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Social Affiliations within Sperm Whale (*Physeter macrocephalus*) Groups

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Christal, J. & Whitehead, H. 2001: Social affiliations within sperm whale (*Physeter macrocephalus*) groups. *Ethology* **107**, 323–340.

Abstract

We examined patterns of affiliation within groups of sperm whales (*Physeter macrocephalus*), particularly concentrating on how short-term spatio-temporal associations reflect long-term relationships. Female and immature sperm whales live in stable, and partially matrilineal, social units. Two or more social units may move together for periods of several days, forming a cohesive group of about 20 animals. We observed that sperm whales in the eastern tropical Pacific quite consistently associated with members of their own social unit more than they did with other animals in their group with whom they did not share a long-term relationship. There was little evidence for preferred, or avoided, affiliations within social units, except in two large and relatively unstable units. In two well-studied groups, individuals did not show consistently favoured positions in the foraging rank relative to other members of their social unit. These results indicate the importance of long-term relationships to female and immature sperm whales, but suggest that relationships are quite homogeneous within social units.

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Introduction

Grouping behaviour entails a variety of costs and benefits to individuals (e.g. as reviewed by Lee 1994). Whilst some of these costs and benefits, especially predator- and food-related factors, potentially affect members of almost all forms of groups, from temporary aggregations to stable social units, others (e.g. access to helpers for rearing of offspring) relate primarily to long-term associations. Costs of intra-group competition may be mitigated by the evolution of a variety of forms of mutualism (Connor 1995): by-product

mutualism, kin selection (Hamilton 1964), reciprocity (Trivers 1971) or pseudo-reciprocity (Connor 1986). Whilst kin selection benefits require the presence of relatives, many of the other forms of mutualism, except by-product mutualism, are contingent on multiple interactions between a given pair of individuals. As such, mutualistic, cooperative relationships are likely to occur predominantly between long-term associates, unless they simply involve by-product mutualism.

In many species with social structures based around long-term social units, inter-unit encounters are commonly avoided or characterized by aggression. This lack of affiliation between social units is generally attributed to resource or reproductive competition (e.g. Cheney 1987). However, inter-unit animosity is not universal. Among, for example, sperm whales, *Physeter macrocephalus* (Whitehead et al. 1991), killer whales, *Orcinus orca* (Baird 2000), and African elephants, *Loxodonta africana* (Moss & Poole 1983), permanent social units commonly associate together. These species are all characterized by a lack of both territoriality and within-unit mating activity, so that factors which might otherwise lead to intense inter-unit competition appear to be reduced. When social units associate, there will be two distinct classes of relationship within the resultant groups. Whilst relationships between members of the same unit are likely to be based on long-term affiliation and cooperation, and frequently genetic relatedness, these aspects of relationships between members of different units will be less strong (with the exact nature of inter-unit relationships contingent on the frequency of associations between the units).

Sperm whales are large and sexually dimorphic (≈ 11 m for adult females; ≈ 16 m for adult males) toothed whales which feed at depths of between 200 and 2000 m, principally on squid (Rice 1989). They generally move at about 4 km/h within large ranges, which span about 1000 km for females (Whitehead & Weilgart 2000). Females and young are found in groups of about 20 animals, which move cohesively (Best 1979; Whitehead et al. 1991). However, each group may consist of two or more stable units which associate together for periods of day (Whitehead et al. 1991). The units, which average about 13 members each (Christal et al. 1998), are partially, but at least sometimes imperfectly, matrilineal in structure (Dillon 1996; Richard et al. 1996; Christal 1998; Christal et al. 1998; Lyrholm & Gyllensten 1998; Bond 1999; Lyrholm et al. 1999).

Within sperm whale groups, there appears to be the potential for cooperative or by-product benefits to accrue between animals in proximity to each other. For example, sperm whales defend themselves cooperatively against predators (Arnbom et al. 1987), and Whitehead (1989) suggested that sperm whales that forage in proximity to others may benefit by catching prey that elude their neighbours, or by gaining information about prey presence through the echolocation of nearby animals (i.e. by-product mutualism). Depending on the nature of these benefits, we might predict different patterns of association within groups. For instance, members of the same unit should associate preferentially if benefits are being transferred mutualistically, except in cases where only by-product mutualism is involved.

