community or no clear architecture of groups except for dyads, triads, and their multiple networks. Lusseau et al. (2003) found that the bottlenose dolphin population in the Doubtful Sound in New Zealand demonstrated a unique fission-fusion social structure as long-lasting associations were a strong feature of the community, unlike results found from other studies carried out on this species.

Rogan et al. (2000) applied cluster analysis without using sociograms to assess social structure in their study of the Shannon Estuary dolphins. They sampled the zones described in this present study, but for their cluster analysis they used 39 dolphins that occurred more than four times during their study period, which was 1 y. The present study's more robust data set confirms the suggestion by Rogan et al. of a highly fluid and dynamic population of dolphins in the Shannon Estuary.

In the analysis for testing the encounter rate of randomly picked individual dolphins, the data for 2005-2006 and 2008-2009 supports the null hypothesis that the probability of a dolphin associating with the same dolphin in consecutive years follows a hyper-geometric distribution. This indicates that the dolphins associate at random and that it is unlikely that strong long-term alliances exist, adding further support to the fission-fusion nature of the social structure of these animals in the Shannon Estuary. The number of marked dolphins in the estuary is not accurately known. The sensitivity analysis suggests that the hypothesis of random association is valid up to a total of ~100 marked individuals. The total number of bottlenose dolphins in the estuary has been estimated at about 130 individuals, and not all dolphins are marked. A maximum of 80 marked animals has been reported by Englund et al. (2008), and this is supported by observations of marked animals making up approximately 60% of the population. Thus, it is unlikely that the marked number exceeds 100 individuals.

To conclude, it was found that bottlenose dolphins identified in the years 2005 through 2009 (excluding 2007) did not exhibit any signs of group fidelity or social stability that has been documented in other dolphin species (e.g., spinner dolphins [Karczmarski et al., 2005], Indo-Pacific bottlenose dolphins [*Tursiops aduncus*; Wiszniewski et al., 2009], and Risso's dolphins [*Grampus griseus*; Hartman et al., 2008]). It must be noted that mother/calf pairs of bottlenose dolphins living in a fission-fusion society will have an extended long-term association as calves are known to stay with their mothers for up to 8 y after birth (Greiller et al., 2003). However, the nature of the study carried out on the Shannon Estuary dolphins, which depends on the existence of clearly marked individuals, would not record these associations between nonmarked individuals such as mothers with unmarked calves or juveniles. Also, should there be gender bias in marking frequency, this technique may also fail to identify long-term associations as sex was not confirmed during this present study. The behaviour engaged in by marked animals may be seasonally dependant as survey trips and photo-identification only took place between April and October in this study. Therefore, it is not known if social structure differs in winter months as there are no data for this season.

Nevertheless, this study shows that the Shannon Estuary dolphins demonstrated a fluid and dynamic social structure with many loose aggregations between individuals. These dolphins appear to be typical of their species, exhibiting a highly social and rapidly changing fission-fusion society. The bottlenose dolphin population in the Shannon Estuary is one large population and should be considered as such in future management plans and conservation efforts.

Acknowledgments

We thank the National Parks and Wildlife Service for the continuous funding of tour boat-based photo-identification studies in the Shannon Estuary; and Geoff and Sue Magee and Gerald, Geraldine, and Paul Griffin for their hospitality on the tour boats. We also thank the researchers who collected these data over the years, especially Andrew Young, Janelle Atkinson, and Conor Ryan; and Dr. Ian O'Connor for all his help throughout.

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