

Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Islands

HAL WHITEHEAD

Department of Biology, Dalhousie University, Halifax, N.S., Canada B3H 4J1

Received July 12, 1988

WHITEHEAD, H. 1989. Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Islands. *Can. J. Zool.* **67**: 2131–2139.

Groups of sperm whales, composed mostly of females and their offspring, which were tracked in the waters off the Galápagos Islands during 1985 and 1987, generally foraged in ranks about 550 m long aligned perpendicular to the direction of travel. While at the surface, they swam in clusters containing a mean of 1.7 whales, and these clusters were spaced out along the rank. When feeding at depth the whales were estimated to be about 40 m apart. The ranks travelled at approximately 2 kn (3.7 km/h) and maintained their headings for periods of several hours. Individuals showed some coordination in the timing of their dives. There were no indications that individual whales, mature males, or first-year calves were more likely to be found in particular positions along the rank. The major benefits for individuals of foraging in a rank are probably gathering information about prey densities, avoiding mutual interference, and possibly catching prey that elude other members of the formation.

WHITEHEAD, H. 1989. Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Islands. *Can. J. Zool.* **67** : 2131–2139.

Des groupes de Cachalots macrocéphales, composés surtout de femelles et de leur progéniture, ont été suivis dans les eaux côtières des Îles Galapagos en 1985 et en 1987; les cachalots cherchaient ordinairement leur nourriture en rangées d'environ 550 m de longueur perpendiculaires à la direction de leurs déplacements. En surface, les cachalots nageaient en petits groupes contenant en moyenne 1,7 animaux, et ces groupes étaient dispersés le long de la rangée. En profondeur, les animaux se tenaient à environ 40 m de distance. Les rangées se déplaçaient à raison de 2 noeuds (3,7 km/h) et maintenaient cette vitesse pour des périodes de plusieurs heures. Il y avait une certaine coordination entre les plongées des individus. Il ne semblait pas y avoir de positions particulières réservées aux mâles à maturité ou aux petits de l'année. Les avantages reliés à la recherche de nourriture en rangées sont probablement de pouvoir acquérir de l'information sur la densité des proies, d'éviter les interférences mutuelles et peut-être aussi de permettre de capturer des proies qui échappent aux autres membres de la formation.

[Traduit par la revue]

Introduction

Sperm whales, *Physeter macrocephalus*, are gregarious (Best 1979). Mature female sperm whales are almost invariably found in association with other females and their young, in groups of about 22 individuals which have a stable composition over periods of years (Ohsumi 1971; Best 1979; Whitehead and Arnborn 1987; Whitehead and Waters 1988). Although males are often found together, their groupings are generally smaller and probably less stable than those of the females (Best 1979). Best (1979) suggests two principal factors for the evolution of gregariousness in sperm whales: mutual caring for calves by females (especially protection against predators), and cooperation in the location and capturing of food. Although there is some evidence supporting the first of these factors (Gordon 1987; Arnborn and Whitehead 1989), cooperative foraging has not yet been studied.

Sperm whales feed on a variety of species and sizes of deep-water fish and squid (Gaskin 1982; Kawakami 1980). Their food preferences vary considerably with geographic area. In some regions they eat almost entirely squid and in others, such as off Iceland, fish are the principal food source (Gaskin 1982; Kawakami 1980). The techniques used to catch prey are not known. Gaskin (1982) concludes that they have the ability to take prey by active hunting, but does not rule out the possibility that they may be able to lure food by some kind of passive stratagem.

Sperm whales studied off the Galápagos Islands in 1985 and 1987 were found to feed at depths of about 400 m principally on histioteuthid squid (Papastavrou 1987; Papastavrou et al. 1989). When foraging, individual whales dived for about

40 min, followed by 10 min at the surface (Papastavrou et al. 1989). While at the surface, sperm whales were seen in small sets of one to four individuals coordinating their movements, which Whitehead and Arnborn (1987) call "clusters" (Fig. 1). Sperm whales appeared to feed in a similar manner both during the day and at night (Papastavrou et al. 1989). Occasionally (approximately once a day) the sperm whales ceased deep diving, and congregated at the surface for a few hours at a time in slow moving "social" clusters containing from 4 to over 20 animals, such as the most distant cluster in Fig. 1 (Whitehead 1987).

In this paper I describe the spatial organization of groups of foraging sperm whales off the Galápagos Islands, and examine the results for evidence of cooperative foraging.

Methods

Collection of data at sea

The research described in this paper was conducted from the 10 m auxiliary sloop *Elendil* with a crew of five to six in the waters around the Galápagos Islands (0°N, 90°W). Research was carried out between 23 February and 20 April 1985 (a total of 30 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- to 14-day periods separated by a few days in port resupplying.

While at sea, groups of sperm whales were tracked acoustically using a directional hydrophone specially built for the project by Dev-Tec Inc. (Pasadena, CA). This allowed us to locate groups of sperm whales and stay within about 2 km of them during most of the tracking time. Among the data collected when tracking sperm whales during daylight were the following.

