

# Marine aquaculture and bottlenose dolphins' (*Tursiops truncatus*) social structure

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**Abstract** In this study, we investigate association patterns of 249 bottlenose dolphin feeding groups off Sardinia Island (Italy) from January 2000–May 2007 and describe how their association behaviour is related to their response to food patches created by a marine fin fish farm. We also tested the hypothesis that dolphins have different social structures with different feeding activities: Associations should decrease during opportunistic feeding behaviours as it is easier to capture prey, and cooperation is not as necessary. Sixteen individually identified bottlenose dolphins were observed participating in both opportunistic and not opportunistic feeding activities, with a mean of  $30 \pm 8$  times and  $9.6 \pm 1$  times, respectively. Bottlenose dolphins show non-random social behaviour during feeding and this behaviour differs depending on their specific foraging activity. Dolphin associations during feeding can be divided into three categories: acquaintances, affiliates, and feeding associates. Association behaviour during fish farm feeding is consistent with our hypothesis that during opportunistic behaviours, benefits from cooperation decrease, as it is easier to capture prey. Group size homogeneity in both feeding activities demonstrates that the number of dolphins engaging in foraging is not necessarily related with cooperation levels. Moreover, an adult dolphin may prefer to associate with a specific individual, independent of the

sex, who shares the same foraging priorities. This study is the first to show how aquaculture is not only directly affecting marine predators but could also indirectly affect their social structure and behaviour.

**Keywords** Social structure · Fission-fusion societies · Aquaculture · Bottlenose dolphins · *Tursiops truncatus*

## Introduction

The study of animal social structures defines an important class of ecological relationships between animals and their nearby conspecifics (Whitehead 1997). Ecological restrictions, by impacting both mating systems and population structure, are formative factors in the evolution of social systems (Clutton-Brock and Harvey 1977). In combination with their genetic underpinnings, the type and structure of individual-based interactions relates to the abundance and distribution of food or predation (Wrangham 1982).

A variety of studies have revealed the structure of social networks in particular mammal communities: Indian Ocean bottlenose dolphins (*Tursiops aduncus*; Connor et al. 2000; Lusseau 2003), African elephants (*Loxodonta africana*; McComb et al. 2001) and chimpanzees (*Pan troglodytes*; Mitani et al. 2002). Using Hinde's (1976) framework for the study of social behaviour based on the type and patterning of dyadic relationships, recent studies have used association indexes to assess the social properties of populations (Cairns and Schwager 1987; Whitehead 1995). The objectives of studies using these methods are to test if the animals have preferred or avoided associates (Myers 1983, Kerth and König 1999; Whitehead and Dufault 1999; Lusseau et al. 2003; Gero et al. 2005; Wittemyer et al. 2005). Additionally, the study of animal

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social behaviour can offer significant insights into the social dynamics of animal populations and possibly propose new management approaches (Anthony and Blumstein 2000).

Common bottlenose dolphins, *Tursiops truncatus* (Montagu 1821), live in fission–fusion societies within which individuals associate in small groups that change in composition, often on a daily or hourly basis (Connor et al. 2000). Fission–fusion societies limit the effect of within-unit competition through unit splits during periods of high competition (Dunbar 1992), and they enhance cooperative effects through unit cohesion when the ecological costs of aggregating are low or benefits of sociality are high (Takahata et al. 1994; van Schaik 1999). Human activities can influence the distribution of food resources, which may promote the evolution of social organizations as a response to fluctuations in the costs of feeding competition (Altmann 1974).

Fission–fusion societies present a good opportunity to examine the costs and benefits of association in dolphin populations affected by human use of coastal waters, especially by fisheries activities and habitat modification (Beddington et al. 1985; Fertl and Leatherwood 1997; Diaz Lopez 2006b).

Marine aquaculture is an important industry that continues to grow more rapidly than all other animal food-producing sectors, with an average annual growth rate for the world of 8.8% per year since 1970, compared with only 1.2% for capture fisheries and 2.8% for terrestrial farmed meat production systems (FAO 2007). Coastal sea-cage fin fish farms have been introduced into an environment that has a natural complement of fish eating predators. Therefore, a science-based response to the conservation problems created by interactions between marine fish farms and dolphins depends critically on accurate knowledge of the impacts caused by the interactions (Díaz López and Shirai 2007). The literature to date has focused on how aquaculture influences dolphin distribution (Wursig and Gailey 2002; Watson-Capps and Mann 2005; Díaz López et al. 2005; Díaz López and Shirai 2007; Ribeiro et al. 2007) and behaviour (Díaz López 2006a), but there is a lack of information on how the dolphins' social structure can be influenced by this activity.

