



Social organization in northern bottlenose whales, *Hyperoodon ampullatus*: not driven by deep-water foraging?

SHANNON GOWANS, HAL WHITEHEAD & SASCHA K. HOOKER

Department of Biology, Dalhousie University

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It is postulated that deep-water foraging in sperm whales, *Physeter macrocephalus*, has led to communal care of young and long-term female bonds. By studying the social organization of a second, unrelated, deep-diving species, the northern bottlenose whale, we investigated the role that deep diving may play in the evolution of cetacean sociality. Northern bottlenose whales in a deep-water canyon, the Gully off Nova Scotia, Canada, form small groups ($\bar{X} \pm \text{SD} = 3.04 \pm 1.86$). Associations within age/sex classes (female/immature, subadult male and mature male) were significantly higher than associations between different classes. Females and immature bottlenose whales formed a loose network of associations, showing no preferential associations with particular individuals or those from specific age/sex classes nor any long-term bonds. Mature and subadult males had stronger associations with individuals in their own class, and associations between some males lasted for several years, although males also formed many short-term associations. Overall the social organization of northern bottlenose whales in the Gully appears to resemble that of some bottlenose dolphins, *Tursiops truncatus*, living in shallow, enclosed bays. Thus deep-water foraging does not appear to necessarily lead to the evolution of long-term bonds between females.

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Social structure is believed to be moulded by selective ecological pressures, especially predation (Wrangham & Rubenstein 1986). For slow reproducing large mammals, the protection of young is particularly crucial, as young often have much higher mortality rates than adults. For a number of species (e.g. silverback jackels, *Canis mesomelas*; Moehlman 1986), protection of the young seems to have been a major influence on the evolved social system. This has been thought to be especially true for whales, which forage at great depth (Whitehead 1996).

Sperm whales feed predominantly on deep-water squid and this foraging behaviour is believed to have been an important factor leading to the evolution of sociality in these whales (Best 1979; Whitehead 1996). Young sperm whales do not appear to be capable of diving to the foraging depths of adults (ca. 400 m) as calves remain at the surface longer than adults and dive for shorter periods and to lesser depths. While on the surface, calves associate with various members of their group (Gordon 1987). When calves are present, female and immature sperm whales in the group stagger their dive schedules, increasing the probability that at least one adult-size animal is at

the surface with the calf (Whitehead 1996). It has been suggested that this communal babysitting (while the mother forages at depth) is responsible for the formation of long-term bonds between female sperm whales, in agreement with the theories of reciprocal altruism or kin selection (Best 1979; Gordon 1987; Whitehead 1996). Male sperm whales show a very different pattern of associations than females: subadult males disperse from the female units and move from the tropics to temperate waters where they form 'bachelor herds'. As they mature, males become more solitary and migrate towards the poles. Socially mature males return to the tropics during the breeding season to mate with females, which remain year-round in tropical and subtropical waters (Best 1979).

Northern bottlenose whales (beaked whale; Family Ziphiidae) share a similar ecological niche to sperm whales; both species live offshore and forage principally on deep-water squid (Papastavrou et al. 1989; Hooker 1999). While sperm whales are certainly deep divers (routinely diving to approximately 400 m for 40 min; Papastavrou et al. 1989), they do not generally dive as deeply as northern bottlenose whales (which routinely dive to 800 m or deeper for 30 min or longer; Hooker & Baird 1999). While little is known about the diving abilities of northern bottlenose whale calves or predation pressures, presumably the same physiological pressures

Correspondence and present address: S. Gowans, Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada (email: sgowans@is2.dal.ca). S. K. Hooker is now at the British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, U.K.

preventing sperm whale calves from diving as deep or for as long as adults would also act on bottlenose whales. We would therefore expect bottlenose whale mothers to face similar ecological pressures caused by their deep-diving behaviour. In addition beaked whales and sperm whales are believed to be only distantly related to each other (Messenger & McGuire 1998). Therefore, comparing the social organization of sperm and northern bottlenose whales may help to elucidate the role that deep-diving behaviour plays in the evolution of long-term bonds between females and communal babysitting of calves.