(i) Positions from a Tracor Transtar satellite navigator. Satellite

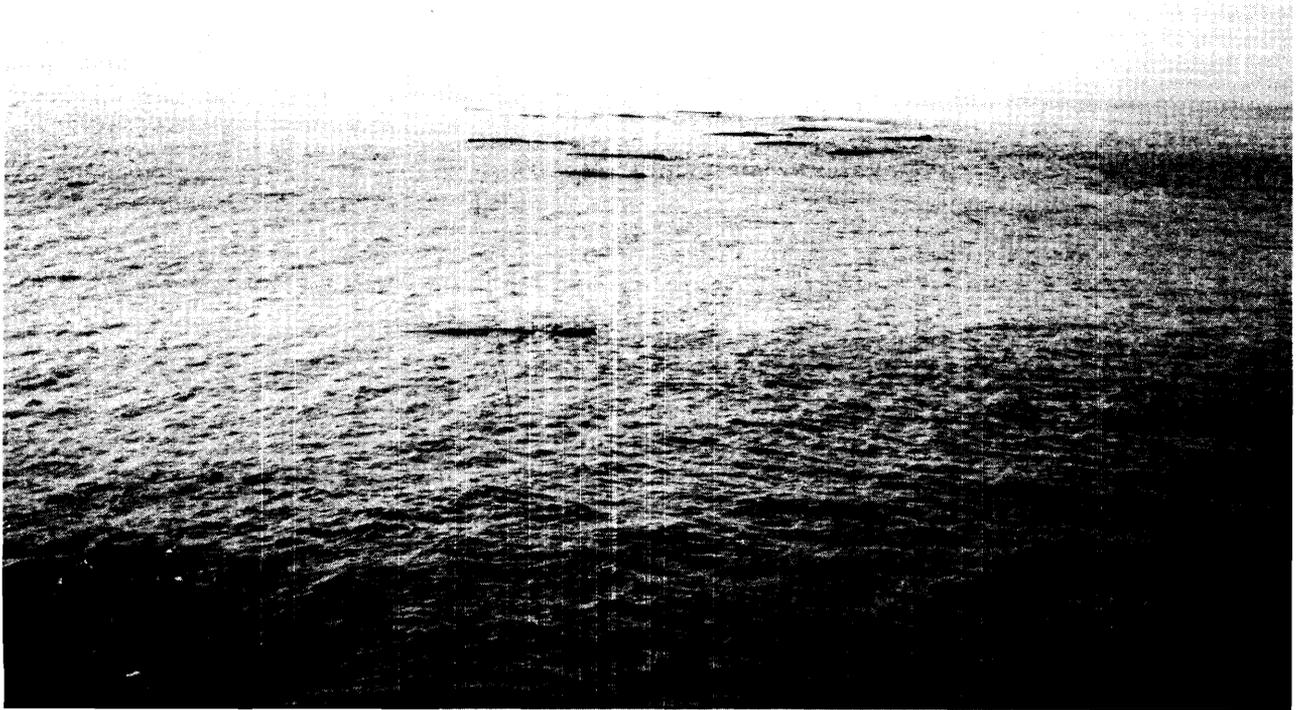


FIG. 1. Three clusters of sperm whales, containing 3 (left foreground), 1 (centre), and at least 12 (behind) individuals. The clusters are aligned in a rank perpendicular to their direction of travel.

fixes were obtained approximately every 2 h both day and night. These were accurate to about 1000 m.

(ii) Ranges and bearings from the vessel to all visible clusters (whales swimming at approximately the same speed in the same direction and within 100 m of one another; Whitehead and Arnborn 1987) every 5 min. Ranges were estimated visually with regular calibrations on whales or objects at known distances (using a range finder based upon the dip below the horizon of an object at the sea surface when observed from a known height as an indicator of range). Bearings were taken from a hand bearing compass or the ship's compass. Also recorded for each cluster were the number of whales, first-year calves, and mature males (distinguishable by their considerably smaller and larger sizes respectively) visible in each cluster, its estimated speed from comparisons with the vessel's knotmeter (when possible), its compass heading, and observations of any behaviour such as fluke-ups (the whale's flukes raised in the air at the start of a dive).

(iii) Photographs of the flukes of whales which are used to identify individuals (Arnborn 1987). These photographs were usually, but not always, taken as the whale fluked-up at the start of a foraging dive. Foraging dives, as indicated by steadily descending depth sounder traces (to ca. 400 m), were almost always preceded by fluke-ups, but on some occasions fluke-ups were not followed by a prolonged dive (Papastavrou et al. 1989). During the 1985 and 1987 Galápagos studies 583 individuals were identified from fluke photographs (Whitehead and Waters 1988).

Most of the animals sighted during the studies were females, calves, or immatures, but mature males sometimes joined the groups being tracked (Whitehead and Arnborn 1987). Particular groups of females and their offspring (calves and immatures) were followed for

durations of between a few hours and a few days. Occasionally, visual and acoustic contact with sperm whales was lost, but more frequently two or more groups of sperm whales associated and we unintentionally transferred our tracking to a different group as they diverged (Whitehead and Arnborn 1987).

Analysis of data

To examine the spatial distribution of clusters of sperm whales, for each 5-min interval the position of each observed cluster was transformed to xy coordinates centred on the centroid (centre of mass of the observed formation with each cluster having a mass of one unit) of the clusters seen within that interval. The y -axis was aligned to correspond to the direction of travel (as indicated by the bearing between adjacent satellite navigator fixes), as shown in Fig. 2.

The principal axis of the cluster positions was determined for each 5-min interval in which greater than three clusters were sighted, using formulae presented by Sokal and Rohlf (1981). The principal axis is the direction accounting for most of the variance in the scatter of points (Sokal and Rohlf 1981). The slope of the principal axis indicates the general linear direction of the points. The ratio of the length of the minor axis to that of the principal axis gives the scatter of the points about the principal axis: if this ratio is near 0.0 then the points are almost collinear, if near 1.0 they are scattered almost circularly.

A statistic proposed by Durbin (1965), and recommended by Cliff and Ord (1981), was used to examine whether clusters were clumped or spaced out when projected onto an axis perpendicular to the direction of travel (the x -coordinate of Fig. 2). The distances between projected clusters were ranked $\{g(1), g(2), \dots, g(n)\}$ ($n + 1$ is the number of clusters sighted during the 5-min interval) and transformed (so that $g(1) + g(2) + \dots + g(n) = 1.0$), and the standardized statistic,

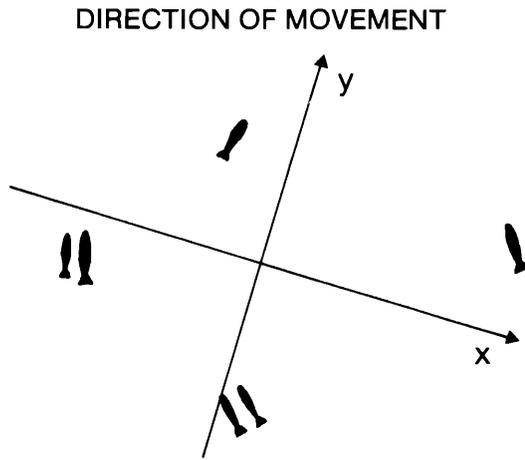


FIG. 2. Coordinate system used to describe sperm whale spatial organization. In this representation there are two clusters containing two whales each and two clusters containing one whale each.

S , was calculated for each 5-min interval as follows:

$$S = (2n - 2 \sum_{j=1}^n jg(j) - (n - 1)/2) / \sqrt{(n - 1)/12}$$

If the clusters were distributed according to a Poisson process (i.e., uniformly and independently of one another over a given segment), then S has an expected value of 0.0 and a standard deviation of 1.0. If the clusters were clumped, then $S < 0.0$, and if the clusters were spaced out, then $S > 0.0$.

To examine the effects of rounding errors in the data (ranges were routinely estimated to the nearest 50 m and bearings to the nearest 10°), a random simulation including rounding errors was carried out. The resultant distribution of S was almost identical to that from the random Poisson process without rounding errors. Thus, rounding is not a potential cause of significantly large values of S .

The consistency with which the whales maintained their direction of movement was examined as follows: the vector mean direction of movement was calculated for all observed headings during each hour; and these hourly means were compared with means 1, 2, 3, . . . , 11 h earlier to calculate the absolute changes in direction of movement for different delay times.