This study focuses on the north-eastern coast of Sardinia Island (Italy) where fin fish aquaculture has been linked with direct and indirect changes in the behaviour of bottlenose dolphins (Díaz López 2006a; Díaz López et al. 2005). A total of 32 photo-identified adult bottlenose dolphins were primarily observed hunting both schooling and solitary prey onshore and around the fish farm area, using cooperative and individual feeding strategies (Díaz López and Shirai 2007). Previous studies, Díaz López (2006a), have shown that aquaculture provides a reliable food source for dolphins through the provision of usually unobtainable prey. Bottlenose dolphins were built up

around the marine fin fish farm as it provides an abundant source of food (Díaz López and Shirai 2007). This opportunistic feeding strategy is comparable with the strategies used in association with trawlers and gillnets, which allows for an increased rate of feeding while decreasing the energy expenditure necessary for foraging (Fertl and Leatherwood 1997; Díaz López 2006a, b).

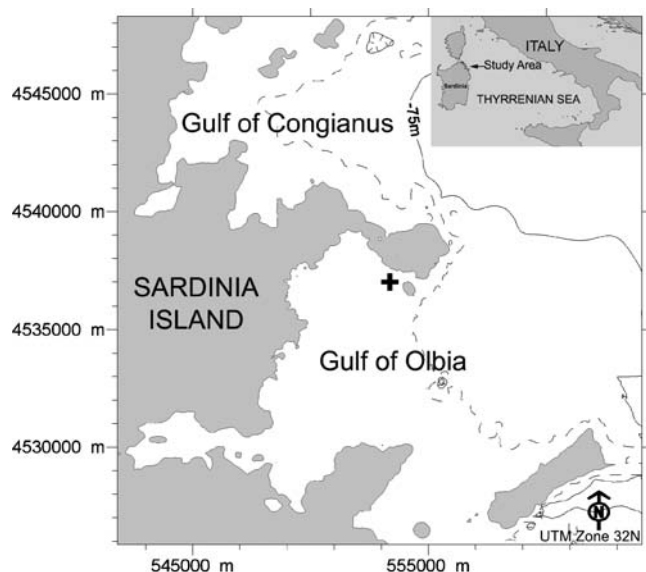
Individual-based studies focusing explicitly the variability of social unit structure in relation to anthropogenic factors are few. In this paper, we describe the patterns of association of bottlenose dolphins on the north-eastern coast of Sardinia and describe the way in which their association behaviour is related to the way they respond to food patches created by a coastal sea-cage fin fish farm.

We were also interested in testing the hypothesis that dolphins will have different social structures with different feeding activities: associations should decrease during opportunistic feeding behaviours around the fish farm area as it is easier to capture prey and cooperation is not as necessary. Any advantage of cooperation is outweighed by the increased competition among group members. Although these data are only from one study site, it is possible to extrapolate to other areas where anthropogenic concentrations of food facilitate bottlenose dolphin opportunistic feeding activities.

## Materials and methods

### Field methods

We used group composition and behavioural data collected from 577 sightings in 474 days at sea between January 2000



**Fig. 1** Map of the north-eastern coast of Sardinia, showing with a cross the location of the marine fin fish farm

and May 2007, with the exception of 2003. On average, we spent 7 months per year conducting observations.

These data were collected as a part of the ongoing long-term study on the north-eastern coast of Sardinia, Italy (Fig. 1). The boundaries of the study area were Salina (40° 55'N) in the south, and Punta Volpe (41°02'N) in the north, and the offshore extent was the 75 m isobath.

Randomization of the surveys was attempted to equally cover all parts of the study area over the course of the study, although the geographic distribution of effort could vary according to weather conditions.

During this study, we distinguish the term group as one or more dolphins observed in the visual area, usually involved in the same activity, following Díaz López (2006b), allowing for the detection of long term associations. A survey was completed for each group of dolphins that was sighted during daylight hours. The group size and age categories were assessed visually in situ, and the data were later verified with photographs and videos taken during each sighting.

Composition of a group was determined by standard photo-identification techniques following Würsig and Jefferson (1990). Attempts were made to photograph the dorsal fins of all animals in a group with four pictures taken for each individual estimated to be in the group (excluding unmarked animals). Only good quality photographs (in focus, unobscured, with the dorsal fin perpendicular to the plane of the photograph and with the dorsal fin large enough to identify small notches) were used in the analyses. Individual dolphins were identified from photographs based primarily on the size, location and pattern of notches on the trailing edge of the dorsal fin and on the back, directly behind the dorsal fin. Individuals without dorsal fin or back notches were excluded from the social analysis to minimise the bias of confusion.