The social organization of a population is based upon the nature and quality of interactions between individuals (Hinde 1976). In most cetacean species (and many terrestrial species) it is not possible to observe interactions, so individuals are assumed to be interacting if they are members of the same group, being found in the same locations at the same time (Whitehead & Dufault 1999). Relationships between pairs of individuals can be described by the characteristics and temporal patterning of their associations. By summarizing the pattern of relationships between individuals, the general social organization can be described (Hinde 1976; Whitehead 1995). Here we use this approach to study the social organization of northern bottlenose whales in the Gully, a deep canyon off the coast of Nova Scotia.

METHODS

Field Data Collection

We collected photographs of northern bottlenose whales from the Gully, Nova Scotia (43.5–44.5°N, 58.5–60°W) during the summers of 1988–1997 from sailing vessels with auxiliary diesel engines. Field seasons varied in length from 3 months in 1990, 1996 and 1997 to only a few days in 1991 and 1992. To minimize any potential disturbance by the boat, we typically approached a group of whales from the side at a speed of less than five knots, slowing down to the whales travelling speed by the time we were within 100 m. Care was taken while positioning the boat parallel to the whales so as to not disturb the group. Only rarely did swimming speed increase when the whales were approached, and when it did, the group was not pursued. More typically, the whales would continue swimming in the same direction and at the same speed and showed no obvious negative reaction to the boat. Often, the whales would approach the vessel and circle the stationary vessel. Extra precaution was exercised when approaching groups containing calves. The boat would approach much slower and remain further away from the whales.

When conditions permitted, we took photographs of the dorsal fin and surrounding flank of bottlenose whales that were within 15 m of the vessel. We photographed sexually dimorphic melon (forehead) profiles in conjunction with dorsal fin photographs and used these photographs to assign age/sex categories (Gray 1882; Gowans et al. 2000); mature male, subadult male, immature male/female (of all ages). It was not possible to distinguish between immature males and females. Most analyses

were restricted to high-quality photographs and to reliably marked individuals (no change in mark over periods of years) known from both left and right sides to ensure equal probabilities of recapture (Gowans & Whitehead 2001). There were 65 reliably marked individuals with high-quality photographs known from both left and right sides (approximately half of the total population of 130 individuals that use the Gully; Gowans 1999), including 31 female/immature males, 15 subadult males and 18 mature males.

Definitions

Group. Whales found within five body lengths (chain rule) and showing coordinated behaviour (e.g. similar heading or surfacing times).

Calf. Small individuals possessing fetal folds or bent over dorsal fins, likely young of the year.

Juveniles. Individuals that were less than two-thirds adult size and were not calves.

Young animals. Calves or juveniles.

We made estimates of the number of individuals in the group frequently and used the maximum estimate in our analysis of group size. We assigned a new group number when 10 min had passed with no whales visible at the surface or when individuals were observed further than five body lengths apart. We also recorded the number of calves and juveniles in each group.

Analysis

We calculated the distribution and mean group size directly from field estimates. We calculated typical group size (the size of the group in which the typical animal found itself on average) from field estimates following the methods of Jarman (1974) where T is the typical group size, n groups were observed and x_j is the number of individuals in group j :

$$T = \frac{\sum_{j=1}^n x_j^2}{\sum_{j=1}^n x_j}$$

Two individuals were considered to be associated if they were photographed within the same group. This was considered to be the most appropriate definition of an association, as animals within groups coordinated their movements, and behavioural interactions between individuals were rarely observed. In addition, different groups were sometimes sampled over short time periods (e.g. less than 10 min), which made temporal definitions of association difficult (Gowans 1999). We calculated estimates of the proportion of time individuals spent together for all dyads using the simple ratio index of association (Cairns & Schwager 1987). Although many studies of cetacean

social organization use the half-weight association index (i.e. Smolker et al. 1992; Bejder et al. 1998), we used the simple ratio index because it is thought to be the least biased of the standard association indices (Ginsberg & Young 1992). Furthermore, the results of tests were similar for both the simple ratio and the half-weight association index. In many groups not all individuals were photographed, nor were all individuals identifiable. Therefore, there were occasions when pairs of individuals were associated but the associations were not detected by our sampling technique, resulting in a downward bias in association indices.