The data were examined for evidence of coordination in the times that whales began their feeding dives. Each hour during daylight in which more than 10 fluke-ups were observed, and for which more than 5 fluke-ups were observed in the preceding and following hours (to eliminate most occasions when sighting conditions were improving or deteriorating), was broken into 5-, 10-, 15-, 20-, and 30-min intervals. The number of flukes observed in each interval was counted. The hypothesis that the flukes were independently allocated to intervals was tested for each hour and duration of interval, using the "G" likelihood-ratio statistic (Sokal and Rohlf 1981).

To examine whether particular individuals had certain positions within the rank where they were more likely to be found than other positions, the x -coordinate (as defined above, Fig. 2) of the transformed position was calculated for each positive identification of each individual from a fluke photograph. If individuals retained a position within the rank, then the x -coordinates should have less variance for identifications of the same individual than for identifications of different individuals. Identifications less than 30 min from the previous identification (corresponding to a short feeding dive, Papastavrou et al. 1989) were not included in this analysis in order to remove biases due to repeat identifications of the same individual during a short period of time (e.g., when whales were lobtailing, thrashing their flukes onto the water surface).

The hypotheses that clusters containing calves or mature males might be found closer to, or further from, the centroid of the distribu-

tion of clusters (along the x -coordinate) than other clusters was tested as follows: using 5-min intervals with more than four clusters sighted, the mean absolute distance (along the x -coordinate) from the centroid was calculated for clusters sighted less or equal to 200 m from the vessel (to eliminate bias due to differential sightability of calves, males, and other whales). The means and standard deviations of these absolute x values were compared for those clusters containing calves, those containing males, and those containing neither males nor calves. A large mean would indicate that the class of individuals was generally found on the edges of the rank, and a small mean would indicate that it was found near the centre.

Significance tests

Formal significance tests, which are given for a few of the analyses presented below, should be treated cautiously as there is considerable autocorrelation in the data. Sample sizes are generally very large, and a better indication of the magnitude and consistency of a measure comes from comparison between the distributions obtained from the data collected during the two years (1985 and 1987) and randomly generated data.

Results

Spatial structure of foraging sperm whales

Sperm whales at the surface were seen in clusters containing from 1 to over 50 animals. The distribution of sizes of clusters less than 300 m from the research vessel (at greater ranges cluster size was sometimes underestimated) during the Galápagos research is given in Fig. 3. There is a small bias towards large cluster sizes in these data as we were more likely to be near a cluster if its size was large: during "social" periods the whales formed fewer but larger clusters and thus the boat was likely to be close to a particular one. However, the mean cluster sizes are not reduced by much when clusters at all ranges to the vessel are included (mean cluster sizes of 3.7 (1985) and 3.2 (1987) animals for clusters less than 300 m from the research vessel reduced to 2.4 (1985) and 2.1 (1987) animals when all clusters are included).

As mentioned above, cluster sizes tended to be larger when the whales were socializing and smaller when they were foraging. The distribution of cluster sizes at the start of foraging dives, as indicated by the number of fluke-ups observed from each cluster during a 5-min interval, is also shown in Fig. 3. By this measure, the mean cluster size of foraging sperm whales was 1.7 animals for both the data from 1985 and 1987.

The horizontal formation of the clusters was examined from the xy plots of their positions (as defined above). The distribution of the ratio of the length of the minor axis to that of the principal axis is given in Table 1, together with a control distribution in which each recorded cluster was randomly positioned using a bivariate normal distribution with equal variances on the two axes. It is clear that the observed clusters (with median ratios of 0.3) were more collinear than those generated randomly (median ratios of 0.5).

Figure 4 shows the distribution of slopes of the principal axes relative to the direction of movement of the whales, together with the slopes of the principal axes from randomly generated data. It is clear that, unlike the random data for which the principal axis is distributed uniformly around the circle, the principal axis of the clusters of whales generally fell between 45 and 90° of the direction of movement.

When projected onto an axis perpendicular to the direction of travel (i.e., the x -coordinate of Fig. 2), the mean inter-cluster distance was 213 m (SD = 192 m) for the 1985 data and 202 m (SD = 182 m) for 1987.

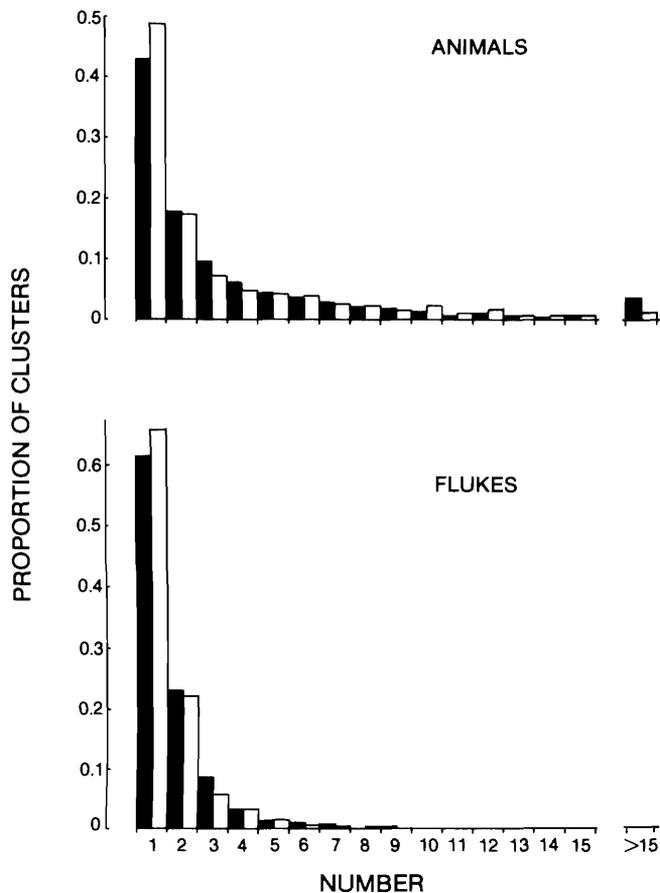


FIG. 3. Distribution of sizes of clusters for 1985 (■) and 1987 (□) seen less than 300 m from research vessel: number of whales visible in each cluster (above) and number of flukes observed from each cluster (below) during 5-min intervals. Sample sizes for whales visible: 2732 clusters (1985) and 3677 (clusters (1987). Sample sizes for flukes visible: 818 clusters (1985) and 1377 clusters (1987).