Underwater observations aided in identification and sex determination. Sex was determined by direct observation of the genital region. Males were identified by a gap between the uro-genital slit and the anus, lack of mammary slits, or observation of an erection. Females were identified by observation of mammary slits.

Behavioural data were collected using focal group continuous sampling (Mann 1999). The definition and duration of each behavioural category was attempted *a posteriori* following data analysis strictly based on objective, non-discrete parameters, including specifically observed behavioural events, area, dive duration, swimming direction and speed, contact among individual dolphins and other variables (Díaz López 2006b).

## Analyses

Bottlenose dolphin groups were only included in the social analyses if the predominant behavioural state was feeding.

Of those data, only individuals sighted more than ten times were considered for the analyses to reduce inaccuracies and biases associated with small sample sizes. Unidentified animals and calves were excluded from the analyses. Calves were excluded because of their unique dependent relationship with their mothers (Mann and Smuts 1999).

We stratified the foraging groups into two exclusive categories: (1) when the dolphins were engaged in feeding in the fish farm (opportunistic feeding; Díaz López 2006a), (2) when the dolphins were engaged in feeding activities onshore (not opportunistic feeding activities).

The animals photographed in the same foraging group were considered associated. We used the half-weight index (HWI) as a measure of association, as it accounts best for observer biases inherent in photo-identification techniques (Cairns and Schwager 1987; following Smolker et al. 1992). This index results in values ranging from zero to one, with zero representing two animals never seen together, and one representing two animals never seen apart.

We pooled the feeding groups into both feeding categories (opportunistic foraging and not opportunistic foraging) and calculated the HWI for each dyad under each feeding category, as well as over all encounters.

Following Whitehead (1997), we plotted the HWI in the different feeding categories for each dyad against each other to determine whether strength of association differed between both feeding behavioural categories.

We used a permutation test, as in Bejder et al. (1998), with modifications, as in Whitehead et al. (2005), to test for non-random associations in each of the feeding activities and for all data combined against the null hypotheses that dolphins associate randomly with one another. The observed association matrix was randomized 3,000 times with 100 flips per permutation for each analysis. The resulting *p* values of permutations were not considered a formal statistical threshold but rather as indicating the strength of evidence of non-random associations; and thus, a Bonferroni adjustment was not required (Gero et al. 2005). Associations were permuted within daily sampling intervals to remove

**Table 1** Mean number of times an individual bottlenose dolphin was sighted engaged in feeding activities. Data are presented as mean ± standard error

Sex class	Pooled data	Opportunistic feeding	Not opportunistic feeding
Males ( <i>n</i> =7)	54.8±18	44.4±15	10.5±3
Females ( <i>n</i> =7)	32.5±9	25.1±8	7.5±1
Unsexed ( <i>n</i> =2)	11±1	5	6±2
Total	39.6±9	31±8	8.6±1

**Table 2** Observed and random mean and standard deviation (SD) of half-weight indexes (HWIs) across the two feeding categories and pooled across feeding behavioural categories

Feeding category	Mean (SD) of observed HWI mean	Mean (SD) of randomized HWI mean	<i>P</i> values
Opportunistic feeding	0.11 (0.13)	0.00003 (0.00003)	< 0.0001
Not opportunistic feeding	0.14 (0.15)	0.00005 (0.00004)	< 0.0001
Pooled data	0.13 (0.13)	0.00003 (0.00003)	< 0.0001

The statistical significance of these was tested by means of a Monte Carlo test using 3,000 random permutations with 100 flips per permutation for each analysis.

possible demographic effects (i.e. mortality, recruitment, or migration to or from the study area; Whitehead 1999).

We identified a dyad as having a preferred association when their association index was twice the mean index, including zero values (as in Durrell et al. 2004). This arbitrary threshold value was chosen because it is approximately twice the expected value if associations were completely random.

A total of three separate hypothesis matrices were formed, one for each combination of sex (male–male, male–female, female–female) classes in which a “1” was scored for each dyad with the combination of sex classes in question and a “0” for all others (following Gero et al. 2005). A preferred association matrix was constructed in which a score between 0 and 2 was given to each dyad for the number of feeding categories in which they formed a preferred association (i.e. a zero was given to dyads that never formed preferred associations, a one was given to dyads that only formed a preferred association in one feeding category, a two was given to pairs that formed preferred associations in both feeding categories).

Mantel tests (Schnell et al. 1985) and matrix correlation coefficients between the elements of each of the hypothesis matrices and the preferred association matrix were carried out to determine if the relative sex of the individuals in a dyad was correlated with the type of association they formed. The statistical significance of these was tested by means of a Monte Carlo test using 1,000 random permutations. The number of random permutations was determined increasing the number of permutations until the *p* value stabilizes (Bedjer et al. 1998).