Here, we investigate relationships among foraging sperm whales, and consider whether patterns of short-term association (spatio-temporal co-ordination) reflect longer-term relationships. We consider whether members of a stable social unit associate more closely with each other than with other individuals present within a group, and whether, within stable units, there are preferred or avoided companionships. We present a case study of two stable units that remained grouped for 1 wk, which illustrates well the patterns of temporal and spatial association within a group.

Methods

Field Methods and Analysis of Photo-Identifications

Field research was carried out off the Galápagos Islands (1°30' S–1°30' N, 89°–92°W) and off the western coast of mainland South America from Panamá (7°N, 80°W) to southern Peru (19°S, 72°W) between 1985 and 1999. We tracked groups of sperm whales for periods of hours to days by listening for their distinctive clicks with a directional hydrophone (underwater microphone) from 10- to 12-m auxiliary sailing vessels (Whitehead & Gordon 1986).

Sperm whales have two general behavioural modes; foraging at depth and socializing/resting near the surface (Whitehead & Weilgart 1991). Whilst foraging, which occupies about 75% of the time, members of a group of females and immatures are usually spread out over 1–2 km of ocean, often forming a rank perpendicular to the direction of travel (Whitehead 1989). Between dives of about 35 min, members of the group breathe at the surface for about 8 min in 'clusters' usually containing 1–3 animals (Whitehead & Weilgart 2000). Clusters are defined as sets of animals which are within 100 m of each other and show co-ordinated behaviour (Whitehead & Arnborn 1987). In practice, animals within a cluster generally swim parallel to and within 1–2 body lengths of each other.

When whales begin their dives, they lift their flukes (tail) into the air. We photographed the flukes to identify individuals (Arnborn 1987; Dufault & Whitehead 1995), and with each photograph we recorded the composition of the cluster (numbers of females/immatures, 1st-year calves, mature males) being photographed as well as the time and location (mostly using Tracor Transtar SATNAV before 1992, and Trimble Transpak GPS afterwards).

Fluke photographs, which allow the unambiguous identification of virtually all sperm whales (except very young calves) from high quality photographs, were processed using the methods of Arnborn (1987) and Dufault & Whitehead (1995). A catalogue of 1859 identified individuals was constructed for the Galápagos Islands and other areas of the Pacific, and the sighting history of each of these individuals was compiled.

We collected particularly detailed data from two groups off the Galápagos. Group 'A2/B' was followed continuously between 28 May and 3 June 1995, except for one gap of 8 h (Christal & Whitehead 2000). The group consisted of two social units which had each been observed separately in previous years: unit

A2 with five members, and unit B with 17 members (Christal & Whitehead 2000). Group 'T', consisting of one social unit with nine members, was followed on 18 d between 10 Mar. and 12 Apr. 1999. During the tracking of these groups we observed no other sperm whales, with the exception of brief appearances by distinctively large, mature males.

Long-Term Relationships: Unit Membership

The social units considered in this analysis are those delineated using the techniques described by Christal et al. (1998): individuals were determined to be members of the same unit if they were identified within 12 h of each other on at least 2 days, with those days being separated by a gap of at least 30 d (unit membership and identification dates for all units, except unit T observed in 1999, are listed in Appendix 1 of Christal 1998). Thus, unit membership was determined on the basis of long-term association, and beyond the requirement that individuals be sighted on the same day, short-term association patterns were not considered. Twenty units were delineated using this method (Table 1). The delineation is not perfect in some cases, partially because occasionally units split or merged, and a few individuals appeared to transfer between units during the course of the study (Christal et al. 1998). Particularly relevant for this paper is the split of unit A2 (containing five members) from unit A between 1991 and 1995.

Short-Term Associations

Two different measures of short-term association were considered:

1 'In cluster together'. Only those clusters involving 2–6 individuals were considered in these analyses, to eliminate most clusters when animals were socializing or resting and not foraging. In some cases, not all members of a cluster were identified due to highly synchronous diving, or poor quality photographs. Data on cluster membership were not available for all sightings of all units, so this measure is considered only for the case study of group A2/B.

2 'Identified within 10 min'. For two animals to be identified within a 10-min interval, not only must their dive cycles be reasonably well-synchronized, but they must also be in fairly close spatial proximity ($< \approx 600$ m), in order for the research vessel to approach both animals and obtain identification photographs. Thus, identification within 10 min indicates close temporal and spatial coordination. In practice, many of the associates identified within this time interval would have been clustered.