The distribution of S (defined above) for the Galápagos sperm whale data is shown in Fig. 5, together with distributions in which the positions of the clusters were assigned by a random Poisson process. In both 1985 and 1987 there was a small but significant (t -tests, $P < 0.01$) tendency for clusters to be spaced out. Overall the clusters in 56% of the 5-min intervals suggested spacing ($S > 0.0$), as compared with 45% for the random data.

This section is summarized in the diagram shown in Fig. 6: foraging sperm whales were seen at the surface in clusters averaging 1.7 animals; the clusters tended to form a rank aligned perpendicular to the direction of travel, as in Fig. 1; along this rank, clusters were an average of about 200 m apart and tended to be more regularly spaced than would be expected if the clusters were distributed randomly.

Temporal processes: speed, consistency of direction, and coordination

Estimated speeds of movement through the water while the whales were at the surface are given in Table 2 and Fig. 7. Means were calculated treating both clusters as units (the display in Fig. 7) and each sighted whale separately. The generally lower estimated speeds when single whales are treated as units are a result of clusters with more whales (those behaving "socially") tending to move more slowly. Also shown in

TABLE 1. Collinearity of clusters of sperm whales

Ratio	No. of observations (random)	
	1985	1987
0.0–0.1	122 (22)	75 (13)
0.1–0.2	205 (55)	160 (56)
0.2–0.3	216 (103)	152 (95)
0.3–0.4	159 (164)	138 (150)
0.4–0.5	145 (193)	107 (138)
0.5–0.6	95 (174)	66 (118)
0.6–0.7	64 (145)	49 (112)
0.7–0.8	38 (127)	36 (84)
0.8–0.9	24 (72)	17 (30)
0.9–1.0	8 (21)	8 (12)
Median	0.30 (0.50)	0.31 (0.47)
Total	1076	808

NOTE: This table gives the distribution of the ratio of the minor axis to the principal axis of the positions of clusters for 5-min intervals in which more than three clusters were seen. The distribution of this ratio when the observed clusters were positioned by a bivariate normal distribution with equal variance in each direction is given in parentheses.

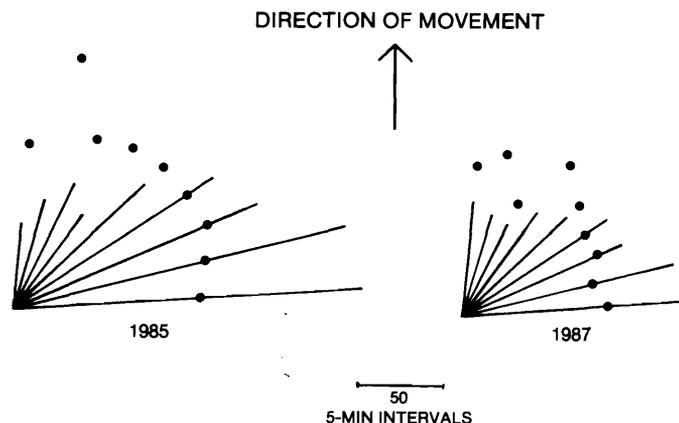


FIG. 4. Slopes of principal axes of observed clusters relative to the direction of movement. The length of the line at t° is proportional to the number of 5-min intervals in which the principal axis was $t \pm 5^\circ$ from the direction of movement. (●) Results from randomly generated data.

Table 2 and Fig. 7 are estimated speeds over the ocean bottom from satellite navigator fixes greater than 30 min apart. The greater variance in these estimates is due to a combination of the distance between the vessel and the whales, currents, and errors in the satellite navigator fixes. Overall, the data show that the whales were generally moving at speeds of 1.25–3.25 kn (2.3–6.0 km/h) both when at the surface and underwater, with a maximum sustained speed of about 5.5 kn (10 km/h).

The results of the analysis of rate of change in mean direction of movement are shown in Fig. 8. It is apparent that the whales changed direction of movement by 15–20°/h so that after a period of about 5–8 h their heading was almost independent of their original heading (mean change of 90°).

The results of the investigation of coordination in the times that whales began their feeding dives are given in Table 3.

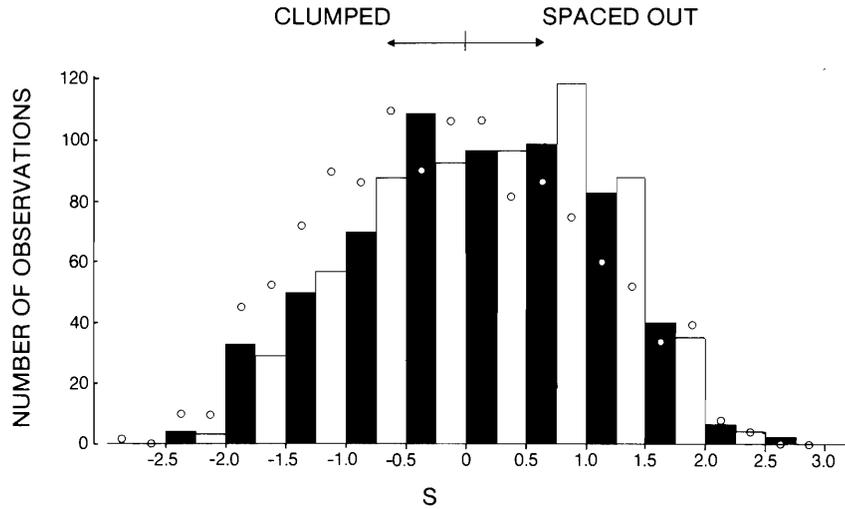


FIG. 5. Distribution of the standardized statistic S which indicates clumping ($S < 0$) or spacing ($S > 0$) for 1985 (■) and 1987 (□) data. (○) Distribution of S when the positions of the clusters were chosen randomly.

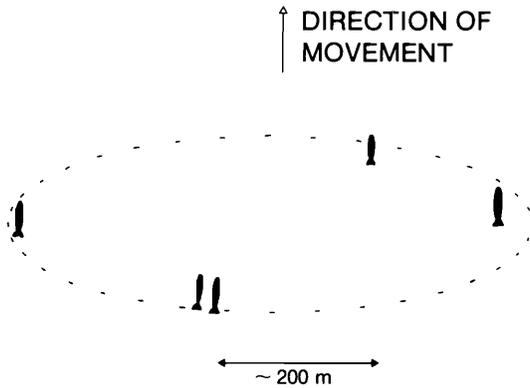


FIG. 6. Spatial organization of foraging sperm whales while at the surface: a representative summary.