The calculation of the HWI, the Mantel tests, matrix correlation coefficients, and the Monte Carlo permutation tests were carried out using the compiled version of SOCPROG 2.3 (Whitehead 2006).

Individual preferences for feeding opportunistically or not opportunistically and differences in group size were tested using a non-parametric Mann–Whitney *U* test performed with Palaentological Statistics, PAST, version, 1.6 (Hammer et al. 2001). Data were presented as mean + standard error. Statistical significance was tested at the  $\alpha < 0.05$  level.

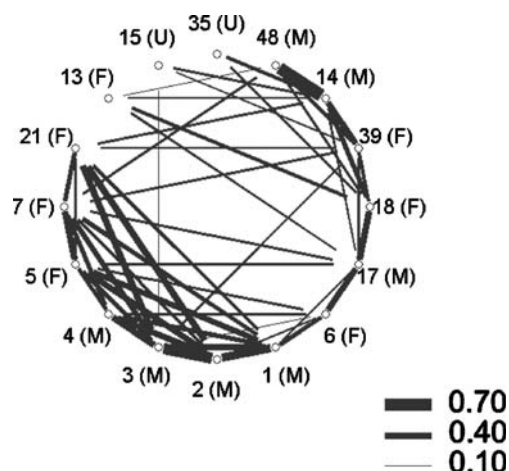
## Results

### Sighting data and survey effort

We selected 249 feeding group sightings for analysis and presentation of data, within which 16 bottlenose dolphins were individually identified (50% of the 32 individuals photo-identified in the study area). Of these, sex was known for 14 dolphins (7 females and 7 males). In total, the 16 dolphins were sighted a mean of  $39.6 \pm 9$  times during the study (Table 1). All dolphins were observed participating in both opportunistic (feeding in the fish farm) and not opportunistic feeding categories, with a mean of  $31 \pm 8$  times and  $8.6 \pm 1$  times, respectively. The number of times that dolphins were engaging in opportunistic feeding in the fish farm area was significantly predominant (Mann–Whitney *U* test  $U_b = 71.5$ ,  $n = 16$ ,  $p = 0.034$ ).

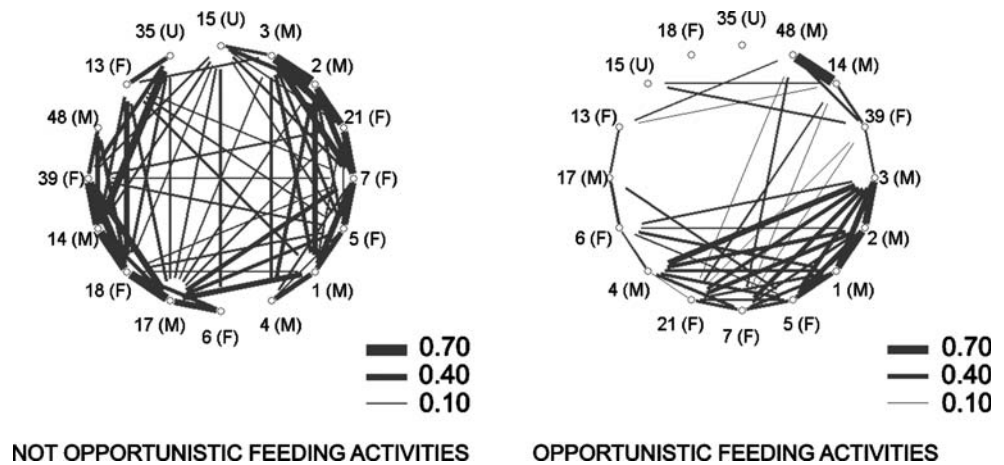
### Is bottlenose dolphins' social structure random?

Using the methodology of Whitehead (1999), we found that the association behaviour of bottlenose dolphins off Sardinia differed significantly from random. Significantly high associations were identified in all data combined, as in both feeding categories, since the standard deviations of



**Fig. 2** Overall sociogram of bottlenose dolphins off Sardinia during feeding activities

**Fig. 3** Sociograms of bottlenose dolphins off Sardinia during opportunistic and not opportunistic feeding activities



observed association indexes were significantly larger than for the randomly permuted data ( $p < 0.001$ , Table 2), indicating that dolphins maintained non-random associations across daily sampling periods (Whitehead 1999).

Overall associations between dolphins can be seen in a sociogram (Fig. 2) where points representing the individuals are arranged around a circle and the thickness of lines between the points indicates the strength of their relationship. They are clearly not random, based on the relative absence and asymmetry of linkages through the axes of the sociogram. In Fig. 3, it is possible to observe clear differences in the shape of the sociograms between feeding categories.