For all analyses except the assessment of preferred companionship (see below), we set the sampling period at 1 day to avoid replicate associations within the same day, which would not necessarily be independent. We calculated and analysed all association indices using SOCPROG 1.2 (Whitehead 1999a).

To determine whether there were differences in the patterns of association between and within age and sex classes, we used a Mantel test to test the null hypothesis that association rates (i.e. probability of being in the same group) were similar between and within classes (e.g. Schnell et al. 1985). We calculated the mean association index (and standard deviation) between each pair of age/sex classes. We identified the maximum associate of each individual (the associate that shared the highest association rate), then averaged the association indices between maximum associates within the age/sex classes and calculated the standard deviation.

Preferred Companionship

To determine whether the patterns of associations between individuals were different from random, we constructed 1:0 association matrices for each 5-day period, such that dyads were assigned a value of 1 if they were photographed within the same group within the sampling period and 0 if they were not. The association matrix was then permuted following the procedure described by Bejder et al. (1998), in which pairs of rows and columns were randomly chosen from the association matrix and the association values inverted between rows (keeping constant the number of identified individuals in each group, and the number of groups in which each individual was observed). As successive association matrices were not independent, we determined the number of permutations required to obtain an accurate P value (testing whether the real data differentiated from random) by conducting increasingly larger numbers of permutations until the P value stabilized (Bejder et al. 1998). As the number of associated pairs that could be permuted was low, we included all quality photographs in the permutations. This resulted in a more powerful test (due to increased sample size) and probably did not bias the test as the results using all quality photographs were more often significant than tests using only high-quality photographs (see Gowans 1999 for more details). Identification of preferred companionship indicated only that individuals were considered associated more often than expected by random, but did not necessarily indicate

that these individuals were actively choosing to remain associated.

Short-term companionship

As individuals move in and out of the Gully over the summer field season (Whitehead et al. 1997), associations may appear significantly different from random simply due to demographic effects (i.e. individuals associated randomly with all animals present in the Gully at that time, and did not associate with those that were not present). By constraining the permutations of the association matrix to short time intervals, these demographic effects can be removed (see Whitehead 1999b). We set the sampling period at 5 days, as single-day sampling periods were too short to contain many associations. As bottlenose whales are estimated to spend on average 10 days in the Gully (SE=5; Gowans 1999), approximately half of the individuals probably moved in or out of the Gully during the 5-day sampling period.

By randomly permuting the group to which individuals were assigned (while keeping the number of groups in which animals were observed constant) within the 5-day sample period, we tested the null hypothesis that there were no preferred companions within the 5-day period. Preferred associations within 5-day periods will reduce the number of pairs of associated individuals, and so decrease the mean association index. Therefore, if the mean association index for the observed data was significantly lower than the randomly permuted data, then the null hypothesis of no short-term (within 5 days) companions was rejected (Whitehead 1999a). Simulated data representing many different social systems were used to test the value of this technique to detect preferred associations (H. Whitehead, unpublished data).

Long-term companionship

To test for long-term companionship, the associations of each individual within the 5-day sampling period were permuted, while keeping the total number of associations of each individual the same. If some pairs of animals were associated or avoiding each other in different sampling periods more often than by chance, this would increase the standard deviations of the association indices. Thus, if the standard deviations of the observed association indices were significantly higher than the randomly permuted data, the null hypothesis (no preferential associates between 5-day sampling periods) was rejected (Whitehead 1999a).

Temporal Pattern

We calculated standardized lagged and null association rates for associations between individuals (Whitehead 1995). Lagged association rates estimate the probability that two animals sighted together at a given time will still be associated at some time lag later. The null association rate indicated the lagged association rate expected, given random association. We standardized lagged and null association rates (by dividing the rate by the number of