For the analysis of between vs. within-unit associations, a sampling period of 2 h was selected, as a compromise between two opposing factors. The longer the sampling period, the greater the probability of artificial lumping of separate groups seen on the same day. However, short sampling periods increase the potential for auto-correlation between samples due to sequential associations between individuals (i.e. if surface intervals remain synchronous over several dive cycles), reducing the effectiveness of the association measure (although not

Table 1: Sperm whale units: number of identified members and number of days two or more members were identified, mean pair-wise association indices within units, and between units and other members of groups, percentage difference between indices, and results of permutation tests for differences between association indices among unit members (where possible)

Unit	Members	Days	Mean pair-wise association index			Permutation test for within-unit associations (p)
			within-unit	between-unit and 'other'	% difference	
A	24	21	0.342	0.219	56.16	0.021
B	22	17	0.386	0.19	103.16	0.010
C	3	2	0.500	0.183	173.22	–
D	15	3	0.248	0.190	30.53	0.765
E	18	13	0.439	0.406	8.13	0.528
F	12	7	0.350	0.362	–3.31	0.046
G	11	4	0.191	0.137	39.42	0.448
H	4	7	0.667	0.325	105.23	–
I	7	6	0.417	0.330	26.36	0.712
J	9	4	0.323	0.201	60.70	0.498
K	13	9	0.292	0.220	32.73	0.594
L	14	15	0.381	0.171	122.81	0.547
M	3	3	0.500	0.518	–3.47	–
N	6	6	0.578	0.115	402.61	0.167
O	8	9	0.130	0.231	–43.72	0.946
P	9	8	0.676	0.360	87.78	0.108
Q	6	3	0.491	0.198	147.98	–
R	11	5	0.331	0.226	46.46	–
S	6	3	0.340	0.299	13.71	–
T	9	18	*	*	*	0.093

* Unit T was never observed with other females or immatures.

compromising statistical tests because in no case did we assume sampling periods to be independent). Two individuals identified in association (according to either of the association measures) on a single occasion within a 2-h sample were considered to be associated within that sample, but no weighting was given to multiple instances of association within a sample.

For the analysis of preferred within-unit associations, sampling periods of a day were used and dyads were considered associated on a day if they were identified within 10 min (or clustered for A2/B) on the day.

Association Indices

The commonly-used association indices (e.g. 'half-weight', 'simple ratio'; Cairns & Schwager 1987) are unsuitable for comparing associations within units vs. between-unit members and other whales. The denominators of these indices all include the number of samples in which either animal of a pair was identified,

regardless of whether the other animal was also identified. In order to be recognized as a member of a unit, an individual must have been identified in at least two identification periods, separated by at least 30 d (Christal et al. 1998). Yet, by definition, non-unit members must not have been identified during more than one of the identification periods for that unit (otherwise they would have been considered members of that unit). Thus, use of these standard indices introduces a bias, since the probability of a particular unit member being identified in the absence of a given non-unit member is greater than that of that unit member being identified in the absence of another member of its unit. To avoid this bias, a custom association index was used for this analysis. This was simply:

$$\frac{\text{number of 2-h samples in which X and Y were associated}}{\text{number of 2-h samples in which X and Y were both identified}}$$

Thus, this association index measures the frequency of association between two individuals, over only those samples during which both individuals were identified.

The simple ratio association index (Cairns & Schwager 1987) was selected for use when examining preferred associations within units and in the case study of associations in group A2/B, following Ginsberg & Young (1992). The problems described above are not present in these cases, since all individuals were known to be present on all days.

Analysis of Variation in Association Indices

The direction of differences between mean pair-wise association indices for 'within-unit' pairs vs. 'between-unit and other' pairs (i.e. between a unit member and any non-unit group member) was tested, over all units, using a sign test. This test considers the relative numbers of positive and negative differences between the two means, using units as cases. Given no association preference in either direction, the numbers of positive and negative differences should be equal. A sign test indicates the significance of any deviations from equality.

For the case study of group A2/B, matrices of association indices were compared with unit membership using the Mantel test (Mantel 1967). The statistical significance of the Mantel statistic was tested by means of a Monte Carlo test, using 1000 random permutations, as recommended by Schnell et al. (1985).