Which types of associations are formed during feeding by bottlenose dolphins?

Analyses revealed that dolphin associations during feeding can be divided into three general categories: (1) acquaintances, which never form preferred associations but are still associated in at least one feeding category (seven males, six females and two unsexed formed this type); (2) affiliates, which consistently form preferred associations across both

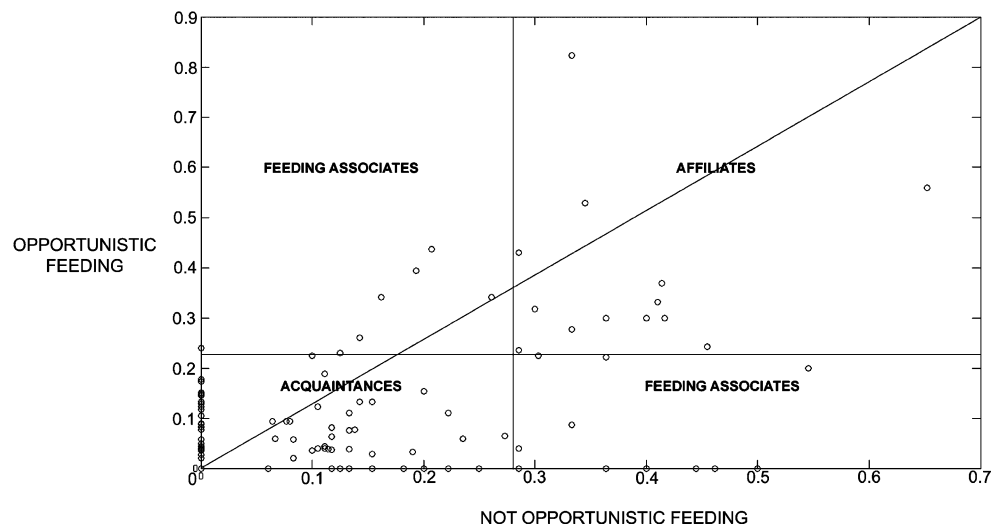
feeding categories (five males and four females); and (3) feeding associates, which form preferred associations within one feeding category (opportunistic or not opportunistic), but not in both foraging categories (six males and three females).

Figure 4 depicts the HWI of each dyad against itself across feeding categories and is used to illustrate the three types of association. The diagonal represents the 1:1 ratio line on which points would be expected to fall if feeding had no relationship with the strength of the association, in which case, the HWI for a given dyad would be equal in both opportunistic and not opportunistic feeding categories. The apparent arc in the data points indicates that dyads with intermediate strength associations were stronger in not opportunistic feeding category, or that the strength of association varied with feeding category.

Preferred associations, group size and relative sex of preferred partners

A total of 109 associations were identified out of a possible 240 dyads, of these 35 were preferred associations (i.e. they

**Fig. 4** Plot comparing dyadic half-weight index (HWI) of bottlenose dolphin pairs between feeding categories. The diagonal represents the 1:1 ratio line on which points would be expected to fall if the behavioural state had no relationship with strength of association. Horizontal and vertical lines mark the threshold value defining preferred associations



**Table 3** Average of bottlenose dolphins associations observed during feeding off Sardinia

	Mean±SE	Percent of observed dyads ( <i>n</i> =109)
Acquaintances	4.7±0.7	68.8
Feeding associates	1.1±0.3	16.5
Affiliates	1±0.3	14.7
Total	6.8±1	100

had association indices above twice the mean index) and 18 were feeding associates (eight engaging in opportunistic and ten in not opportunistic foraging activities). Although three dolphins (two unsexed and one female) did not form any preferred associations, 13 dolphins formed at least one preferred association. On average, each individual associated with  $6.8 \pm 1$  partners, of which  $2.1 \pm 0.5$  were preferred (Table 3).

Group size during feeding activities ranged from singletons to groups of seven dolphins and showed a median group size of 2 (mean= $2.5 \pm 0.09$ ). Group size did not vary between both opportunistic and not opportunistic feeding categories (Mann–Whitney *U* test  $U_b=5,091$ ,  $n_{\text{opportunistic}}=194$ ,  $n_{\text{not opportunistic}}=55$ ,  $p=0.6$ ; median=2 for both categories).

When comparing relative sex (both males, both females, opposite sex), tests against the distribution of preferred associates were not significant (Mantel *Z* test, permutations=1,000,  $n=16$ ,  $p_{m-m}=1$ ,  $p_{f-f}=1$ ,  $p_{f-m}=1$ ; Table 4). Therefore, the relative sex of preferred partners is not related with the number of preferred associations, indicating that during feeding activities bottlenose dolphins choose male and female partners equally.