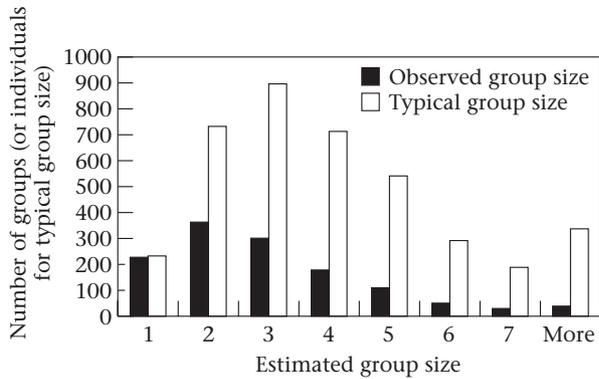


Figure 1. Distribution of observed and typical group sizes of bottlenose whales in the Gully. Typical group size (Jarman 1974) is the group size as experienced by a typical individual whale.

recorded associates on each occasion) as not all individuals in the group were identified. We used jackknife techniques to assess the precision of the estimated lagged association rates (Sokal & Rohlf 1995).

Models describing temporal patterns of association were then fitted to the full data set using maximum likelihood and binomial loss techniques to determine best fit. We used jackknife techniques to calculate the standard error of the model terms, which gives a conservative estimate of the precision of the terms (Sokal & Rohlf 1995). The models included the two types of associates described by Whitehead (1995): (1) constant companions: stable associations over time, changed only by birth or death; (2) casual acquaintances: associated individuals dissociate over time. Models with each animal possessing a combination of different levels of associate were fitted.

Adult–Young Interactions

As relatively few calves and juveniles were photographically identifiable, it was not possible to examine interactions between young animals with adults in the same systematic ways that interactions between adults were analysed. However the photographic-identification history of calves and juveniles can be used to investigate the possibility of babysitting and the general pattern of adult–offspring interactions. We examined the sighting history of all young animals from 1988 to 1998 to

identify their associates. We assumed that young animals should associate most often with their mothers and that mothers should associate most often with their offspring. We used these assumptions to identify potential mothers and/or babysitters. We also examined identification histories of young animals to determine whether they were observed alone at the surface.

RESULTS

The modal group size was three animals, which closely corresponded to the mean ($\bar{X} \pm SD = 3.04 \pm 1.86$, $N = 1281$, range 1–14; see Fig. 1). The typical group size (Jarman 1974) was 4.17. Although it was not possible to analyse group composition precisely (as not all individuals were identified and sexed in each group; see Gowans 1999 for more details), groups were often composed of individuals of different age and sex classes. Calves were present in 3.9% of the groups and, on average, only one calf was present in each group ($\bar{X} \pm SD = 1.2 \pm 0.40$, $N = 50$). Juveniles were present in 7.5% of the groups and, when present, there tended to be only one juvenile per group ($\bar{X} \pm SD = 1.2 \pm 0.39$, $N = 96$).

Association patterns between and within classes were not similar (Mantel test: $t = 2.12$, $N = 645$, $P = 0.017$): associations within the age and sex classes were generally higher than the associations between classes. Both subadult and mature males had generally higher association indices with other males of their same class, and also had overall higher association indices than females (Table 1). Seventeen male–male dyads had an association index greater than 0.20 and 10 male–male associations exceeded 0.25, while five female/immature male associations exceeded 0.20 and none were greater than 0.25. Maximum association indices (highest association index of each individual with all other animals) were variable, indicating that some individuals had high association indices with their maximum associate, while others had much lower indices (Table 1). The high values for mature males associated with other mature males indicated that the maximum associate of a mature male was most often another mature male. Similarly subadult males were maximum associates with other subadult males. Female/immature males did not show a clear age or sex class preference for their maximum associate, although the inclusion of immature males with females in this category may have obscured the patterns of association.

Table 1. Mean and maximum association simple ratio indices (SD) within and between the different age/sex classes

	Female/immature	Subadult male	Mature male
Mean associate			
Female/immature	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)
Subadult male	0.01 (0.01)	0.04 (0.05)	0.02 (0.02)
Mature male	0.01 (0.01)	0.02 (0.02)	0.02 (0.02)
Maximum associate			
Female/immature	0.14 (0.08)	0.06 (0.07)	0.10 (0.10)
Subadult male	0.11 (0.08)	0.23 (0.27)	0.13 (0.14)
Mature male	0.14 (0.10)	0.12 (0.13)	0.19 (0.17)

Individuals were considered associated if they were photographed in the same group in the same day.

