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PATTERNS OF VISUALLY OBSERVABLE BEHAVIOUR AND VOCALIZATIONS IN GROUPS OF FEMALE SPERM WHALES

by

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(With 5 Figures)

(Acc. 31-V-1991)

Introduction

In social vertebrates individuals often need to spend a significant proportion of their time and/or energy maintaining social bonds. This may cause conflict with the desirability of optimizing food intake (DUNBAR & DUNBAR, 1988), especially for species in which food is gathered incrementally, and food intake is time limited. The female sperm whale (*Physeter macrocephalus*), whose fitness is likely to be closely tied to both socialization and the proportion of time spent foraging, might be expected to be an exemplar of a species with such a dilemma.

Female sperm whales, together with their offspring, are invariably found in groups with 10-30 members (BEST, 1979; WHITEHEAD & WATERS, 1990). These groups seem to be reasonably stable in composition over periods of years (OHSUMI, 1971; WHITEHEAD & WATERS, 1990), and there is some evidence that members may be genetically related (ARNBOM & WHITEHEAD, 1989). Within groups there appears to be communal caring for calves (GORDON, 1987), and female sperm whales are

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known to display considerable altruism towards injured group members (Caldwell *et al.*, 1966).

Best (1979) proposed two possible principal functions for the sociality of female sperm whales: protection of calves from predators and increasing feeding efficiency by communal foraging. Recent evidence suggests that the first of these, calf protection, is likely to be more important (Gordon, 1987; Arnbom & Whitehead, 1989; Whitehead, 1989). Sperm whales seem to be able to successfully defend themselves and their calves against their major natural predator, the killer whale, *Orcinus orca*, by forming cohesive cooperative groups (Arnbom *et al.*, 1987).

In most ocean areas, female sperm whales feed largely on mesopelagic and bathypelagic squid (Kawakami, 1980). These squid average about 1 kg in mass and are generally not found in large aggregations (Whitehead, 1989). Best (1979) calculates that a female must consume approximately 300 squid per day. As sperm whales are able to defend themselves effectively against all natural predation, in the absense of significant human hunting it is likely that their populations are generally food-limited. Therefore, with individuals trying to maximize their catch of relatively small, widely dispersed prey, the time that can be devoted to foraging may be an important component of fitness.

Off the Galápagos Islands we have found that female and immature sperm whales spend much of their time diving, apparently searching for food. While foraging, they normally dive to about 400 m below the surface for about 40 min (Papastavrou *et al.*, 1989). Dives are separated by approximately 10 min spent breathing at the surface (Papastavrou *et al.*, 1989), when the whales are seen in clusters of 1-3 individuals (Whitehead, 1989). At the end of each surface period a sperm whale raises its flukes into the air to commence a dive. While foraging, members of a group often align themselves parallel to one another in a rank approximately 550 m long arranged perpendicular to the direction of travel (Whitehead, 1989). This rank sweeps through the ocean at about 2 knots (3.7 km/hr) (Whitehead, 1989).

However, female and immature sperm whales do not spend all their time in this foraging routine. From time to time members of the group can be seen together at the surface in a few large clusters for periods of an hour or more (Whitehead, 1987). Particularly during these longer surface periods, a variety of activities may be seen from above the water surface. These include dramatic displays such as leaps from the water as well as more prosaic consequences of activities principally taking place beneath the surface.

Sperm whale sounds were first described by WORTHINGTON & SCHEVILL (1957), who heard impulsive 'clicks' about half a second apart. Despite one report to the contrary (PERKINS *et al.*, 1966), which attributed a wide variety of sounds to sperm whales, it is generally agreed that sperm whales produce only clicks (BACKUS & SCHEVILL, 1966). BACKUS & SCHEVILL (1966) noted that the clicks, which were often made up of a series of pulses, were broadband from about 200 Hz to 32 kHz, with the dominant frequency around 5 kHz; that the interval between clicks generally varied from about 0.025 to 1.250 s; and that the whole click lasted about 2-24 ms. WATKINS (1980) reported that clicks displayed little directionality, showed no change in character with depth, and though sound levels were highly variable, could be heard at distances of over 10 km under good conditions. BACKUS & SCHEVILL (1966) proposed echolocation as a probable function of these click trains which WEILGART & WHITEHEAD (1988) call 'usual' clicks. This echolocation hypothesis has been supported by the work of NORRIS & HARVEY (1972), GORDON (1987), MULLINS *et al.* (1988), and WHITHEAD & WEILGART (1990). However WATKINS (1980) believed that sperm whale clicks are not directional enough, too regular in interclick interval, not given often enough, too loud, and too long in duration to be primarily used for echolocation. Instead, he proposed that usual clicks are mainly social signals.

BACKUS & SCHEVILL (1966) alluded to 'short, irregularly spaced sequences of clicks which are repeated several times within the space of a few tens of seconds'. These stereotyped, repetitive patterns, composed of short series of 3 to 40 or more clicks were later called 'codas' by WATKINS & SCHEVILL (1977). Codas are usually about 0.5 to 1.5 s in duration and can be precisely repeated from 2 to 60 or more times. Higher rates of clicking, 60-80 or more clicks/s which are perceived by humans as 'creaks', have been noticed by NORRIS & HARVEY (1972), WATKINS (1980), GORDON (1987) and MULLINS *et al.* (1988).

Sperm whale vocalization patterns have been informally related to the type of behaviour in which the whales are engaged (WATKINS & SCHEVILL, 1977; WHITEHEAD, 1987). When at depth, and probably foraging for food, individuals generally produce usual clicks. In contrast, when the whales are at the surface they are often silent, although sometimes codas or creaks are heard.

In this paper we investigate the relationships between visible activities and vocalizations, and use these relationships to examine temporal patterns of behaviour in the sperm whale. We are particularly interested in how foraging alternates with more social behaviour.

Methods

1. *Field methods.*

The data used in this paper were collected from the 10 m auxiliary sloop Elendil with a crew of 5-6 in the waters around the Galápagos Islands, Ecuador (0°S, 90°W). Research was carried out between 23 February and 20 April 1985 (a total of 30 24-hr days spent tracking sperm whales) and 3 January and 28 June 1987 (57 days spent tracking sperm whales). The vessel was at sea for 5-14 day periods separated by a few days in port resupplying.