## Discussion

These results clearly demonstrate that bottlenose dolphins off Sardinia show non-random social behaviour during feeding activities, and their social behaviour differs depending on the feeding activity in which they are engaged.

Partner preferences are expected in by-product mutualisms in which individuals differ in the ability to provide or use by-product benefits (Wrangham 1982; Connor 1995). In Sardinia, these differences may relate to varying foraging strategies influenced by food patches created by a coastal sea-cage fin fish farm. Additionally, we were able to show that bottlenose dolphins have preferences for opportunistic feeding in the fish farm area, as observed in precedent studies (Díaz López and Shirai 2007).

In a social context, opportunistic feeding activities reduce the level of association between dolphins. Our results show that bottlenose dolphin associations appear to be weaker when engaging in opportunistic feeding activities than during not opportunistic feeding activities. These observations were consistent with our hypothesis that during opportunistic behaviours the benefits derived from cooperation (mainly characterized by enhanced foraging efficiency due to the absence of natural predators in the area) decrease, as it is easier to capture prey. The costs associated with increased competition among group members could be greater than the advantages associated with cooperation. Moreover, dolphins find it easier to exploit a concentrated food source (Díaz López 2006a), thus the level of associations is reduced. These results are supported by a parallel study in the fish farm area (Díaz Lopez 2006a), where cooperative feeding strategies were observed less frequently (34%) than individual feeding strategies (66%) by dolphins hunting both schooling and solitary prey.

During not opportunistic feeding behaviours (characterized by searching and foraging on patches of food that are soon dispersed) strong associations could play an important role. According to the similarity principle (de Waal and Luttrell 1986), it is likely more beneficial to forage with individuals that share similar foraging tactics, as by-product benefits are likely higher between individuals that forage in the same manner. Individuals could receive by-product benefits by coordinating their behaviours with specific individuals (Brown 1983; Mc Donald and Potts 1994; Gero et al. 2005). Cooperative hunting has been reported in several mammals and even in bird species (e.g. Brown 1983; Mc Donald and Potts 1994; Gazda et al 2005; Díaz López

**Table 4** Breakdown of associations by sex type as a percentage of dyads (excluding two unsexed individuals)

Sex class	Never observed associated (%)	Acquaintances (%)	Affiliates (%)	Feeding associates		<i>P</i> values
				Opportunistic (%)	Not opportunistic (%)	
Male–male	19	38	24.5	9.5	9	$p > 0.05$
Female–female	14	62	10	5	9	$p > 0.05$
Male–Female	8	57	16	10.5	8.5	$p > 0.05$

The *p* value is from the Mantel test comparing sex class to all others

2006a). Accounts of cooperative behaviour in feeding bottlenose dolphins include fish being herded into a ball (Leatherwood 1975; Bel'kovich et al. 1991; Diaz Lopez 2006a), fish driven ahead of dolphins swimming in a crescent formation (Leatherwood 1975; Würsig 1986; Diaz Lopez 2006a), against mud banks (Leatherwood 1975), or trapped between dolphins attacking from either side (Würsig 1986).

Associations presented in feeding groups of bottlenose dolphins can be divided into three general categories: (1) acquaintances, which never form preferred associations but are still associated in at least one feeding category; (2) affiliates, which consistently form preferred associations across both feeding categories; and (3) feeding associates, which form preferred associations within one feeding category (opportunistic or not opportunistic), but not in both foraging categories. Interestingly, sexes were not as segregated as in other described populations. Male alliances of Indian Ocean bottlenose dolphins (*Tursiops aduncus*) have been shown to herd oestrus females to increase the males' mating opportunities (Connor et al. 2000). The results shown here demonstrate that preferred associations are formed in both feeding activities independently of the relative sex of preferred partners. Our Mantel tests analyses did not reveal significant relationships in dyadic associations among the sex classes. This finding suggests that an adult dolphin (male or female) may prefer to associate with a specific individual independently of the sex who shares the same foraging priorities. Thus, the apparent differences between the two species reflect the specific ecological conditions more than the species-specific characteristics (e.g. Boesch 1996). This circumstance confirms that food acquisition drives the social organisation of these hunting groups and it would explain why both sexes have similar association dynamics (Lusseau et al. 2003). Similar social behaviour, denominated bisexuality bonded community model has also been observed in West African chimpanzees (Boesch 1996) in which females and males are equally social.

The observed group size homogeneity in both feeding categories demonstrates that the number of dolphins engaging in feeding activities is not necessarily related with levels of cooperation. Therefore, in bottlenose dolphins, the group composition and not the group size plays an important role during feeding activities. This has also been seen in chimpanzees where group composition depends on feeding competition and the formation of hunting parties (Boesch 1996; Mitani and Watts 1999).