Table 2. Permutation tests for preferential association within 5-day periods

Data set	Mean association index		P value
	Observed data	Random data	
All individuals ($N=113$)	0.0139	0.0152	0.0002
Female–female associations ($N=31$)	0.0180	0.0191	0.0748
Subadult male–subadult male associations ($N=15$)	0.0575	0.0684	0.0078
Mature male–mature male associations ($N=18$)	0.0269	0.0329	0.0001

If the mean association indices for the observed data was significantly lower than the random data, then the null hypothesis that there is no preferential association over short time periods was rejected.

Table 3. Tests for preferred companionship between 5-day periods

Data set	SD of mean association index		P value
	Observed data	Random data	
All individuals ($N=113$)	0.0524	0.0508	0.0147
Female–female associations ($N=31$)	0.0441	0.0446	0.7866
Subadult male–subadult male associations ($N=15$)	0.1341	0.1308	0.0215
Mature male–mature male associations ($N=18$)	0.0718	0.0648	0.0097

If the standard deviation of the mean association indices for the observed data was significantly higher than the random data, then the null hypothesis that there is no preferential association over long time periods was rejected.

The mean association index for the observed data was significantly lower than the randomly permuted data (permuting the group to which individuals were assigned) in all cases except female/immature associations with other female/immatures (Table 2). Unlike the two classes of older males, females and immature males showed no significant preferential association (whether due to affinity or animosity) with other female/immatures over short periods (5 days). Similarly, the standard deviation of the mean association index of the observed data was significantly higher than the randomly permuted data (randomly permuting the associations of each individual) for all cases except female/immatures (Table 3). Therefore there was evidence for long-term preferential association among mature and subadult males, but not among females and immature males.

Temporal Pattern

The standardized lagged association rate was higher than the null (or random) association rate for all individuals for time lags less than approximately 1100 days (roughly 3 years; Fig. 2). Therefore, individuals were more often associated than expected at random for periods of less than 3 years. Lagged association rates were highest for short time lags, and decreased after approximately 100 days (roughly one field season), indicating that many associations between individuals did not last more than one field season. The lagged rate further declined after

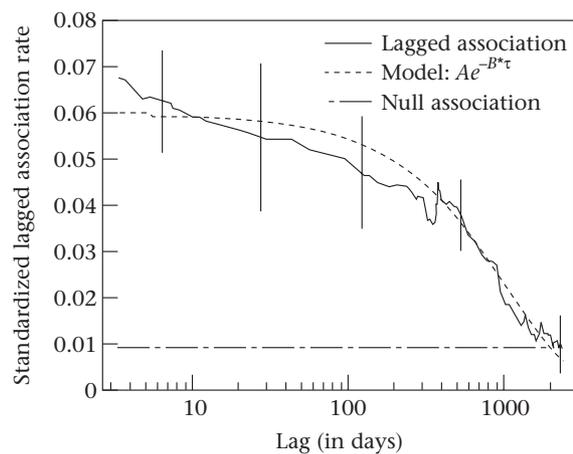


Figure 2. Standardized lagged association rates of all reliably marked individuals (with jackknifed estimates of precision) showing fitted model and null associations.

approximately 350 days until the association rates were roughly random after lags of about 3 years. There were no data collected over lags of 100 days to lags of slightly less than 1 year and there were relatively few data collected over 1-year lags, as many individuals were not sighted in successive years. The model that best described the pattern of associations was:

$$g(\tau) = Ae^{-B*\tau}$$

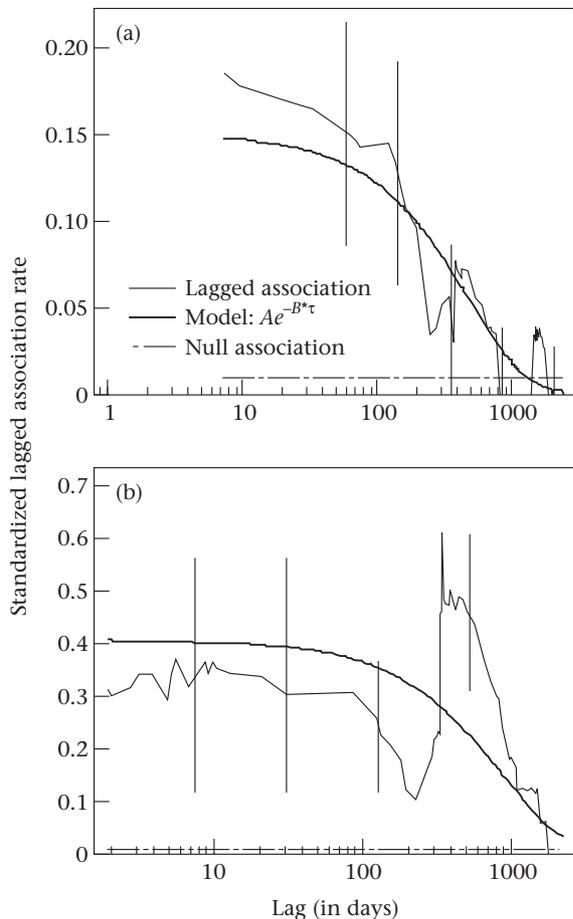


Figure 3. Standardized lagged association rates (with jackknifed estimates of precision) for (a) female/immatures and (b) mature males, showing fitted models and null association rates.

where: $g(\tau)$ equals the lagged association rate at a lag of τ time units; $A=6.0 \times 10^{-2}$ (SE 1.1×10^{-2}); $B=9.5 \times 10^{-4}$ (SE 2.6×10^{-4})/days $^{-1}$; τ is the time lag.

This model represents casual acquaintances. The error bars were quite large, indicating a lack of precision in estimating the pattern, but the model fit the observed pattern well (Fig. 2).

By age and sex class

There were insufficient data to estimate accurately standardized lagged association rates for subadult males. However, the best-fit model for both female/immatures and mature males was the same model that fit the full data set ($Ae^{-B\tau}$; Fig. 3), although sample sizes of individuals in each class were small. The model terms were: female/immature males: $A=0.15$ (SE 0.092); $B=2.1 \times 10^{-3}$ (SE 1.2×10^{-2})/days; mature males: $A=0.41$ (SE 0.16); $B=1.0 \times 10^{-3}$ (SE 3.0×10^{-4})/days.

The peak in associations between mature males at approximately 2 years (700 days) was most likely a sampling artefact. After lags of approximately 100 days, the lagged association rate of both female/immatures and mature males declined steeply, indicating many dissociations over the winter. Although the parametric estimates

are imprecise, they indicate that male–male associations last longer than those between females.

Adult–Young Interactions

Between 1988 and 1997, we photographically identified 16 young animals. Three calves were observed on multiple days within the same field season and one of those (no. 1272) was also observed as a juvenile. Five juveniles were observed on multiple days within the same year, and two of the three (nos. 1146 and 1239) were observed in more than one year. Of these eight young animals, it was possible to identify three probable mothers (Table 4). All of the probable mothers had been sexed as female/immature based on melon photographs, or genetically sexed as female, and were almost always associated with their probable offspring in the first year the young were observed. Based solely on association patterns, individual no. 131 would be identified as the probable mother of juvenile no. 1146, however melon photographs indicate that no. 131 was a subadult male when he was associating with no. 1146. Individual no. 45 was categorized as a female/immature by melon photographs and therefore was more likely to be the mother of no. 1146, even though she was observed less often with the juvenile than no. 131. Calf no. 1023 showed the clearest example of babysitting in the data set as it was associated twice with individual no. 143, which was genetically sexed as male. During one of these encounters, individual no. 143 was the only animal present with the calf.

Groups never consisted of solitary calves, however, in four of the 96 groups with juveniles, adults were not observed. While observing groups consisting of both adults and calves ($N=50$), calves were left alone at the surface in five groups for up to 7 min, usually at the beginning or end of a surfacing interval. Juveniles were left alone at the surface during eight of the 88 encounters with groups containing both juveniles and adults.