We listened for the clicks of the sperm whales with a directional hydrophone specially built for the project by Dev-Tec Inc. (Pasadena, CA). This allowed us to locate groups of sperm whales and track them for periods of days, staying within about 2 km of the whales during most of the tracking time (night and day). Groups principally consisted of female sperm whales and their young, but these were sometimes accompanied by large, mature males (WHITEHEAD & ARNBOM, 1987; WHITEHEAD & WATERS, 1990).

We define a 'cluster' to be a set of individuals within 100 m of one another coordinating their movements (WHITEHEAD & ARNBOM, 1987). During daylight, the ranges, bearings and composition (maximum number of observed: large males, first-year calves and other whales) of all visible clusters of whales were recorded every 5 min, together with the number of occurrences of any observable activities. In this paper, we use 'activity' for specific observable actions (as well as cluster sizes and speed and consistency of movement) and 'behaviour' for general states. The activities recorded included (Fig. 1):

Fluke-up: flukes raised above the water surface, usually at the start of a deep dive;

Breach: a leap from the water, showing at least half the body;

Lobtail: a thrash of the flukes onto the water surface;

Spyhop: a slow raising of part of the whale's head above the water surface (indicating that the whale is lying nearly vertically in the water);

Sidefluke: a portion of the flukes visible above the water surface but oriented vertically (indicating that the whale is turning sharply).

Additionally, we estimated the speed of the whales (to the nearest 0.5 knot (0.9 km/hr) from comparison with the mechanically measured speed of the research vessel), and heading (in degrees magnetic from compasses) of clusters when they were sufficiently close for these measures to be determine with reasonable accuracy.

While tracking sperm whales, for 5 min each hour (on the hour) we recorded the underwater sounds (or lack of sounds) of the whales through a Benthos AQ17 omnidirectional hydrophone (10 m depth), Barcus-Berry "Standard" or Ithaco 453 preamplifier, and Uher 4000, Sony TC770 or Nagra IV-SJ tape recorders. High-pass roll-off filters (starting at 10 kHz) in the preamplifiers were used to minimize wave noise. Recordings were made at 19 cm/s. Occasionally, hourly recording sessions were missed due to distant or fast-moving whales, or because of technical problems.

2. *Laboratory acoustic methods.*

The 1,696 5-min sessions of acoustical recordings from both 1985 and 1987 were first analyzed aurally by signalling to a computer when codas and creaks (high repetition rate click series with interclick intervals less than 0.1 s; WHITEHEAD & WEILGART, 1990) were heard. Since recordings were often not the full 5 min in length, only the first 4 min of each session was used. Sessions with poor signal-to-noise ratios and sessions that were under 4 min in length were eliminated from the statistical analysis (124 sessions eliminated).

A 16-s section of each session with acceptable signal-to-noise ratio was chosen so that it did not contain obvious extraneous sounds, such as the banging of the boat's rudder,

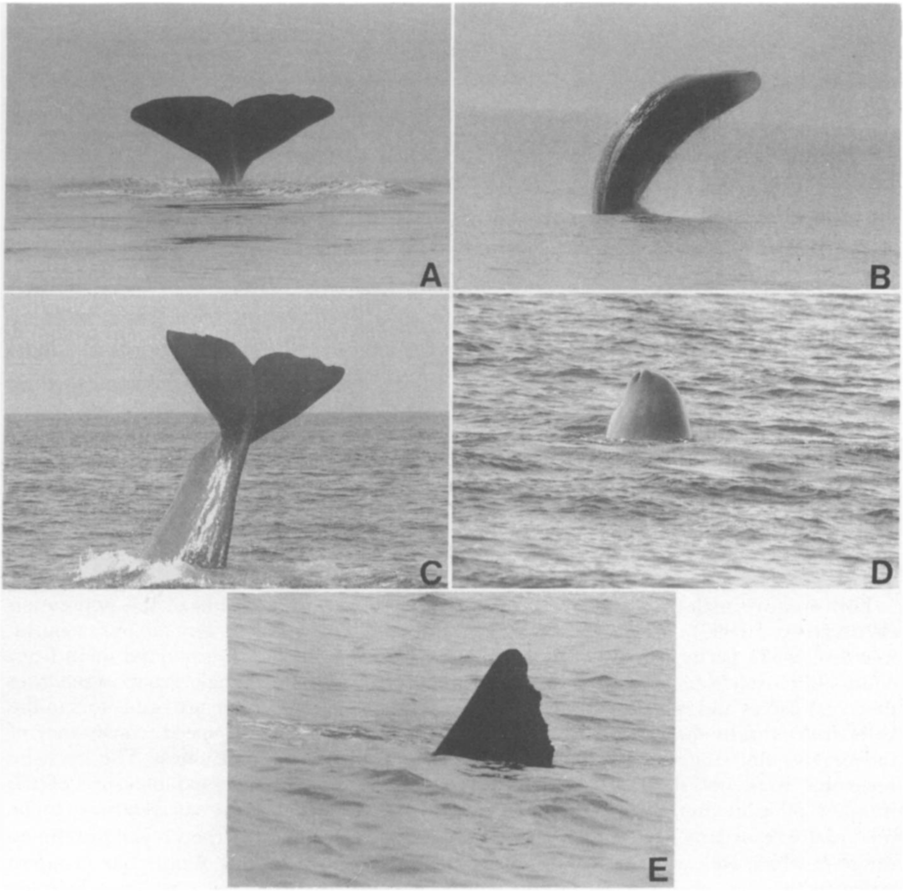

Fig. 1. Fluke-up (a), breach (b), lobtail (c), spyhop (d), and sidefluke (e).

or vocalizations of other cetaceans, or any sperm whale codas, creaks or slow clicks (distinctive vocalizations made by males; Weilgart & Whitehead, 1988). This meant that the section consisted almost entirely of usual clicks. The number of clicks in the 16-s section was counted automatically using a digital oscilloscope and computer, and used to compute a click rate in clicks/s for the session (Whitehead & Weilgart, 1990). Very high click rates (>ca. 60 clicks/s) appeared to be the result of groups meeting rather than of any within group behavioural change (Whitehead & Weilgart, 1990). Therefore, in this paper we use a measure of whether more than or less than 20 clicks/s were heard as a crude indicator of the group's output of usual clicks.