Our findings have implications for the "social complexity" hypothesis for large brain evolution in primates and a few other mammalian taxa (e.g. Connor et al. 1992). The genetic relatedness of individuals is unknown and could play an important role in group composition, as it does in other cetaceans, which tend to divide according to matrilineage (Connor et al. 1998).

We suggest that the main management issues raised by this study relates to the dolphins' habitat. The feeding opportunities for dolphins that are created by human activities have become part of their "way of life", part of their habitat requirements. Assessing the consequences of fisheries and habitat modification with relatively obvious effects on marine predators can be difficult. The effects of human activities (i.e. aquaculture, fisheries) are not only directly affecting marine predators but, as this paper shows, could also indirectly affect their social structure and behaviour.

When top predators display complex social responses to activities not directed at them, the task of studying all possible effects in the food chain can become even more challenging. Further work should focus on elucidating how human activities induce social and spatial changes in marine top predators.

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## References

- Anthony LL, Blumstein DT (2000) Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce  $N_e$ . *Biol Conserv* 95:303–315
- Altmann SA (1974) Baboons, space, time, and energy. *Am Zool* 14:221–248
- Beddington JR, Beverton RJ, Lavigne DM (1985) *Marine Mammals and Fisheries*. George Allen and Unwin, London
- Bejder L, Fletcher D, Brager S (1998) A method of testing association patterns of social animals. *Anim Behav* 56:719–725
- Bel'kovich VM, Ivanova EE, Yefremenkova OV, Kozarovitsky LB, Kharitonov SP (1991) Searching and hunting behavior in the bottlenose dolphin (*Tursiops truncatus*) in the Black Sea. In: Pryor K, Norris KS (eds) *Dolphin societies: Discoveries and puzzles*. University of California Press, Berkeley, pp 38–67
- Boesch C (1996) Social grouping in Tai chimpanzees. In: McGrew WC, Marchant LF, Nishida T (eds) *Great Ape Societies*. Cambridge University Press, Cambridge, pp 101–113
- Brown JL (1983) Cooperation—a biologist dilemma. *Adv Stud Behav* 13:1–37
- Cairns SJ, Schwager SJ (1987) A comparison of association indices. *Anim Behav* 35:1454–1469
- Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. *J Zool* 183:1–39
- Connor RC (1995) The benefits of mutualism: a conceptual framework. *Biol Rev* 70:427–457
- Connor RC, Smolker RA, Richards AF (1992) Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc Natl Acad Sci USA* 89:987–990
- Connor RC, Mann J, Tyack PL, Whitehead H (1998) Social evolution in toothed whales. *Trends Ecol Evol* 13:228–232