To examine whether members of units associated randomly, we used the Monte Carlo permutation method of Bejder et al. (1998), with a modification described by Whitehead (1999). In this method, the associations among members of the unit are permuted in such a way that the number of associations (other animals identified within 10 min) of each animal on each day is left unchanged (Whitehead 1999). For each random permutation, the simple ratio association indices between all pairs of individuals are calculated. We use the standard deviation of these association indices as a test statistic

(Whitehead 1999), because preferred re-associations of pairs of animals between days will produce some abnormally high indices, whereas avoided associations will give unusually low ones. The null hypothesis that associations are independent between days (given the number of associations of each individual on each day) is rejected when the standard deviation of the real association indices is greater than 95% of the standard deviations calculated from random data. In the method of Bejder et al. (1998), the permutation routine is sequential and so the permutations are not independent. Thus, a greater number of permutations are needed than in standard Monte Carlo methods. We used 50 000 permutations of the data which gave repeatable p -values for each unit (Bejder et al. 1998). For some units, especially those with few members, the associations could not be permuted subject to the constraints, and no test could be performed.

Spatial Analysis

The spatial analysis asks whether, within a group, units or individuals had preferred positions within the foraging formation. This analysis was only possible for the group A2/B followed in 1995 and the group consisting only of unit T followed in 1999. For other groups where we have sufficient long-term data to distinguish units, locations were from SATNAV, which does not give sufficient precision (≈ 1000 m vs. ≈ 100 m for the GPS used in 1995 and 1999) for such analyses.

The positions of identified animals relative to the mean track of the moving group were estimated as follows: for each identification i , at time t_i and in position (x_i, y_i) , we considered all other identifications within 1 h, which we called 'neighbouring identifications'. If there were less than five neighbouring identifications, then the position of this identification relative to the group was not calculated. For A2/B, 238 identifications (out of 262) fulfilled the 'five-neighbours' criterion, and they had a mean of 12.5 neighbouring identifications each. There were 330 suitable identifications for T (out of 498), with a mean of 6.2 neighbouring identifications each.

The movement of a group at the time of identification i was estimated by quadratic regressions of the x - and y -coordinates of these neighbouring identifications on time (t):

$$x = a_1 + a_2t + a_3t^2$$

$$y = b_1 + b_2t + b_3t^2.$$

An example of a 'mean track' calculated by making such quadratic regressions on the neighbouring identifications is shown in Fig. 1. The estimated heading of the group (relative to the x -axis) at the time of identification i was:

$$\theta = A \tan[(b_2 + 2b_3t_i) / (a_2 + 2a_3t_i)].$$

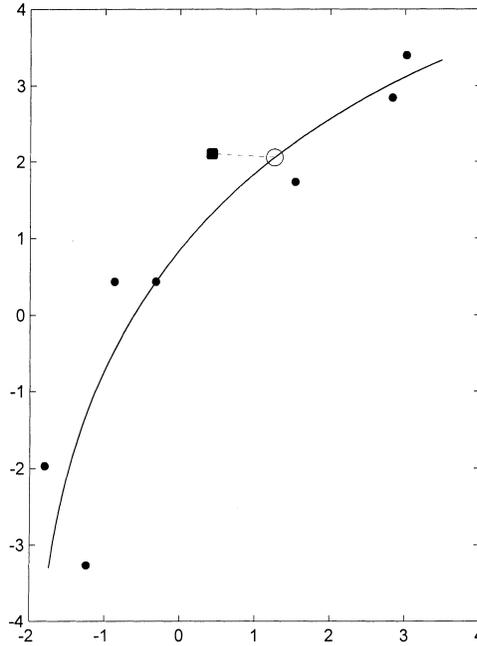


Fig. 1: Illustration of regression technique for determining the relative position of one identification (marked by '■'; ID#3287, 1 June 1995 at 08:15 h). Positions of identifications within 1 h are shown (●) and a quadratic position–time regression is fitted through them. The expected position of the original identification, given its time, is marked by a '○', and the dashed line indicates the displacement. Scales are in km

The deviation of identification i from the mean track of the group was estimated by:

$$d_x(i) = x_i - (a_1 + a_2 t_i + a_3 t_i^2)$$

$$d_y(i) = y_i - (b_1 + b_2 t_i + b_3 t_i^2).$$

The deviation of one point from the mean track is illustrated in Fig. 1, and a sequence of identifications relative to the calculated mean track is shown in Fig. 2. Four measures of the position of identification i relative to the mean track of the group were calculated:

$$\text{total displacement : } \sqrt{(d_x(i))^2 + d_y(i)^2}$$

$$\text{right/left displacement : } (d_x(i)\sin(\theta) - d_y(i)\cos(\theta))$$

$$\text{forward/backward displacement : } (d_x(i)\cos(\theta) - d_y(i)\sin(\theta))$$

$$\text{sideways displacement : } \text{abs}(d_x(i)\sin(\theta) - d_y(i)\cos(\theta)).$$