TABLE 2. Estimated speeds in knots (1 kn = 1.85 km/h) from vessel's knotmeter "through water," for both clusters and whales, and "over bottom," from satellite navigator fixes at least 0.5 h apart

	1985	1987
Speed through water		
Clusters	2.02 ± 0.84	1.90 ± 0.65
Whales	1.94 ± 1.03	1.76 ± 0.61
Speed over bottom	2.11 ± 1.20	2.01 ± 1.03

NOTE: Values are means ± SD.

Whales within a group tended to coordinate their fluke-ups, especially over shorter time scales.

To summarize this section: the ranks of foraging sperm whales travelled at about 2 kn (3.7 km/h), roughly the same speed that individual clusters were seen to move at the surface, and maintained a particular heading for periods of several hours; individuals within the rank showed some coordination in their fluke-ups.

Individuals, calves, and mature males

This section investigates the hypotheses that particular

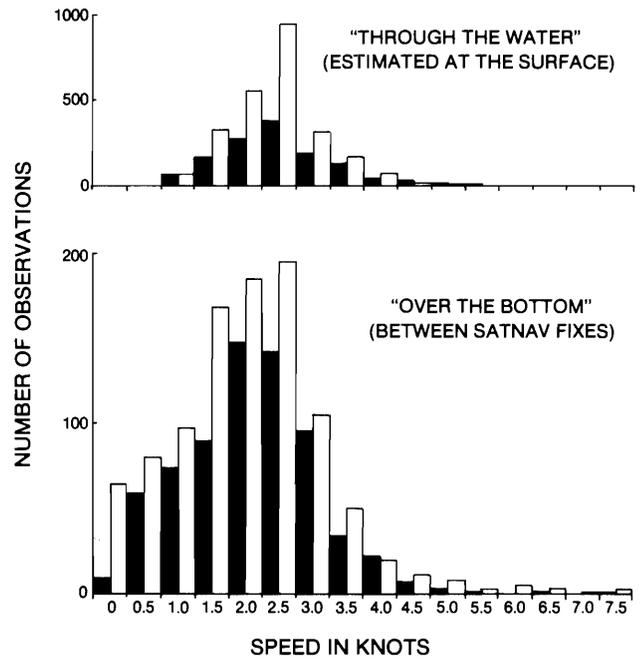


FIG. 7. Speeds of movement of Galapagos sperm whales: estimated for clusters while at the surface (above) "through the water," and between satellite navigator (SATNAV) fixes (below) "over the bottom," for 1985 (■) and 1987 (□).

individuals or classes of individuals (calves and mature males) had certain positions within the rank where they were more likely to be found than other positions. For neither the 1985 nor 1987 data sets was there significantly less variation in the x -coordinates of an individual than between individuals, both within days ($F_{61,75} = 0.876$ (1985), $F_{117,178} = 1.132$ (1987); $P > 0.10$ in both cases) and between days ($F_{204,74} = 1.169$ (1985), $F_{276,139} = 1.165$ (1987); $P > 0.10$ in both cases). Given the quite substantial sizes of the data sets considered here, these results suggest that it is unlikely that individuals often maintained positions within the rank for much more than about 1 h. Similarly, there was no significant difference (t -tests, $P > 0.10$) in the mean x value for either year between

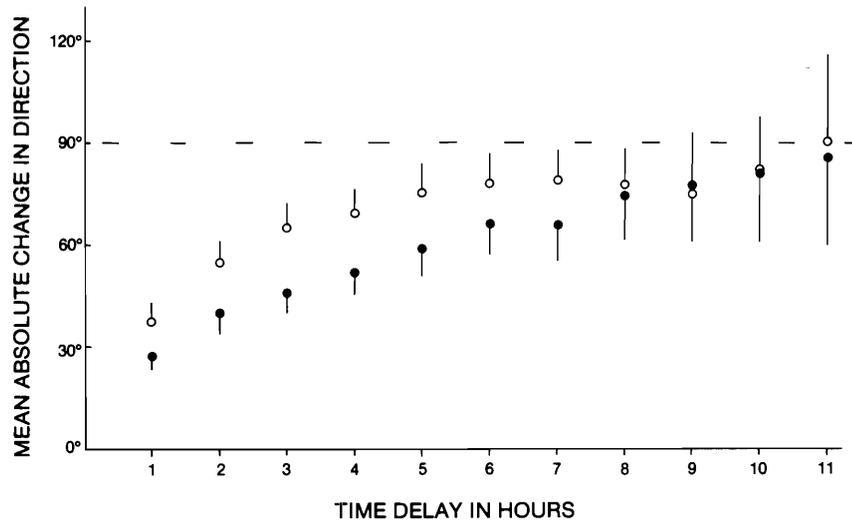


FIG. 8. Mean absolute change of vector mean heading in degrees for different time intervals for 1985 (●) and 1987 (○). Bars from each point represent ± 1 estimated SE.

TABLE 3. Coordination and spacing in the timing of fluke-ups

Time interval (min)	Hours showing significant:		Total hours
	coordination ($P(G) < 0.05$)	spacing ($P(G) > 0.95$)	
5	57/47	0/0	89/84
10	49/38	0/0	89/84
15	44/28	1/2	89/84
20	37/23	2/0	89/84
30	28/10	—	89/84

NOTE: The table summarizes the results of tests using the "G" likelihood-ratio statistic that flukes were independently allocated to intervals. Significantly large values of the G statistic suggest that the whales were coordinating their fluke-ups, and significantly small ones suggest that they were spacing them out. The number of hours for which G was significantly large or small ($P < 0.05$ or $P > 0.95$) are given for 1985 and 1987 (following a slash).

clusters containing either calves or males and clusters containing neither (Table 4).

Thus, the data suggest that neither individuals nor special classes of whale were found preferentially in a particular position within the rank of foraging sperm whales. Individuals probably frequently changed their position along the rank, and males and calves were not significantly closer to, or further from, the centroid of the rank than other whales.

Discussion

Errors and problems

Much of the analysis of this paper is based on visual estimates of numbers of whales, ranges, speeds, and bearings. It is important to consider how the undoubted measurement errors and consistent biases in these estimates may have affected the results in this paper. Another potential problem is that data from both foraging and nonforaging whales are used in most analyses, but the principal purpose of this paper is to describe the formation of foraging whales.

In general, the data were edited as seemed appropriate for each analysis to try and avoid obvious biases. For instance, clusters sighted at longer ranges were omitted for some analyses, as the number of whales in these clusters may have been underestimated. Sometimes, by analysing just fluke-ups, non-

TABLE 4. Mean absolute x-coordinate (distance in metres from centroid perpendicular to direction of travel) for clusters containing first-year calves, mature males, and neither calves nor males

Clusters containing	1985		1987	
	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$
Calves	97	306 \pm 249	35	175 \pm 120
Mature males	32	216 \pm 210	20	237 \pm 138
Neither calves nor males	575	282 \pm 249	400	199 \pm 216

foraging whales could be virtually eliminated, although sperm whales occasionally fluke-up when not foraging. In the other cases the addition of data when the whales are not foraging will generally only produce small biases, as sperm whales off the Galápagos foraged approximately 80% of the time that they were followed (H. Whitehead and L. Weilgart, in preparation), and when not foraging were in a few large clusters constituting only a small part of the data set.