3. *Visual and acoustic variables.*

Variables representing mean rates of visually observable activities were calculated from the 5-min observational records during the 30 min before, and 30 min after, each acoustic recording session. Thus visual records are compared with the closest hourly recording session. When visibility was restricted by fog or for other reasons, the observational records for that hour were not used. There were at least some observations of whales (allowing cluster size, etc. to be estimated) in all hours with acceptable visibility. The following visual and acoustic variables were used for statistical analysis:

Mecs: Mean cluster size for clusters seen within 500 m of boat (for 1-hr periods with more than five such clusters, and excluding mature males and first-year calves);

Macs: Maximum cluster size seen during 1-hr period (excluding mature males and first-year calves);

Speed: Mean scalar speed recorded from whales (in knots);

Prop: Mean vector speed with all speeds standardized at 1.0 (only when 5 or more speeds recorded)—an indicator of the consistency of the headings of different clusters (*e.g.* if all clusters were moving northwest then Prop = 1.0; if one cluster was moving north, three east, one south and one west then:
$\mathrm{Prop} = \sqrt{[(1\times1 + 3\times0 + 1\times-1 + 1\times0)^2 + (1\times0 + 3\times1 + 1\times0 + 1\times-1)^2]}/6 = 0.333$);

Fluker: Fluke-up rate per whale seen at the surface in each 5-min period;

Breachr: Breach rate per whale seen at the surface in each 5-min period;

Lobr: Lobtail rate per whale seen at the surface in each 5-min period;

Spyr: Spyhop rate per whale seen at the surface in each 5-min period;

Sflkr: Sidefluke rate per whale seen at the surface in each 5-min period;

Coda: Codas heard per 4 min recording session;

Creak: Creaks heard per 4 min recording session;

Lowc: Lowc = 1 if measured usual click rate less than 20 clicks/s, Lowc = 0 if measured usual click rate greater than 20 clicks/s.

Both mature males and first-year calves constituted less than 4% of the population (Whitehead, 1990), and as they seemed to contribute little to any of our acoustic measures or to perform many of our tallied activities we have also excluded them from counts of cluster size. Thus our analysis refers to members of female groups excluding first-year calves and mature males. The visual measures given above are indicators of the behaviour of individuals while at the surface, their gregariousness, speed, consistency of movement, and the rates at which they performed different activities. The acoustic measures were not standardized per individual, as we had no good measure of the number of individuals close enough to the hydrophone for their vocalizations to be potentially recordable. However, we were normally within 500 m (the very approximate range at which we can record codas and creaks; unpublished data) of only one group of sperm whales at any time. Although they varied somewhat in size, groups contained about 20 members (Whitehead & Waters, 1990), so that our coda and creak numbers are roughly those to be expected per individual in 80 min (20×4 min). Usual clicks can be heard at much greater ranges (up to about 5,000 m with our equipment) so that Lowc is only an approximate measure of whether or not usual clicks were being produced by all groups present within about this radius. Because of this imperfect standardization, the acoustic variables (especially Lowc) are less satisfactory representations of the behaviour of individual whales than those derived from visually observable activities.

Whitehead *et al.* (1989) argue that the rate of observing defecations per fluke-up may be used as an indicator of general feeding success. We use the same measure here over periods of calendar months, as in Whitehead *et al.* (1989).

4. *Statistical methods.*

None of the acoustic or visual variables used in this paper were normally distributed untransformed or with square-root or logarithmic (plus one) transformations (Kolmogorov-Smirnoff tests; $p < 0.01$). This invalidates standard parametric tests of hypotheses. However, in the analysis described below we were generally concerned with finding patterns in the data, rather than rigorous hypothesis testing. In such 'data analysis', normality is desirable, but not essential. When necessary and possible, we used non-parametric significance tests.

As the data were collected on an hourly schedule while following particular groups of sperm whales, the sampling units are not independent. Most variables show considerable autocorrelation with lags of up to about 7 hr (Table 1). For significance tests, a reduced data set containing only records collected at 0800 and 1600 hours was used. This reduces some of the problems of non-independence of sampling units. However, we recognize that our results only formally pertain to the sperm whales around the Galápagos Islands during the periods of our study.

The durations of bouts of a particular type of behaviour were estimated from a time series of a variable for which a high value (greater than a given cutoff value) signified that the type of behaviour was taking place. Let T(h) be the number of hourly records for which a record for the following hour existed, and the record for that hour and all the preceding h-1 hours had values of the variable greater than the cutoff, but the record h hours earlier had a value less than the cutoff (*i.e.* the number of records h hours into a bout for which it could be determined whether they marked the end of the bout or not). Of these T(h) records, let L(h) be the number in which the subsequent record had a value less than the cutoff (*i.e.* those marking the end of a bout). We can then test, using the likelihood-ratio G test (SOKAL & ROHLF, 1981), whether the probability that a bout ends after h hours is independent of h. If it is, then the process can be considered Poisson, and the bout lengths should be negatively exponentially distributed. The mean bout duration can be estimated from $\Sigma T(h)/\Sigma L(h)$ and its coefficient of variation from $1/\surd(\Sigma L(H))$. If the process cannot be considered Poisson, then we can estimate the probability that a bout lasts h hours from:

$$p(h)=[L(h)/T(h)]\prod_{i=1}^{h-1}(1-L(i)/T(i))$$

Standard errors for the p(h) can be derived using binomial theory. The mean bout duration is:

$$\sum_{h=1}^{\infty} h.p(h)$$

and its standard error can also be estimated from binomial theory.

Statistical analysis was generally carried out using the SYSTAT routines (WILKINSON, 1987).

Results

1. Statistical summary of visually observed activities and vocalizations.

Basic statistics for the visual and acoustic variables are given in Table 1. Although the mean cluster size was about 2.5, much larger clusters were seen on occasion. Clusters were usually well coordinated in their headings. Codas, creaks, and all visually observable activities, except fluke-ups, showed wide variation in their rates of occurrence.