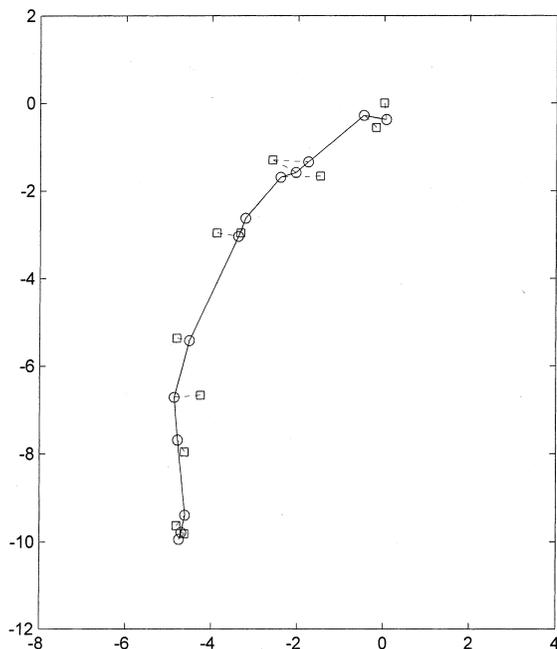


Fig. 2: Recorded positions of identifications ('□') of sperm whales and expected positions ('○', using quadratic regression technique) between 14:39 h and 17:42 h on 31 May 1995. Scales are in km

These measures were then used to ascertain whether certain individuals, or units for A2/B, were consistently further/closer to the mean position of the group (total displacement), on one side or the other (right/left), in front or behind (forward/backward), or further/closer to the mean track of the group (sideways).

Tests of Relative Position

The four measures of position relative to the mean track of the group were not obviously related to the estimated speed of movement of the group (inspection of scatterplots, $r^2 < 0.01$). However, they were not normally distributed (Lilliefors test, $p < 0.05$ for all four measures) and there were significant differences between days (Kruskal–Wallis test: $p = 0.046$ for total displacement, $p = 0.068$ for sideways displacement, $p > 0.10$ for other measures, for A2/B) and possibly other forms of non-independence.

To test for differences between units A2 and B, whilst removing these problems of non-normality and non-independence, we calculated mean values of each measure for each individual over the whole week. These were normally distributed for each unit (Lilliefors tests, $p > 0.05$). We then tested using univariate and multivariate t-tests for differences between the units.

To test for differences between individuals, we calculated the mean value of each individual on each measure on each day, and tested for individual effects

using a repeated-measures MANOVA design (with days being blocks). Residuals following this procedure were normally distributed for A2/B (Lilliefors test, $p > 0.05$ for all four measures) but not for T (Lilliefors test, $p < 0.05$ for all four measures), and so the results for group T should be treated cautiously.

Results

For 16 of the 19 units which grouped with other units, the mean pairwise 'within-unit' association index was greater than that for 'between-unit and other' pairs (Table 1), indicating an association preference for members of an animal's own unit (the magnitude of which appeared to vary between units). The three exceptions share no obvious features that distinguish them from the other units, and in two of these cases (units F and M), the negative difference is small. The direction of the association preference was significant over all units (sign test, $p = 0.004$).

A total of 79 clusters (size 2–6, mean 3.1) were included in the analysis of group A2/B. Each of the 22 group members was identified in 3–15 of these clusters (mean 9.2). Members of the group showed a significant preference for clustering with members of their own unit (Table 2, Fig. 3). This preference was also significant for the '< 10 min' association measure.

Most of the units showed no indication of preferential association among members (Table 1). Exceptions were units A, B and F. The Monte Carlo test for unit F was barely significant at $p < 0.05$ (Table 1). Units A (from which A2 split) and B were two of the best-studied units in our study, but they also had particularly large numbers of members (Table 1) and were relatively unstable (Christal et al. 1998). Examination of the patterns of association within units A and B revealed some hints of a relationship between short-term associations and past or future changes in unit membership, but no clear pattern. Because the Monte Carlo test constrains permuted associations so that the number of associates of any individual is fixed on any day (Whitehead 1999), changes in unit membership (through recruitment, death, merges, splits or transfers) between days will not, in themselves, result in significant p-values. The general picture of homogeneous associations within units is exemplified by our best-studied unit, T, which was identified on 18 days, never grouped with other units.