The probable effects of biases, errors, and the inclusion of data from nonforaging whales on the analyses in this paper are considered in Table 5. There are a few probable small biases but in general the effects of the problems are to make the results conservative; biases, errors, and the inclusion of nonforaging whales make it less likely that significant results will come from the analyses. For instance, clusters of foraging sperm whales are probably more collinear, more perpendicular to the direction of travel, and more consistent in their headings than indicated by the results presented above.

How representative are the results?

Sperm whales feed on a great variety of food in different ocean areas (Kawakami 1980), presumably in a variety of different ways. How representative, then, are the results in this paper of sperm whale foraging patterns in general? The results were obtained from about 33 groups of sperm whales followed for varying lengths of time during a total of 87 days within a 29-month period only between January and June in one geographic area. The consistency of most of the results between the 2 years of our study, and in our subjective obser-

vations of the behaviour of the whales over shorter periods, strongly suggests that the foraging formation described in this paper is typical of groups of female sperm whales off the Galápagos Islands feeding on histioteuthid squid.

Sperm whales have been informally described as swimming in "rows" or "lined up almost like soldiers" by whalers (Caldwell et al. 1966) and one of the three schools described by Ohsumi (1971) was in "a rank, 50 m spread." Some of these observations probably refer to the formations within clusters in which animals often swim abreast, but foraging in steadily moving ranks may also be reasonably common outside the Galápagos.

The rank formation was not universal off the Galápagos, and even when feeding in a rank there were variations. For instance, the whales changed direction of movement faster in 1987 than in 1985, perhaps because of differences in the food availability, their environment, or location within the Galápagos area (Whitehead et al. 1988). Male sperm whales can forage singly (e.g., Mullins et al. 1988), and given the considerable variability in the food of sperm whales in different ocean areas we might expect variation in their feeding behaviour.

Watkins and Schevill (1977) used an acoustic array to track sperm whales underwater on a number of occasions. They found sperm whales to generally scatter as they dived, and suggest that such scattering may facilitate foraging. However, their whales, all judged to be over 12 m in length and thus probably adult males (Best 1979), did not appear to form ranks as described in this paper.

Formation underwater

The results derived in this paper describe the formation of the sperm whales at the surface. How do they relate to the formation at feeding depth, where spatial organization will have most effect on feeding success? The clusters observed at the surface probably generally break up as the whales dive, with individuals diverging as they descend (Watkins and Schevill 1977; H. Whitehead, unpublished depth sound records). This likely results in the sperm whales at depth forming an approximate one-dimensional rank with individuals spaced out along it. Each cluster at the surface represents approximately (time at depth)/(time at surface) clusters at feeding depth. Therefore, an approximate interindividual distance at depth can be calculated as follows:

$$\frac{\text{spacing of clusters at surface} \cdot \text{time at surface}}{\text{mean cluster size} \cdot \text{time at depth}}$$

The mean intercluster interval at the surface was 213 m, the mean cluster size when feeding was 1.7, the mean time at the surface was 10 min (Papastavrou et al. 1989), and the mean time at depth was 30 min (a dive time of 40 min minus diving and surfacing 400 m at 80 m/min (Papastavrou et al. 1989)). This gives an approximate interindividual distance at feeding depth of 42 m.

The length of the rank formed by a group of foraging sperm whales can be approximated by

$$\text{spacing at depth} \cdot \text{mean group size} \cdot \text{proportion of time at depth}$$

With a mean group size of 22 individuals (Whitehead and Waters 1988), and the numbers used above, this is estimated to be about 555 m.

TABLE 5. Summary of possible biases and errors, and the differences between foraging and nonforaging whales, on the analyses in this paper. Presented last for each analysis is the considered overall effect of these problems on the validity of the results for foraging sperm whales

<i>Cluster size</i>	
Bias:	vessel nearer large clusters, occasional fluke-up when not foraging
Errors:	visual estimation of cluster size
Foraging:	larger clusters when not foraging
Overall:	slight bias towards large cluster sizes
<i>Ratio: minor axis/principal axis</i>	
Bias and errors:	errors in range and bearing will tend to lead to overestimates in the ratio and add to its variance
Foraging:	whales probably less aligned when not foraging
Overall:	foraging whales probably more collinear than indicated in Table 1
<i>Slope of principal axis</i>	
Bias and errors:	errors in range and bearing estimation, errors in satellite navigator fixes (especially with short times between fixes), and currents
Foraging:	whales move less consistently when not foraging
Overall:	ranks of foraging whales probably more perpendicular to direction of travel than indicated in Fig. 4
<i>Intercluster distance</i>	
Bias:	clusters missed at long range or when many clusters visible
Ranges and bearings:	rounded
Errors:	errors in range and bearing estimation, errors in satellite navigator fixes (especially with short times between fixes), and currents
Foraging:	probably similar when foraging and not foraging
Overall:	perhaps a small overestimation of intercluster distances, errors small compared with natural variation
<i>Clusters spaced</i>	
Errors:	errors in range and bearing estimation, errors in satellite navigator fixes (especially with short times between fixes), and currents, clusters missed at longer ranges
Foraging:	probably less spaced when not foraging
Overall:	clusters probably more spaced than suggested by data
<i>Speed through water</i>	
Bias:	inability to remain with fast-moving whales (very rare)
Errors:	estimation errors
Foraging:	slower speeds when not foraging
Overall:	small bias towards slow moving whales
<i>Speed over bottom</i>	
Bias:	inability to remain with fast-moving whales (very rare)
Whales not moving:	in straight lines
Errors:	satellite navigator errors and currents, distance between whales and vessel
Foraging:	slower speeds when not foraging
Overall:	small bias towards slow moving whales, plus errors
<i>Consistency in heading</i>	
Errors:	errors in heading estimates
Foraging:	probably less consistent when not foraging
Overall:	consistency probably greater than shown in Fig. 8
<i>Coordination in fluke-ups</i>	
Errors:	flukes not seen at longer range
Overall:	little effect of errors and biases
<i>Position of individuals and classes of individual in rank</i>	
Errors:	estimates in range and bearing, only a portion of rank visible at any time
Foraging:	if preferred positions existed they would probably break down when not foraging
Overall:	preferred positions may not have been detected

Therefore, when feeding, groups consisting of female sperm whales and their offspring generally formed a rank of about 13 individuals (the proportion feeding at any time) spaced about 40 m apart and travelling about 2.5 kn (4.6 km/h). However, the considerable variation in the data and the tendency for individuals to coordinate their dives indicate that the formation at any time is likely to vary considerably from this "average" scenario. The coordination in fluke-ups partly results from occasions when many, and sometimes most, of the individuals within a group ended their "social" periods at the surface together, and so synchronized their dives.