TABLE 1. Summary statistics for visually observable and acoustic variables and degree of autocorrelation in sample

Variable	Sample size	Min.	Max.	Mean	S.D.	Unit	Auto-correlation to Lag of:
Mecs	879	1	24.8	2.55	2.53	whales	7 hr
Macs	932	1	52	5.69	5.83	whales	7
Speed	739	0.5	4.83	1.99	0.65	knots	11
Prop	440	0.14	1.00	0.81	0.18		2
Fluker	932	0	1.50	0.209	0.169	/whale	4
Breachr	932	0	1.70	0.037	0.109	/whale	6
Lobr	932	0	4.37	0.046	0.226	/whale	3
Spyr	932	0	1.00	0.021	0.072	/whale	2
Sflkr	932	0	1.00	0.035	0.075	/whale	2
Coda	1572	0	115	4.05	10.24	codas	6
Creak	1572	0	138	2.52	7.83	creaks	4
Lowc	1751	0	1.00	0.198	0.398		>12

1 knot = 1.852 km/hr. The autocorrelation with the lag given above and all with smaller lags (except possibly one) were significantly different from 0.0 ($p<0.05$); the autocorrelation with a lag of one hour greater than that given, and usually all greater lags, were not significantly different from 0.0 ($p>0.05$). In general, significant autocorrelations were greater than 0.1 and non-significant ones less than 0.1.

2. Relationships between variables.

Spearman correlation coefficients between variables calculated on the reduced data set (to avoid autocorrelation) are shown in Table 2. Correlations are mostly significant ($p<0.05$) and often quite large ($r_S = >0.3$). All variables are positively correlated with one another with the exception of speed, consistency of heading (Prop), and fluke-up rate, which are positively correlated with each other and negatively correlated with the other variables.

The relationships between the variables are revealed in more detail by the results of a principal components analysis on the entire data set (Table 3). Four principal components had eigenvalues greater than 1.0, and so may be considered worthy of further examination.

The first principal component, explaining 31% of the variance, relates large clusters, low speeds, little consistency of heading, few fluke-ups and many spyhops and sideflukes, with large numbers of codas and creaks but few usual clicks. It contrasts foraging behaviour, with animals spread out in small clusters along a consistently moving rank and fluking-up at the start of deep dives, with aggregative behaviour, during which animals

TABLE 2. Spearman correlation coefficients between visual and acoustic variables using reduced data set (just 0800 hours and 1600 hours)

	Mecs	Macs	Speed	Prop	Fluker	Brch	Lobr	Spyr	Sftr	Coda	Creak
Macs	*0.85*										
Speed	-0.04	-0.01									
Prop	-0.10	-0.18	*0.49*								
Fluker	*-0.49*	*-0.49*	0.06	*0.25*							
Breachr	0.13	*0.19*	-0.10	0.01	*-0.17*						
Lobr	*0.18*	*0.16*	-0.06	*-0.16*	*-0.16*	*0.46*					
Spyr	*0.26*	*0.38*	*-0.32*	*-0.35*	*-0.21*	*0.26*	*0.30*				
Sflkr	*0.25*	*0.34*	*-0.37*	*-0.38*	*-0.25*	*0.21*	*0.31*	*0.60*			
Coda	*0.39*	*0.42*	-0.05	-0.01	*-0.22*	*0.27*	0.17	*0.30*	*0.34*		
Creak	*0.35*	*0.37*	0.06	0.08	-0.07	0.07	*0.20*	*0.27*	*0.24*	*0.36*	
Lowc	*0.38*	*0.25*	*-0.26*	*-0.20*	*-0.38*	*0.26*	*0.30*	0.01	0.17	0.16	-0.06

Correlations significantly ($p<0.05$) different from 0.0 in italics. Sample sizes for individual correlations vary between 63-140.

TABLE 3. Results of principal components analysis of relationships between variables

	Principal components			
	1	2	3	4
Eigenvalues	3.73	1.61	1.45	1.26
% of variance accounted for	31.09	13.41	12.08	10.52
Loadings:				
Mecs	0.82	0.35	0.01	-0.14
Macs	0.83	0.24	0.17	-0.12
Speed	-0.38	0.30	0.44	-0.09
Prop	-0.48	0.39	0.19	-0.04
Fluker	-0.65	-0.19	0.30	0.25
Breachr	0.24	0.24	-0.13	0.74
Lobr	0.29	0.30	-0.09	0.71
Spyr	0.46	-0.60	-0.23	0.01
Sflkr	0.49	-0.57	-0.20	0.07
Coda	0.68	-0.08	0.53	0.03
Creak	0.57	-0.11	0.70	0.02
Lowc	0.41	0.55	-0.47	-0.31

clustered closely together at the surface, manoeuvring beside one another (as shown by sideflukes and spyhops). Usual clicks were heard most frequently during foraging, and codas and creaks during aggregation. This first principal component represents an important continuum in the behaviour of the whales, which we will refer to as *Sociality*. Large values of *Sociality* indicate that the whales were aggregating at the surface and small values indicate that the group was dispersed and diving. At these times we believe that the whales were mainly foraging, as there is no other obvious reason for them to undergo the physiological burden of deep diving. However, occasionally there may be functions other than foraging for the behaviour represented by low values of *Sociality*. Intermediate values may suggest either intermediate behaviour by all members of the group (*e.g.* moderate-sized clusters), or that part of the observation hour was spent aggregated at the surface and part dispersed and diving, or that some members of the group aggregated and others did not, or some combination of these effects.

The other components are much less important, each explaining less than 15% of the original variance. The second principal component contrasts fast, silent, coordinated movement such as that observed when sperm whales fled after an attack by killer whales (ARNBOM *et al.*, 1987), with occasions of considerable manoeuvring close to the surface by slow moving whales. Low values of the third principal component represent quiet, slow moving whales, with occasional spyhops and sideflukes. The fourth component largely represents high rates of the aerial displays, breaches and lobtails, which seem to be relatively unrelated to our other measures (WATERS & WHITEHEAD, 1990).