Table 2: Comparison of short-term association indices within and between units A2 and B in 1995, matrix correlation (r) and significance of the Mantel test (p)

Association measure	Mean pair-wise association index			Mantel tests	
	within A2 (n = 10)	within B (n = 135)	between A2 and B (n = 85)	r	p
Clustered	0.254	0.066	0.014	0.376	<0.001
< 10 min	0.197	0.078	0.052	0.209	0.003

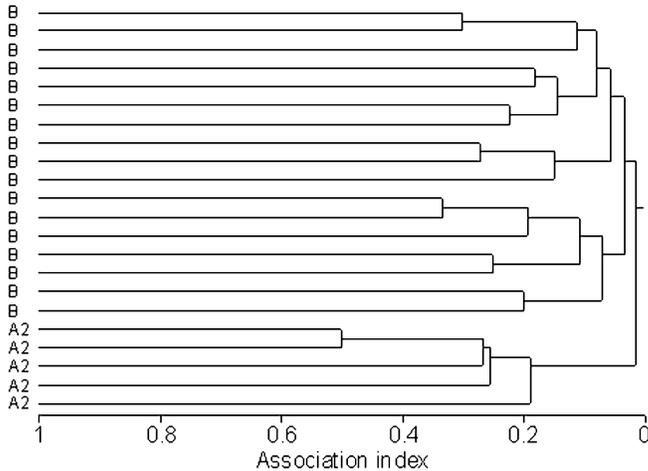


Fig. 3: Average linkage cluster analysis of the association matrix using the 'in cluster together' association measure, for members of group A2/B

Associations between dyads within this unit were quite uniform, with simple ratio indices having a mean of 0.45, $SD = 0.04$, and a range of 0.28–0.63; the permutation test did not reject a null hypothesis of no preferred companionships (Table 1).

In group A2/B, the two units differed significantly in the mean relative positions of their members relative to the mean track as expressed by the four displacement measures – total, right-left, forward-back, and sideways (Wilks' $\Lambda = 0.519$, $p = 0.019$). Members of unit A2 were significantly further from the mean position of the group, both overall (660 m vs. 510 m), and perpendicular to the track (420 m vs. 320 m), than members of unit B (Table 3, t-tests, $p < 0.05$). The differences in total displacement between units are quite dramatic, with all members of unit A2 having greater mean total displacement from the track than all members of unit B, with the exception of #812 (Fig. 4).

Inspection of the data suggests that the greater displacement from the mean track of the group shown by the smaller unit, A2, is the result of members of the two units often favouring contrasting left-right displacements over periods of a few hours. For example, on 27 May 1995, A2 was on the right of the rank in the morning, and on the left around midday (Fig. 5).

In contrast to the between-unit results, there were no significant ($p > 0.05$) differences between individual members of groups A2/B or T in the four measures of relative position (repeated-measures ANOVA) when tested singly (Table 3) or as a multivariate whole (Wilks' $\Lambda = 0.418$, $p = 0.710$ for A2/B; Wilks' $\Lambda = 0.759$, $p = 0.589$ for T). The results were also non-significant when A2 and B were tested separately (Unit A2: Wilks' $\Lambda = 0.537$, $p = 0.983$; Unit B: Wilks' $\Lambda = 0.332$, $p = 0.141$).

Table 3: Relative position of individuals in groups A2/B and T, together with results of tests for differences between positions of units (t-tests on individual means) and individuals (repeated-measures ANOVA's on daily means of individuals)

Measure	Mean (SD) in km				Significant differences between (p)		
	A2/B	Unit A2	Unit B	Unit T	Units A2 & B	Individuals in A2/B	Individuals in T
Total displacement	0.54 (0.37)	0.66 (0.36)	0.51 (0.36)	0.41 (0.53)	0.009	0.165	0.805
Right/left displacement	0.00 (0.46)	0.10 (0.51)	-0.03 (0.44)	0.01 (0.41)	0.183	0.564	0.500
Forward/back displacement	0.00 (0.47)	-0.08 (0.55)	0.03 (0.44)	0.02 (0.54)	0.067	0.873	0.712
Sideways displacement	0.34 (0.30)	0.42 (0.30)	0.32 (0.30)	0.25 (0.32)	0.021	0.227	0.638