Formations and feeding success

Foraging information can potentially improve the feeding success of individuals in several different ways which I will list in order of decreasing sophistication. (1) Individuals cooperate to chase and catch individual prey. (2) Individuals may be alerted to the presence of prey, which they would otherwise not encounter, by other members of the formation (Crook 1965). This is sometimes called "local enhancement" (Pulliam and Caraco 1984). Such information exchange may be deliberate, as when an individual signals that it has encountered prey, or inadvertent when feeding behaviour itself provides other members of the formation with information about the food source. (3) Prey which evade one member of the formation may be taken by a neighbouring member. (4) Animals which are foraging in the same area on a spatially dispersed and relatively stationary food source will interfere with each other less if they travel in a rank rather than close to or behind one another.

Histioteuthid squid, the sperm whales' principal prey in the Galápagos area, weigh about 1 kg or less (Clarke 1980) and are probably not strong swimmers. Based on their morphology and results from other cephalopod species, they are probably limited to escapes consisting of just a few jets propelling them tens of metres (R. K. O'Dor, personal communication). It is unlikely that several sperm whales are needed to chase and capture them so that benefit 1 is unlikely to apply in this instance. The lack of consistent positions within the rank also suggests that behaviourally sophisticated cooperative capture techniques are not generally employed.

For individuals to gain benefit from the direct use of food sources discovered by others, the resource must be patchy and the patches must be large enough so that several individuals can benefit from the location of a patch (Pulliam and Caraco 1984). From examining the numbers of squid buccal masses of each type found together in sperm whale stomachs, Clarke (1980) makes inferences about the gregariousness of the squid. Although he concludes that histioteuthids are gregarious, only rarely were more than a total of 10 histioteuthids found in a stomach together and never more than 18. We never observed obvious sudden changes from the steadily moving rank formation which might be expected to accompany the discovery of a large patch of food. This suggests that the patches of histioteuthids were not sufficiently large to allow a group of over 20 sperm whales continuous food for a substantial period. However, if histioteuthids, although not occurring in large patches, showed gradients in density, information on the feeding success of other individuals in the rank might usefully allow an individual, or the formation as a whole, to redirect its movements. Evidence presented by Gordon (1987) and Mullins et al. (1988) suggests that the patterns of vocalizations of feeding sperm whales, audible at several kilometres, may indicate feeding success. Additionally, if sperm whales

echolocate to find food (see below), echoes from a neighbour's clicks might be used to find prey.

As sperm whales can almost certainly swim faster and for more prolonged periods than the histioteuthids, benefit 3 is only likely to apply if the squid can detect and respond to the sperm whales before the sperm whales detect the squid. Although Watkins (1980) disagrees, Berzin (1971), Caldwell et al. (1966), Norris and Harvey (1972), and Gordon (1987) think it likely that sperm whales may find their prey using echolocation. They certainly make loud clicks, audible to hydrophones at up to 5 km, most of the time they are at feeding depth (Mullins et al. 1988). Despite other views (Moynihan 1985), there is evidence that at least some species of squid possess a sense of hearing (Hanlon and Budelmann 1987). Therefore, whether sperm whales receive benefit 3 from their formation foraging will depend on whether the squid can hear the sperm whales substantially before the whales detect the echoes of their clicks from the squid, and if so, on what evasive action the squid take.

The probable sluggishness of histioteuthids together with the likely range at which sperm whales can detect them suggests that foraging directly behind another sperm whale will not be profitable. If slow-swimming, slowly renewing prey are to be found at a particular depth, as suggested by the evidence presented by Papastavrou et al. (1989), then rank feeding appears to be an efficient way of minimizing interference among whales feeding together.

Individual sperm whales may be benefitting from the squid that avoid other members of their formation (3), but it seems probable that the major benefits of foraging in a rank are gathering information about prey locations and densities (2), and avoiding mutual interference among sperm whales which are grouped for reasons unrelated to foraging (4).

Significance of grouping

If 4 were the only benefit of formation foraging, the evolution of gregariousness in sperm whales cannot be explained by an increase in foraging efficiency. Although there is evidence that members of groups of female sperm whales cooperate in raising their young and assisting with defense against predators, immature whales, which are also generally found in groups, do not (Caldwell and Caldwell 1966; Berzin 1971; Best 1979; Arnbohm et al. 1987; Gordon 1987; Arnbohm and Whitehead 1989). The groups of immature whales are less stable in composition and less cohesive behaviourally (Caldwell et al. 1966), and large mature males are often found alone (Best 1979). This suggests that in some circumstances there are benefits to foraging together, probably in the form of information exchange (2) or capture of prey which try to evade other members of the formation (3), but not always. In contrast, killer whales, *Orcinus orca*, of both sexes, which feed on more elusive prey than sperm whales and thus gain more benefit from cooperative foraging (1, 2, 3), generally remain in stable cohesive groups throughout their lives (Bigg et al. 1987).

To conclude, it is quite likely that formation foraging is sometimes beneficial to sperm whales, and at the very least it minimizes mutual interference, but it is unlikely that it has been the major force for the evolution of gregariousness amongst female sperm whales.

Comparison with other species

Other marine (as well as terrestrial) vertebrates forage in ranks. Several schooling dolphin species and other small

odontocetes such as pilot whales, *Globicephala* spp., and killer whales are often found in schools that are "broader rather than long relative to the direction of school movement" (Norris and Dohl 1980). Norris and Dohl (1980) suggest that an increased rate of finding large patches of dispersed prey (benefit 2 above) is a likely function of this formation. Rank formations are also found outside the Cetacea. For instance, Broni (1985) describes jackass penguins, *Spheniscus demersus*, as using a "line-abreast" formation, and rank foraging may occasionally be found in terrestrial carnivores, such as wolves, *Canis lupus* (references in Mech 1970).