In Fig. 2, the second, third and fourth principal components are plotted against the first, *Sociality*. It is clear from the fan-shaped spread of points in each plot that there was little variation in the second, third or fourth components with low *Sociality*, in contrast to the considerable variation in all three components when *Sociality* was high. It seems that the behaviour of the whales, as described by the variables used in this paper, was rather stereotyped when they were foraging, but much less so during aggregation at the surface. In Fig. 2 the third component shows rather little variation when negative, in comparison to considerable scatter when positive. Low values of component three, then, represent whales lying quietly at the surface in a rather standardized manner.

In order to specifically examine the relationship between visually observable activities and vocalizations, we carried out a canonical correlation analysis. The results, summarized in Table 4, refer to an analysis of the entire data set. However, an analysis was also carried out on the reduced data set (to minimize the effects of autocorrelations) which showed the first two canonical correlations to be significantly different from zero ($\chi^2 = 28.1$, $df = 16$, $p = 0.031$). The first set of canonical loadings are very similar to the first principal component: high rates of

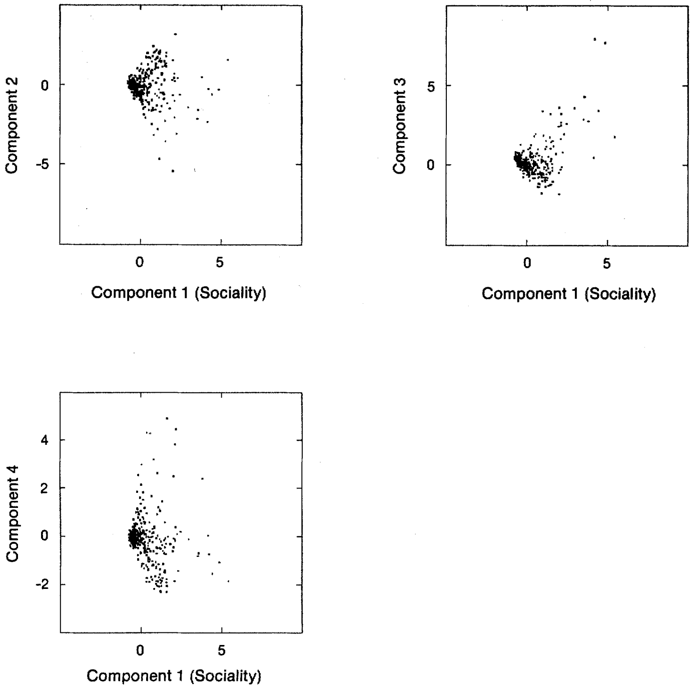

Fig. 2. Scores on second, third and fourth principal components plotted against the first (*Sociality*).

Table 4. Canonical correlation analysis of the relationship between visual observable activities and vocalizations

	Canonical variate		
	1	2	3
Canonical correlations:	0.723	0.486	0.210
Canonical loadings:			
Mecs	-0.948	0.068	0.125
Macs	-0.846	0.468	0.182
Speed	0.205	0.056	0.321
Prop	0.321	-0.270	0.781
Fluker	0.728	0.237	0.202
Breachr	-0.157	0.019	-0.123
Lobr	-0.224	0.031	-0.391
Spyr	-0.181	0.315	-0.371
Sflkr	-0.210	0.351	-0.244
Coda	0.642	0.642	-0.419
Creak	0.503	0.788	0.356
Lowc	0.764	-0.642	0.064

creaks and codas, and few usual clicks, were heard when cluster sizes were large, and fluke rates low. The second pair of canonical variates is less easily interpretable, and, given the much lower loadings, seems less important.

As visual data were lacking at night, and the data for some visual variables were not always collected during the day (Table 1), we sought simple representations of the first principal component, *Sociality*, from visual and acoustic data. The first acoustic canonical variate (0.038 × Coda + 0.040 × Creak + 1.94 × Lowc) is correlated with *Sociality* (first principal component) with $r = 0.772$. Only three visual variables, Mecs, Macs and Fluker, have absolute loadings greater than 0.5 on the first canonical variate, and of these Mecs and Macs are highly correlated (Table 2). A simplification of the first visual canonical variate (0.278 × Mecs–2.03 × Fluker) represents the first visual canonical variate well ($r = 0.994$), and is also closely correlated with *Sociality* ($r = 0.848$). These two measures will be referred to as *Sociality* (acoustic) and *Sociality* (visual) respectively. They have a correlation of $r = 0.593$.

3. Behavioural patterns.

Histograms showing the proportion of hourly records at different values on the *Sociality* continuum are presented in Fig. 3. The bimodal distribution of *Sociality* (acoustic) is due to the discrete values (0 and 1) taken by Lowc. For both *Sociality* (visual) and *Sociality* (acoustic) 76% of the observations have values less than 0.5. While *Sociality* appears to be a continuum, the results suggest that the groups spent very roughly three quarters of their time in the standard, foraging, mode of behaviour, and about a quarter engaged in other, generally more social, behaviour. WHITEHEAD & WEILGART (1990) arrive at a similar result from an analysis of usual click rates.

In order to examine the temporal alternation of behaviour we initially define *Aggregation* as values of *Sociality* (acoustic/visual) greater than 0.5, and *Foraging* as values less than 0.5. As is shown below, the exact value chosen for the cutoff between these two types of behaviour is not critical.