DISCUSSION

The initial expectation of this study was that the social organization of bottlenose whales would resemble that of sperm whales, caused by similar ecological pressures (since both are teuthivorous deep divers; Benjaminsen & Christensen 1979; Papastavrou et al. 1989; Hooker & Baird 1999). However the patterns of association of bottlenose whales were very different from those found in sperm whales (Table 5).

The 'groups' of bottlenose whales considered here are synonymous with the 'clusters' used to describe sperm whale social structure. Mean cluster size for Galapagos female and immature sperm whales was 2.6 (Whitehead & Weilgart 1991), similar to that of the bottlenose whales ($\bar{X}=3$; Fig. 1). However, adult male sperm whales are rarely found in clusters, except when in association with females and immatures (e.g. Christal 1998). Despite the similar group/cluster sizes of bottlenose and female/immature sperm whales, the social dynamics are very different. Bottlenose whales appear to live in a

Table 4. Maximum associates of young animals observed on more than 1 day over the study duration

Young animal	Age class*	Year (days)	Maximum associate of young animal	Sex of maximum associate	Percentage of time spent by		
					Young with maximum associate	Maximum associate with young	Maximum associate with juvenile following year
301	Juvenile	1990 (3)	None				
642	Juvenile	1993 (4)	507†	Female/immature	100	100	Not observed in 1994
682	Juvenile	1993 (3)	54	Female‡	58	73	Not observed in 1994
1023	Calf	1996 (2)	143	Male‡	35	17	0
1146	Juvenile	1996 (1)	None				
	Juvenile	1997 (2)	131	Subadult male	100	100	99
			45§	Female/immature	25	61	70
	Juvenile	1998 (10)	131	Subadult male	99	99	—
			45§	Female/immature	75	70	—
1239	Juvenile	1997 (3)	54†	Female	100	90	90
		1998 (5)	54†	Female	75	90	—
1272	Calf	1997 (3)	159§	Unknown	91	42	54
1334	Juvenile	1997 (1)	1332†	Female/immature	100	100	99
	Juvenile	1998 (3)	1332†	Female/immature	99	99	—

*Calves possessed fetal folds or bent dorsal fins, juveniles were less than two-thirds of adult size.

†Strong support for mother-offspring pair.

‡Genetically sexed.

§Moderate support for mother-offspring pair.

Table 5. Associations patterns amongst sex classes of sperm and bottlenose whales, and several populations of bottlenose dolphins

	Sperm whale	Bottlenose whale	Bottlenose dolphin*		
	Eastern Tropical Pacific	The Gully	Monkey Mia, Australia	Sarasota, Florida	Moray Firth, Scotland
Female–female associations	Strong (mostly life-long bonds)	Loose network (no preferential companions)	Loose network	Loose network	Loose network
Male–male associations	Weak (brief associations only)	Some long-term associations	Strong (most bonds last decades)	Strong (most bonds last decades)	None detected
References	Whitehead & Arnborn 1987; Christal et al. 1998	This study	Smolker et al. 1992; Connor et al. 1999	Wells 1991	Wilson 1995

*It has been suggested that bottlenose dolphins are not monophyletic. The Monkey Mia, Australia population may actually belong within the genus *Stenella*, and there may be other taxonomic differences between other populations (see Rice 1998). However following Rice 1998, we classify all of the populations discussed in this paper as *Tursiops truncatus*.

fission–fusion society in which the associates of an individual frequently change, although some individuals, especially males, form long-term (1–2 year) associations (Fig. 2). Very much in contrast to sperm whales, female bottlenose whales showed no preferential association for particular individuals or even particular age/sex classes. Instead male bottlenose whales appear to have more structured relationships with each other, in contrast to the predominately solitary male sperm whales (Christal 1998).