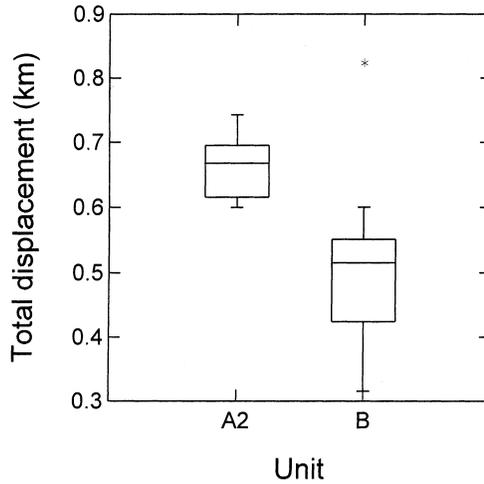


Fig. 4: Box plot showing differences in mean total displacement of individuals of the two units from their expected positions, given the movement of the group. '*' indicates an outlier from the general distribution of members of the cluster (whale #812)

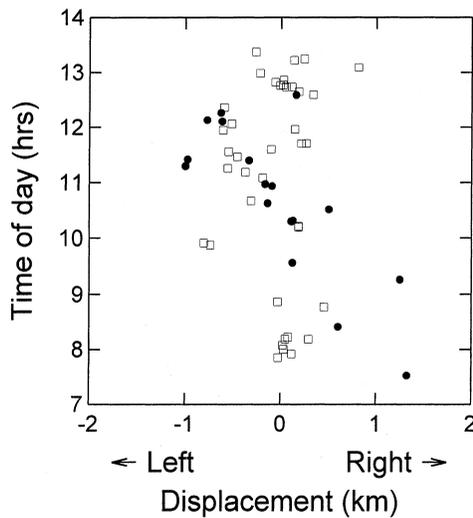


Fig. 5: Left-right displacement about mean track with time of day on 27 May 1995 in km for members of unit A2 (●) and unit B (□). Points are slightly 'jittered' so that they are not coincident

Discussion

In the analysis of association patterns of unit members within groups, there is one principal factor which has the potential to introduce biases. This is the

problem of multiple groups. If members of two separate groups (one of which contains a known unit) are identified within a given sampling period, then members of the group which does not include the unit of interest will be considered to be 'others' (i.e. potential associates of the unit members), and included in analyses. Since groups are by definition separate entities, the probability of association between members of the unit and members of the other group, using a short-term measure (i.e. identified within 10 min), is effectively zero. Thus, false inclusion of members of other groups would bias the mean pair-wise 'between-unit and other' index downwards, thereby artificially increasing the difference between 'within-unit' and 'between-unit and other'. Whilst the selection of a 2-h sampling period would seem likely to have minimized this problem (as groups were very rarely observed at the same time or photographed within a few hours), it is possible that residual effects remain. Whilst such effects may have introduced a slight bias in particular cases, it does not seem likely that this bias would have been of sufficient frequency and magnitude to explain the widespread lower values for mean 'between-unit and other' indices. This bias is not a factor in the results presented for the A2/B group, because no other groups were seen during the week-long study of this group.

The results of these analyses indicate that individual sperm whales within groups associate preferentially with members of their own unit. This preference is apparent not only in terms of cluster membership, but also in the looser (< 10 min) measure of spatio-temporal proximity. In the case of group A2/B, this was at least partially the result of members of the two units favouring opposite sides of the foraging rank. Thus, the spatio-temporal distribution of individuals within a foraging group of sperm whales is not random; those individuals that hold long-term relationships (i.e. are members of the same unit) are more likely to be close together spatially and to exhibit synchronized diving behaviour.