Acknowledgements

I thank all those who helped collect the data at sea, but especially Tom Arnbom, Mel Brooks, Leesa Fawcett, Cheryl Hendrickson, Bill Lambert, Katherine Lynch, Vassili Papatavrou, Sean Smith, Caroline Smythe, Jennifer Staniforth, Susan Staniforth, Susan Waters, and Linda Weilgart. In Ecuador, the Charles Darwin Research Station, the Instituto Oceanográfico de la Armada, and the Galápagos National Park Service provided considerable assistance. The 1985 Galápagos study was funded by M. Clark, F. C. P. Whitehead, the Green Island Foundation, and the Connecticut Cetacean Society. The 1987 Galápagos study was funded by the Natural Sciences and Engineering Research Council of Canada, the International Whaling Commission, and the Dalhousie University Research Development Fund. World Wildlife Fund loaned equipment for both studies. I am grateful to Tom Arnbom and Susan Waters who analysed the photographic data, and to Ron O'Dor for information about squid. Ellie Dorsey, Annick Faucher, Linda Weilgart, and two anonymous reviewers made useful comments on the manuscript.

- ARNBOM, T. 1987. Individual identification of sperm whales. *Int. Whaling Comm. Rep. Comm.* **37**: 201–204.
- ARNBOM, T., and WHITEHEAD, H. 1989. Observations on the composition and behaviour of groups of female sperm whales near the Galapagos Islands. *Can. J. Zool.* **67**: 1–7.
- ARNBOM, T., PAPANAVROU, V., WEILGART, L. S., and WHITEHEAD, H. 1987. Sperm whales react to an attack by killer whales. *J. Mammal.* **68**: 450–453.
- BERZIN, A. A. 1971. The sperm whale. Pacific Scientific Research Institute of Fisheries and Oceanography, Moscow. (Translated from Russian by Israel Program for Scientific Translations, No. 600707, Jerusalem, 1972.)
- BEST, P. B. 1979. Social organization of sperm whales, *Physeter macrocephalus*. In *Behavior of marine animals*. Vol. 3. Edited by H. E. Winn and B. L. Olla. Plenum Press, New York. pp. 227–289.
- BIGG, M. A., ELLIS, G. M., FORD, J. K. B., and BALCOMB, K. C. 1987. Killer whales. A study of their identification, genealogy, and natural history in British Columbia and Washington State. Phantom Press, Nanaimo, B.C.
- BRONI, S. C. 1985. Social and spatial foraging patterns of the jackass penguin *Spheniscus demersus*. *S. Afr. J. Zool.* **20**: 241–245.
- CALDWELL, M. C., and CALDWELL, D. K. 1966. Epimeletic (care-giving) behavior in Cetacea. In *Whales, dolphins, and porpoises*. Edited by K. S. Norris. University of California Press, Berkeley, CA. pp. 755–789.
- CALDWELL, D. K., CALDWELL, M. C., and RICE, D. W. 1966. Behavior of the sperm whale *Physeter catodon* L. In *Whales, dol-*

- phins, and porpoises. Edited by K. S. Norris. University of California Press, Berkeley, CA. pp. 677–717.
- CLARKE, M. R. 1980. Cephalopods in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Rep.* No. 37.
- CLIFF, A. D., and ORD, J. K. 1981. Spatial processes. Pion, London.
- CROOK, J. H. 1965. The adaptive significance of avian social organization. *Symp. Zool. Soc. Lond.* **14**: 181–218.
- DURBIN, J. 1965. Discussion on Professor Pyke's paper. *J. R. Stat. Soc. Ser. B*, **27**: 437–438.
- GASKIN, D. E. 1982. The ecology of whales and dolphins. William Heinemann Ltd., London.
- GORDON, J. C. D. 1987. Behaviour and ecology of sperm whales off Sri Lanka. Ph.D. thesis, University of Cambridge, Cambridge.
- HANLON, R. T., and BUDELMANN, B.-U. 1987. Why cephalopods are probably not "deaf". *Am. Nat.* **129**: 312–317.
- KAWAKAMI, T. 1980. A review of sperm whale food. *Sci. Rep. Whales Res. Inst. Tokyo*, **32**: 199–218.
- MECH, L. D. 1970. The wolf. The Natural History Press, Garden City, NY.
- MOYNIHAN, M. 1985. Why are cephalopods deaf? *Am. Nat.* **125**: 465–469.
- MULLINS, J., WHITEHEAD, H., and WEILGART, L. S. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Can. J. Fish. Aquat. Sci.* **45**: 1736–1743.
- NORRIS, K. S., and DOHL, T. P. 1980. The structure and function of cetacean schools. In *Cetacean behavior: mechanisms and functions*. Edited by L. M. Herman. Wiley, New York. pp. 211–261.
- NORRIS, K. S., and HARVEY, G. W. 1972. A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon*). In *Animal orientation and navigation*. Edited by S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, and R. E. Belleville. NASA Spec. Publ. No. 262. pp. 397–417.
- OHSUMI, S. 1971. Some investigations on the school structure of sperm whale. *Sci. Rep. Whales Res. Inst. Tokyo*, **23**: 1–25.
- PAPANAVROU, V. 1987. Feeding ecology of sperm whales *Physeter macrocephalus* in the Galapagos Islands. M.Sc. thesis, University of Bristol, Bristol.
- PAPANAVROU, V., SMITH, S. C., and WHITEHEAD, H. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Can. J. Zool.* **67**: 839–846.
- PULLIAM, H. R., and CARACO, T. 1984. Living in groups: is there an optimal group size? In *Behavioural ecology*. Edited by J. R. Krebs and N. B. Davies. Blackwell, Oxford. pp. 122–147.
- SOKAL, R. R., and ROHLF, F. J. 1981. *Biometry*. 2nd ed. W. H. Freeman and Co., New York.
- WATKINS, W. A. 1980. Acoustics and behavior of sperm whales. In *Animal sonar systems*. Edited by R.-G. Busnel and J. F. Fish. Plenum Press, New York. pp. 283–289.
- WATKINS, W. A., and SCHEVILL, W. E. 1977. Spatial distribution of sperm whales (*Physeter catodon*) underwater. *Deep-Sea Res.* **24**: 693–699.
- WHITEHEAD, H. 1987. Sperm whale behavior on the Galapagos grounds. *Oceanus*, **30**: 49–53.
- WHITEHEAD, H., and ARNBOM, T. 1987. Social organization of sperm whales off the Galapagos Islands, February–April 1985. *Can. J. Zool.* **65**: 913–919.
- WHITEHEAD, H., and WATERS, S. 1988. Social organization and population structure of sperm whales off the Galapagos Islands, Ecuador (1985 and 1987). *Int. Whaling Comm. Sci. Comm. Doc. No. SC/40/Sp 3*.
- WHITEHEAD, H., PAPANAVROU, V., and SMITH, S. C. 1988. Sperm whales and El Niño off the Galapagos Islands. *Int. Whaling Comm. Sci. Comm. Doc. No. SC/40/Sp 4*.