The distribution of lengths of bouts of *Aggregation* as suggested by *Sociality* (acoustic) was not significantly different from that expected from a negative exponential distribution (G-test, $\chi^2 = 1.75$, $df = 4$, $p > 0.1$). The mean bout duration was 2.2 hr (se 0.25 hr). However, the durations of bouts of *Sociality* (visual) greater than 0.5 were significantly different from negative exponential (G-test, $\chi^2 = 17.69$, $df = 5$, $p < 0.005$), with

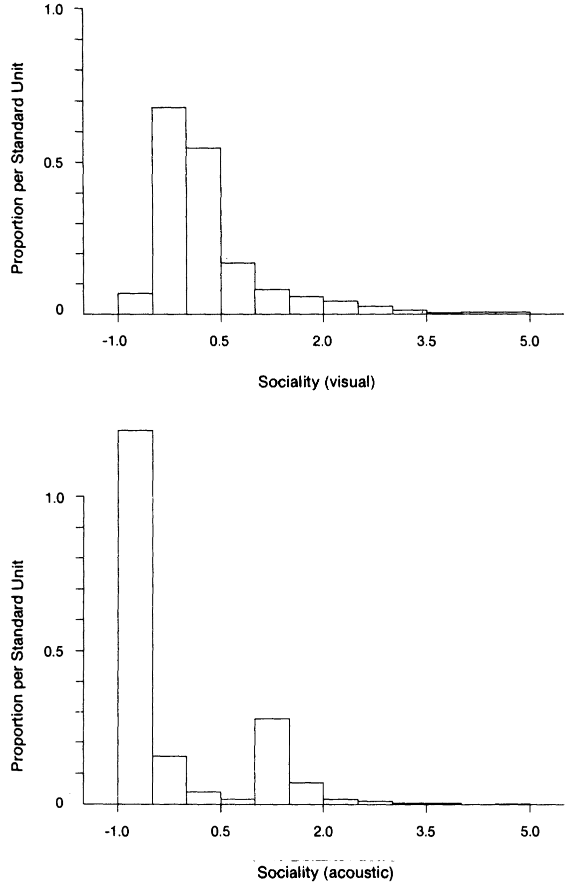

Fig. 3. Histograms of the measures of *Sociality* from visually observable activities (above) and recordings of vocalizations (below).

bouts tending to last either about 1 hr or 5-6 hr (Table 5). Using the formulae given in the Methods section the mean duration of bouts of *Aggregation* was estimated to be 3.5 hr (se 0.33 hr). The chosen value of the cutoff between *Aggregation* and *Foraging* (0.5) is not crucial. With cutoffs of 0.0 of 1.0, mean bout durations were within two standard errors of those with cutoffs of 0.5 for both measures.

Again using a cutoff of 0.5, the durations of bouts of *Foraging* were examined in a similar manner. Neither measure suggested a distribution significantly different from negative exponential (G-test, $\chi^2 = 3.98$, df = 7, $p > 0.1$ and $\chi^2 = 2.45$, df = 4, $p > 0.1$, respectively). The mean

TABLE 5. Probabilities that bouts of *Aggregation* had different durations, p(i), as indicated by visual and acoustic variables

Duration of bout	Variable			
	Sociality (visual)		*Sociality* (acoustic)	
	p(i)	s.e.	p(i)	s.e.
1 hr	0.29	0.035	0.51	0.037
2	0.10	0.018	0.23	0.033
3	0.12	0.025	0.08	0.019
4	0.05	0.014	0.06	0.020
5	0.17	0.045	0.07	0.029
6	0.27	0.062	0.00	—
>6	0.00	—	0.05	0.022

bout durations for *Foraging* were 6.3 hr (se 0.81 hr) using *Sociality* (acoustic) and 8.0 hr (se 2.1 hr) using *Sociality* (visual).

There was significant (Kruskal-Wallis test, $p = 0.033$) and consistent variation in the degree of *Sociality* (visual) within bouts of *Aggregation* (defined using a cutoff of 0.5). Mean values of *Sociality* (visual) rose to a peak about 3 hours after the start of a bout before falling again towards its end (Fig. 4).

4. Temporal variation.

Variation in our measures of *Sociality* was examined on three time scales (between years, between months, and with time of day) using Kruskal-Wallis non-parametric tests on the reduced data set (except for time of day when the full data set was used).

There was no significant difference in either measure of *Sociality* between 1985 and 1987 (for *Sociality* (visual) the mean value was higher in 1985, and for *Sociality* (acoustic) it was higher in 1987), or between calendar months ($p > 0.3$ for all tests). However, there was significant variation with time of day ($p < 0.001$ for both measures). As shown in Fig. 5, during daylight both visual and acoustic measures of *Sociality* rose to a pronounced peak in late afternoon and fell rapidly just before sunset (1800 hours off the Galápagos on the equator). Trends during darkness, as indicated by *Sociality* (acoustic), are less clear.

Using units of calendar months, as in WHITEHEAD *et al.* (1989), there was no apparent relationship ($r = -0.002$, $df = 7$) between mean *Sociality* and feeding success as indicated by defecation rates. There was also no significant relationship between defecation rates and the proportion of

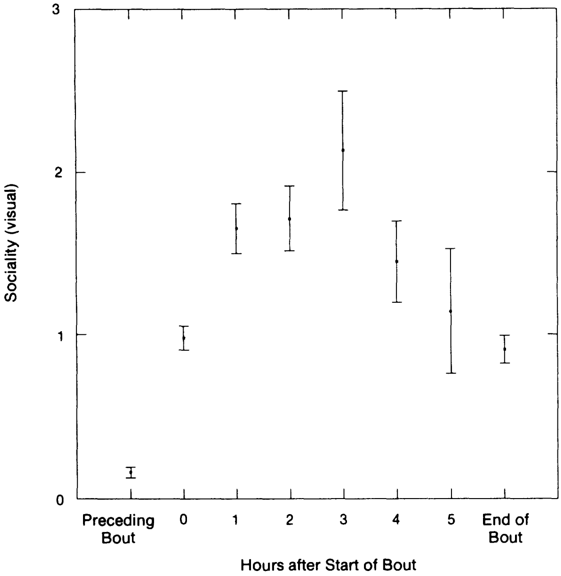

Fig. 4. Mean values of *Sociality* (visual) (± standard error bars) for the one hour preceding the start of a bout of *Aggregation* (defined with a cutoff of 0.5), the 1-hr periods after the start of the bout, and the last 1-hr period of the bout.