- Connor RC, Wells RS, Mann J, Read AJ (2000) The bottlenose dolphin: social relationships in a fission–fusion society. In: Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, pp 91–126
- de Waal FBM, Luttrell LM (1986) The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatol* 46:215–234
- Díaz López B (2006a) Bottlenose dolphin (*Tursiops truncatus*) predation on a marine fin fish farm: some underwater observations. *Aquatic Mammals* 32:305–310 DOI 10.1578/AM.32.3.2006.305
- Díaz López B (2006b) Interactions between Mediterranean bottlenose dolphins (*Tursiops truncatus*) and gillnets off Sardinia, Italy. *ICES J Mar Sci* 63:946–951 DOI 10.1016/j.icesjms.2005.06.012
- Díaz López B, Bernal Shirai JA (2007) Bottlenose dolphin (*Tursiops truncatus*) presence and incidental capture in a marine fish farm on the north-eastern coast of Sardinia (Italy). *J Mar Biol Assoc UK* 87:113–117 DOI 10.1017/S0025315407054215
- Díaz López B, Marini L, Polo F (2005) The impact of a fish farm on a bottlenose dolphin population in the Mediterranean Sea. *Thalassas* 21:53–58
- Durrell JL, Sneddon IA, O’Connell NE, Whitehead H (2004) Do pigs form preferential associations. *Appl Anim Behav Sci* 89:41–52
- Dunbar RM (1992) Time: a hidden constraint on the behavioural ecology of baboons. *Behav Ecol Sociobiol* 31:35–49
- Fertl D, Leatherwood S (1997) Cetacean interactions with trawls: a preliminary review. *J Northw Atl Fish Sci* 22:219–248
- FAO (2007) The state of world fisheries and aquaculture 2006. FAO Fisheries and Aquaculture Department. Food and agriculture organization of the United Nations, Rome, 2007
- Gazda SJ, Connor RC, Edgar RK, Cox F (2005) A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proc R Soc B* 272:135–140
- Gero S, Bejder H, Whitehead J, Mann J, Connor RC (2005) Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp. *Can J Zool* 83:1566–1573 DOI 10.1139/Z05–155
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeo Electronica* 4:1–9
- Hinde RA (1976) Interactions, relationships and social structure. *Man* (London) 11:1–17
- Kerth G, König B (1999) Fission, fusion and non-random associations in female Bechstein’s bats (*Myotis bechsteinii*). *Behaviour* 136:1187–1202
- Leatherwood S (1975) Some observations of feeding behaviour of bottlenosed dolphins (*Tursiops truncatus*) in the Northern Gulf of Mexico and (*Tursiops cf. T. gilli*) off southern California, Baja California and Nayarit, Mexico. *Mar Fisheries Review* 37(9):10–16
- Lusseau D (2003) The emergent properties of a dolphin social network. *Proc R Soc Lond B* 270(Suppl 2):S186–S188 DOI 10.1098/rsbl.2003.0057
- Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, Dawson SM (2003) The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations: can geographic isolation explain this unique trait. *Behav Ecol Sociobiol* 54:396–405
- Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. *Mar Mamm Sci* 15:102–122
- Mann J, Smuts BB (1999) Behavioural development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, 136:529–566
- McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs as repositories of social knowledge in African elephants. *Science* 292:491–494
- McDonald DB, Potts WK (1994) Cooperative displays and relatedness among males in a lek-mating bird. *Science* (Washington, D.C.) 266(5187):1030–1032
- Mitani JC, Watts DP (1999) Demographic influences on the hunting behavior of chimpanzees. *Am J Phys Anthropol* 109:439–454
- Mitani JC, Watts DP, Muller MN (2002) Recent developments in the study of wild chimpanzee behaviour. *Evol Anthropol* 11:9–25
- Myers JP (1983) Space, time, and the pattern of individual associations in a groups-living species: sanderlings have no friends. *Behav Ecol Sociobiol* 12:129–134
- Ribeiro S, Viddi FA, Cordeiro JL, Freitas TO (2007) Fine-scale habitat selection of Chilean dolphins (*Cephalorhynchus eutropia*): interactions with aquaculture activities in southern Chiloé Island, Chile. *J Mar Biol Ass UK* 87:119–128 DOI 10.1017/S0025315407051594
- Smolker RS, Richards AF, Connor RC, Pepper JW (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123(1–2):38–69
- Schnell GD, Watt DJ, Douglas ME (1985) Statistical comparison of proximity matrices: applications in animal behaviour. *Anim Behav* 33:239–253
- Takahata Y, Suzuki S, Okayasu N, Hill D (1994) Troop extinction and fusion in wild Japanese macaques of Yakushima Island, Japan. *Am J Primatol* 33:317–322
- van Schaik CP (1999) The socioecology of fission–fusion sociality in orangutans. *Primates* 40:69–86
- Watson-Capps JJ, Mann J (2005) The effects of aquaculture on bottlenose dolphin (*Tursiops* sp.) ranging in Shark Bay, Western Australia. *Biol Conserv* 124:519–526
- Whitehead H (1995) Investigating structure and temporal scale in social organizations using identified individuals. *Behav Ecol* 6:199–208
- Whitehead H (1997) Analyzing animal social structure. *Anim Behav* 53:1053–1067
- Whitehead H (1999) Testing association patterns of social animals. *Anim Behav* 57:F26–F29
- Whitehead H (2006) Compiled version of SOCPROG 2.3 [computer program]. Available from <http://myweb.dal.ca/~hwhitehe/social.htm/>
- Whitehead H, Dufault S (1999) Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Adv Stud Behav* 28:33–74
- Whitehead H, Bejder L, Ottensmayer A (2005) Testing association patterns: issues arising and extensions. *Anim Behav* 69:e1–e6
- Wrangham RW (1982) Mutualism, kinship and social evolution. In: *Current problems in sociobiology*. Cambridge University Press, Cambridge, pp 269–289
- Wittemyer G, Douglas-Hamilton I, Getz WM (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim Behav* 69:1357–1371 DOI 10.1016/j.anbehav.2004.08.018
- Würsig B (1986) Delphinid foraging strategies. In: Schusterman RJ, Thomas JA, Wood FG (eds) *Dolphin cognition and behaviour: A comparative approach* Lawrence Erlbaum Associates, Hillsdale, NJ, pp 347–359
- Würsig B, Gailey GA (2002) Marine mammals and aquaculture: conflicts and potential resolutions. In: Stickney RR, McVay P (eds) *Responsible marine aquaculture*. CAP International Press, New York, pp 45–59
- Würsig B, Jefferson RA (1990) Methods of photo-identification for small cetaceans. Report of the International Whale Commission, Special Issue no 12:43–52