Highly structured male associations are also found in bottlenose dolphins off Sarasota, Florida, U.S.A. and Monkey Mia, Australia, although social organization in bottlenose dolphins varies between populations (Table 5). In both Sarasota and Monkey Mia, females form loose

networks of associations, associating with many different individuals, and most do not preferentially associate with any particular individual (Wells 1991; Smolker et al. 1992). Most of the mature male bottlenose dolphins in these populations form long-term bonds with one or two other mature males, which have lasted up to 20 years. Stable relationships between males probably form in order to cooperatively monopolize a female during the breeding season (Connor et al. 1992). However, because consortships rarely last for the entire breeding season and because individual females may consort with many different males in a single season, the mating system is probably promiscuous (Wells 1991; Smolker et al. 1992; Connor et al. 1996). Bottlenose dolphins off Sarasota and Monkey Mia are also found in similar sized groups as

bottlenose whales in the Gully (Australia: \bar{X} =4.8, Smolker et al. 1992; Florida: \bar{X} =4.8, Wells et al. 1980; Gully: \bar{X} =3).

Bottlenose dolphins in Moray Firth, Scotland, U.K. are an interesting comparison, as no male alliances have been found and group sizes tend to be larger than off Monkey Mia and Sarasota; \bar{X} =6.5 (Wilson 1995). Coastal bottlenose dolphins in the southern California Bight, U.S.A. show more fluid association patterns than Monkey Mia, Sarasota or Moray Firth study areas, with each dolphin associating with a number of different individuals and having few long-term companions (Weller 1991). Unfortunately, the sex of the few individuals in long-term associations was not known, and therefore, it is difficult to assess whether these were male alliances (Weller 1991). Bottlenose dolphins off California were also found in much larger groups than the other coastal populations of bottlenose dolphins (California: \bar{X} =22.7, Defran & Weller 1999), however, this definition of group was less conservative (encompassing a larger geographical area) than other studies, making direct comparisons of group size difficult.

Chimpanzees, *Pan troglodytes*, also live in fission–fusion societies that share some similarities with bottlenose dolphins, although chimpanzee communities are more closed than those of bottlenose dolphins and the strength of male alliances are less variable in chimpanzees. Strongly bonded philopatric males form the core of stable groups while females have looser relationships. Males often form alliances with each other to gain access to valuable resources or to increase their dominance status (Nishida & Hosaka 1996). In Ngogo, Uganda, males within alliances cooperate to sequester oestrous females and prevent other males from mating with them, while permitting alliance partners to mate (Watts 1998), similar to alliances of bottlenose dolphins in Monkey Mia (Connor et al. 1992). However, neither male chimpanzee nor bottlenose dolphin alliances have been observed cooperatively sequestering females in other locations (Watts 1998; Connor et al. 2000).

While male bottlenose whales do form associations that may last for years, similar to bottlenose dolphins and chimpanzees, they have not been observed cooperating together to gain access to females, or any other resource. The only aggressive interaction we observed between bottlenose whales occurred in 1998 when two mature males were observed repeatedly head-butting each other. These two males had been previously associated with each other (in 1989, 1990, 1994) and then were observed separately in 1996 and 1997 (Gowans & Rendell 1999). Interactions between individual bottlenose whales are difficult to record as only very rarely can the nature or directionality of interactions (who does what to whom) be observed. Therefore, the possibility that male bottlenose whales form stable bonds to cooperate to increase mating opportunities will await further detailed observations.

Communal care of young in sperm whales may result from kin selection as the long-term associates of female sperm whales are predominately relatives. Alternatively, babysitting may be a form of reciprocal altruism between long-term associates (Whitehead 1996). As female

northern bottlenose whales do not seem to form stable associations with other females, even for short periods (Table 2), it appears unlikely that communal care of young would evolve. Bottlenose whale calves and juveniles were occasionally left alone at the surface and juveniles sometimes surfaced on their own. One calf was observed associating solely with a male, however, it was not clear whether the male in this case had altered his behaviour to provide care for the calf, thus providing alloparental care, or whether the calf had changed its behaviour in order to accompany the immature male in the absence of its mother. While babysitting may occur in northern bottlenose whales, it is not as common as in sperm whales, so the communal care of young may not be an important factor in the evolution of bottlenose whale sociality.

Given the differences in social organization between sperm and bottlenose whales, it appears that the factors involved in deep-water foraging, predominately the care of young while mothers forage at depth, do not necessarily lead to similar social patterns. While the evolution of strong female bonds and communal care of calves in sperm whales may have been driven by deep diving, there appears to be at least one alternative strategy used by deep-diving cetaceans.

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