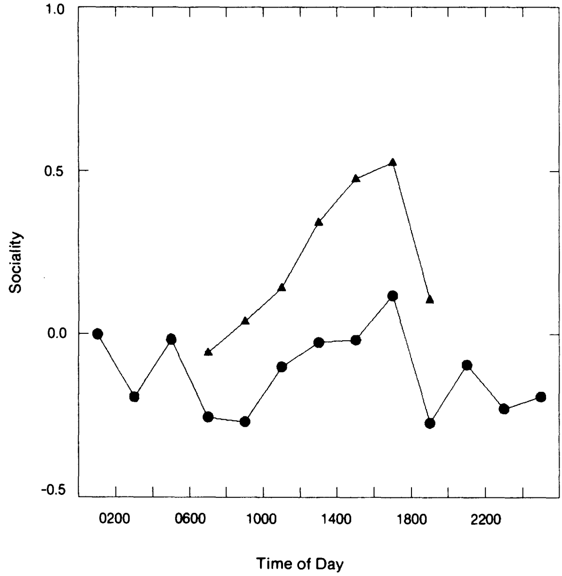

Fig. 5. Diurnal variation in *Sociality* from measures of visually observable activities (▲) and recordings of vocalizations (•), for each 2 hr during the day.

days (for which continuous records of more than seven hours were available) that contained long (>3 hr) bouts of *Aggregation* ($r_S = -0.147$, df $= 5$, $p > 0.10$) as indicated by *Sociality* (visual). There was a stronger, but still not statistically significant, relationship between the rate of occurrence (per hour spent foraging as indicated by *Sociality* (visual)) of short (<2 hr) bouts of *Aggregation* ($r_S = 0.360$, df $= 7$, $p > 0.10$) and defecation rate.

Discussion

The strong correlation that we found between visually observable activities and the rates at which different types of vocalizations were heard (canonical correlation of 0.723) is remarkable given the imprecision with which both sets of measures can be recorded. Other social odontocetes make a much wider range of vocalizations, including clicks, pulsed sounds, and whistles. In recent years relationships between visually observed activities and vocalizations have been examined for killer whales (FORD, 1989), pilot whales, *Globicephala melas* (WEILGART & WHITEHEAD, 1990), and beluga whales, *Delphinapterus leucas* (SJARE & SMITH, 1986; FAUCHER, 1989). Although statistically significant relationships between rates of different types of vocalizations and visually observable behaviour were found in all these studies, in no case was the correlation as strong and clear as our results on sperm whales. This may be partially a result of their deep-diving habits, leading to very different patterns of vocalizations when they are foraging at depth compared to when they are aggregating close to the surface. In addition, the much more limited range of vocalizations heard from sperm whales may explain this unusually close relationship between vocalizations and visually observable activities. In contrast to the mixture of clicks, pulsed sounds and whistles produced by other social odontocetes, sperm whales seem to only make clicks.

Acoustic behaviour will vary with factors other than those considered in this paper, such as group composition. For instance, WEILGART (1990) found codas to be heard significantly more frequently from groups containing first-year calves, or which were accompanied by mature males. However, these effects were small in comparison with those represented by the *Sociality* axis described in this paper.

The strong relationships between sperm whale vocalizations and visually observed activities are useful when considering the functions of the vocalizations. They support the generally held opinions that usual clicks, heard while the whales are foraging, are used for echolocation (BACKUS & SCHEVILL, 1966; GORDON, 1987) and codas, heard during aggregation, are used for communication (WATKINS & SCHEVILL, 1977). In this analysis, creaks appear to be used in similar circumstances to codas, and thus might be considered to be also a form of communication. However, GORDON (1987) and MULLINS *et al.* (1988) present evidence which suggests that creaks may be used by sperm whales as echolocation during feeding. In our recordings, there appeared to be two types of creaks: a) lengthy (> 10 s) series of clicks in rapid succession which were heard with many usual clicks; and, b) shorter series with fewer clicks which were frequently heard with codas. The latter were more numerous, and, as we were unable to find an objective way of meaningfully separating the two types of creaks, in the analysis presented in this paper creaks appear to take on the characteristics of codas. The shorter, coda-like creaks could be used as echolocation in social circumstances, or may be a form of communication, as has been suggested for some click series of other odontocetes (WATKINS & WARTZOK, 1985).

The female sperm whales that we studied spent roughly one quarter of their time at or near the surface in large slow moving clusters. These periods could be distinguished by both the visually observable activities and recordings of vocalizations, although, because of the problems in standardizing acoustic measures per individual, the visual records are more accurate indicators of the behavioural modes of the whales. Intermediate states between *Foraging* and *Aggregation* were also present (Fig. 3; WHITEHEAD & WEILGART, 1990). Aggregative periods at the surface seemed to last either about 1 hr, or about 5 hr, and to take place particularly in the afternoons, ending at dusk. Within longer periods, *Sociality* peaked near the middle of the period. In contrast, the durations of the more stereotyped *Foraging* periods were negatively exponentially distributed, showing no tendency to last a specified time. We have termed the periods when the whales were at or near the surface as having high levels of *Sociality*, mainly because of the proximity of whales to each other and apparent communication through codas. These periods may be important in maintaining social bonds within the stable groups, which become somewhat dispersed during *Foraging*.

However, the primary function of prolonged periods at the surface is not necessarily social. Male sperm whales, which are much less gregarious than females but dive to similar depths, sometimes lie quietly alone at the surface for periods considerably longer than the usual 10 min between dives (*e.g.* MULLINS *et al.*, 1988). This may suggest a need for certain breaks in the usual diving routine, perhaps for sleep, digestion, or to reduce lactate concentrations in the blood. Weddell seals (*Leptonychotes weddelli*) intersperse bouts of deep diving to several hundred metres with periods of a number of hours spent at or near the surface (KOOYMAN, 1989). Although northern elephant seals (*Mirounga angustirostris*) have been found to dive almost continuously for several days, there is evidence that during at least some of these dives the seals may sleep (LE BOEUF *et al.*, 1986). If sperm whales need reasonably frequent breaks from their diving routine of an hour or more at or near the surface, then, for members of closed groups, it is probably adaptive to take these rests together. Without temporal synchronization, resting individuals might have to expend energy 'keeping up' with the steadily moving rank of foraging group members. And resting together in a tight group will almost certainly lessen the possibility of successful attack by killer whales or other predators. Sperm whales resting together may need to communicate information, perhaps about potential predation, changes in formation, or whether to restart feeding. Therefore, under this scenario, lying at the surface in closely packed, slow-moving groups, and from time to time communicating through codas, might simply be an adaptive response to a physiological need to spend substantial time periods at the surface. However, even though the primary function of these periods may not be to maintain social bonds, they could still contribute to the behavioural cohesion of the group.