The apparent segregation of social units within groups of sperm whales seems to contrast with reports for other species. Individuals from associating 'family groups' of elephants are described as mixing freely (Moss & Poole 1983). This intermingling of social units may reflect the fact that particular family groups show association preferences for other family groups which are known or presumed to share a common ancestry (Moss & Poole 1983). Therefore, when family groups aggregate, even those individuals which are members of different families have relationships based on repeated associations, and are more closely related than members of two randomly selected family groups would be. Around Vancouver Island, British Columbia, the social structure of fish-eating 'resident' killer whales is strongly matrilineal, with no dispersal of either males or females from their mother's group. The closest parallel to the sperm whale unit is the 'subpod', with a mean of about seven individuals whose members spend > 95% of their time travelling together (Bigg et al. 1990). Within subpods, individuals have a clear preference for swimming closer to their nearest relatives, but when joining and socializing with other subpods, which are often related, bonds seem to

weaken (Osborne 1986; Bigg et al. 1990). As with elephants, this seems to be a rather different pattern to that of the sperm whales. However, we are not aware of any studies in which the extent of segregation or intermixing of social units has been explicitly examined, as it has in the current study. The degree of intermixing may vary depending on how long the social units have been together, as well as the relatedness between them.

In contrast to the picture with killer whales (Baird 2000) and lions (*Panthera leo*; Stander 1992), and the between-unit results for sperm whales, we could generally find no indication of preferential association or spatial position within sperm whale units. The principal exceptions were two of the largest and best studied units, A and B. During the study, unit A split whilst unit B received at least three transfers from other units (Christal et al. 1998). This perhaps suggests two general types of sperm whale unit, or a continuum between them: relatively unstable units with some internal structure of associations (such as units A and B), and smaller, more stable units within which associations are quite homogeneous (such as unit T). These indications of generally homogeneous relationships within units are consistent with the lack of evidence for individual specific positions in feeding ranks studied off the Galápagos in 1985 and 1987 (Whitehead 1989), and no significant correlations between genetic relatedness and association index within A2/B (Christal 1998).

Our results strongly suggest that long-term relationships within stable units are of considerable significance to female and immature sperm whales, and that animals receive sufficient benefit from such relationships that they conspicuously retain them when the units group. However, the nature of these benefits remains unclear. Babysitting, often suggested as a principal function for sociality in female sperm whales (Best 1979; Gordon 1987; Whitehead 1996a), had no immediate significance for members of either unit A2 or unit B in 1995, because there were no juveniles in the group (Christal & Whitehead 2000). The prospects of future babysitting may have been important for these animals. Another candidate for the value of long-term relationships is the communal sharing of information about ephemeral, but partially predictable, resources over the sperm whales' large spatial ranges (Whitehead 1996b). These whales may affirm such relationships by short-term associations. More standard benefits of grouping, such as increased feeding rates achieved by foraging in a rank (Whitehead 1989) or communal vigilance or defence against predators (e.g. Arnbohm et al. 1987; Weller et al. 1996), would not seem to need long-term relationships, and may explain the short-term grouping of stable units (Whitehead et al. 1991).

To preferentially associate with members of their own unit within foraging groups, sperm whales need to identify other individuals whilst foraging at depth and at ranges of several hundred metres. Watkins (1980) has suggested a social orientation function for the loud clicks that sperm whales make almost continuously during their deep dives. This could work if an animal can identify another from its click characteristics, or by using its own echolocation to scan the companions' bodies. However, it is likely that echolocation for prey, rather than

identification of self or others, is the primary function of such clicks (Gordon 1987; Goold & Jones 1995; Møhl et al. 2000).

Acknowledgements

The research was funded by the Natural Sciences and Engineering Research Council of Canada, the Whale & Dolphin Conservation Society, the National Geographic Society, the International Whaling Commission, Cetacean Society International and the Green Island Foundation. Field work was carried out under the auspices of the Charles Darwin Research Station, with the permission of the Galápagos National Parks Service, the Instituto Nacional de Pesca, and the Armada de Ecuador. We acknowledge the valuable contribution of the many people who have taken part in the field research since. We are particularly grateful to Godfrey Merlen for his ongoing photo-identification work, and for logistical help in the field. Thomas Lyrholm, Erland Lettevall and The Whale Conservation Institute contributed identification photographs taken off the Galápagos Islands in 1988–89 and 1993–94. Tom Arnbom, Susan Waters, Susan Dufault and Luke Rendell helped analyse the individual identification photographs. JC was supported by a Canadian Rhodes Scholars Foundation Scholarship and a Commonwealth Scholarship. The manuscript was improved by reviews from Robin Baird, Richard Connor, Martha Leonard, Luke Rendell, Daniel Ruzzante, and two anonymous reviewers.

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Received: June 19, 2000

Initial acceptance: September 16, 2000

Final acceptance: October 29, 2000 (J.-G. Godin)