Does our evidence help distinguish the possible principal functions of the periods of *Aggregation?* Reduction of lactate concentrations built up during a series of deep dives usually takes only a matter of an hour in other marine mammals (KOOYMAN, 1989), so that the shorter periods at the surface may be a response to this physiological requirement but it is unlikely that longer 5-6 hr aggregative periods are needed for recovery from diving. If periods of digestion were needed, we would expect their frequency, and perhaps duration, to be related to the feeding success of the whales. However, our results do not suggest this. The behavioural patterns that we observed seem more consistent with the characteristics of mammalian sleep or rest (*e.g.* HUME, 1983). They lasted a rather standard length of time usually at a certain time of day, but occurred after *Foraging* bouts of a variety of durations, and, over periods of more than a few days, showed similar long term averages. Although periods with low values of our third principal component may well represent rest or sleep, the wide variety of behaviour observed and recorded while aggregating at the surface (Fig. 2), strongly suggests that the whales are not always simply resting during these periods.

If the maintenance of social bonds was the primary function of these prolonged periods at the surface, what kinds of patterns might we expect to observe? We can find no immediately obvious reason why the durations of periods of socialization, or intervals between them, should or should not be negatively exponentially distributed. However, the proportion of time spent socializing might be expected to have a reasonably constant longterm average, except that in very poor conditions nutritionally stressed animals would probably increase their foraging time, and in times of food surplus more time might be spent socializing. Although there is some evidence that the population of female sperm whales off the Galápagos is near density-dependent equilibrium, probably because of food limitation (WHITEHEAD, 1990), sperm whales are sufficiently large to be able to store enough energy to average variation in food abundance over quite long time periods. Therefore the lack of change in the degree of *Sociality* with feeding success, even through the particularly poor 'El Niño' season of 1987 (WHITEHEAD *et al.*, 1989), would not be remarkable even if maintaining social bonds was the primary function of these periods.

On shorter time scales, whatever their primary function, it makes sense to fit periods of *Aggregation* at the surface into a daily schedule in such a way as to mimimize the disruption to *Foraging*. There is some dispute in the literature as to whether sperm whale feeding shows a diurnal pattern (CLARKE, 1980). Significant variation in gut contents or defecation rates with time of day could itself be a result of diurnal patterns of *Aggregation*. The predominance of *Aggregation* in the afternoon may correspond to a lowering in expected feeding success at this time of day, but this is not necessarily the case.

In conclusion, there are strong correlations between the types of vocalizations heard from female sperm whales and their visually observable activities. They spend about three quarters of their time in fairly stereotyped foraging behaviour, consisting of repeated dives, and one quarter of their time moving slowly at or near the surface, often closely clustered. The principal function of these periods at the surface is not yet clear, but our data are consistent with it having significance in the maintenance of social bonds.

Summary

Hourly records of the visible activities and vocalizations of groups of female and immature sperm whales, *Physeter macrocephalus*, off the Galápagos Islands were used to investigate relationships between vocalizations and visible activities, and to examine patterns of behaviour. There were strong correlations between most recorded variables, and multivariate analysis showed the rates of performing visually observable activities and vocalizing to be largely represented by an axis which is termed *Sociality*. About three quarters of the time sperm whales engaged in relatively stereotyped foraging for food, diving regularly, moving steadily, appearing only briefly at the surface in small clusters, and making regularly spaced trains of 'usual' clicks. However, for periods which usually lasted either about one or about five hours, and often in the afternoon, the whales would aggregate at the surface, usually in large, slow-moving clusters, often making patterned series of clicks called 'codas'. There was considerable variation in the behaviour observed, and sounds heard, during these periods of *Aggregation*. The mean levels of *Sociality* did not vary significantly between years, with season or with a measure of feeding success. The results are consistent with the hypothesis that a primary function of these periods at the surface is the maintenance of social bonds, although other functions are not excluded.

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Zusammenfassung

Das sichtbare Verhalten und die Vokalisationen von Gruppen von weiblichen und unreifen Pottwalen (*Physeter macrocephalus*) vor der Küste der Galápagos Inseln wurden stündlich aufgezeichnet um die Beziehung zwischen Vokalisationen und Verhalten zu untersuchen, und um Verhaltensmuster zu erforschen. Die Korrelationen zwischen die meiste registrierte Variabeln sind groß, und multivariate Analysen zeigten, daß die relative Geschwindigkeit der Verrichtung sichtbaren Verhaltens und der Vokalisation weitgehend durch eine Achse representiert ist, die als 'Gesellschaftlichkeit' bezeichnet wird. Etwa drei Viertel der Zeit waren die Pottwale mit relativ stereotyper Futterbeschaffung beschäftigt. Sie tauchten regelmäßig, bewegten sich ständig, erschienen nur für kurze Zeit und in kleinen Gruppen an der Oberfläche und führten 'gewöhnliche' Klicken von regelmäßigen Abständen in Folgen aus. In Zeiträumen, die entweder ungefähr eine Stunde oder ungefähr fünf Stunden dauerten und oft nachmittags, sammelten sich die Wale jedoch an der Wasseroberfläche an, meist in großen sich langsam bewegenden Gruppen, und sie führten dann gemusterte Serien von Klicken aus, die 'Kodas' genannt werden. Während dieser Perioden der Ansammlung wurden erhebliche Variationen sowohl im Verhalten als auch in den Tönen beobachtet. Das Durchschnittsniveau der *Gesellschaftlichkeit* zeigte keine wesentlichen Veränderungen von Jahr zu Jahr, von Jahreszeit zu Jahreszeit oder auch mit dem Maßtab des Erfolgs bei der Nahrungsaufnahme. Diese Ergebnisse stehen im Einklang mit der Hypothese, daß die primäre Funktion dieser Perioden an der Oberfläche darin besteht die gesellschaftlichen Bindungen aufrechtzuerhalten, obgleich dies andere Funktionen nicht ausschließt.
