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Movements, distribution and feeding success of sperm whales in the Pacific Ocean, over scales of days and tens of kilometers

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Abstract

Movement patterns of groups of female and immature sperm whales (*Physeter macrocephalus*), which were followed over periods of 0.5–2.5 days in the South Pacific, were correlated with defecation rates to investigate foraging behavior, estimate the probable size of patches of prey and the distances between them. Relationships between environmental measures and the distribution and feeding success of groups of sperm whales were also examined. Feeding success and movement patterns were highly variable between groups. Groups with low feeding success moved in a rather straight line while those with high feeding success usually zigzagged over areas about 25–40 km across. As groups with low feeding success traveled in a straight line for 100 to 240 km, distances between 'good quality' patches of prey seemed to be on the order of at least 100 km. Both the mean swimming speed and the proportion of time the whales spent foraging showed no significant correlation with either feeding success or movement patterns, suggesting that the groups keep searching for food while traveling in a straight line. There was no relationship between the feeding success of a group and the measures of sub-surface biomass or an index of underwater relief measured along its track. This could be explained by either space or time lags between peaks in secondary productivity and peaks in prey density, and/or by some groups of sperm whales feeding on spawning squid.

Key words: Sperm whale, *Physeter macrocephalus*, distribution, movements, feeding success, spatial scales

Introduction

Habitat description and its utilization by an animal is central to the study of its ecology (Johnson, 1980). Recent studies of sperm whale (*Physeter macrocephalus*) habitat over spatial scales of hundreds to thousands of km have shown that sperm whales are usually found in areas of high relief which are characterized by intense scattering layers (Jaquet & Whitehead, 1996). However, as the relationships between the distribution of a predator and the distribution of its prey are invariably scale-dependent (Schneider & Piatt, 1986; Horne & Schneider, 1994; Jaquet, 1996), these recent studies over large scales cannot be extrapolated to smaller scales. Investigating habitat utilization by sperm whales is a difficult task as they forage at depths of several hundred meters, severely reducing opportunities for direct observation. Therefore, knowledge concerning the environmental factors influencing sperm whale distribution over spatial scales of less than one hundred km and the extent to which they are feeding in a particular habitat is still very limited.

In ecological studies, relative movements of predators and prey are likely to affect how correlations between their distributions change with scale (Veit *et al*., 1993). If the relationship between the distribution of a predator and the distribution of its prey is studied at too small a scale, coherence will seem to be absent as predators are seldom exactly aligned with prey. On the other hand, if the system is studied at too large a scale, little will be learned of the small scale relationships. Over small spatial scales, Rose & Leggett (1990) suggested that the best scale to choose is the one that corresponds to the patch size of aggregations of both predators and prey.

Relationships between predator and prey distributions over scales of 1 to 10 km have been conducted successfully on various marine species that forage near the surface and/or for which the main prey are fairly well known. Woodley & Gaskin (1996) demonstrated that over a spatial scale of 5 km by 5 km, North Atlantic right whales (*Eubalaena glacialis*) were closely associated with copepod abundance. Veit *et al*. (1993) used a spatial

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scale of 1.8 km by 1.8 km to examine the relationship between pelagic predators (birds and fur seals) and Antarctic krill (*Euphausia superba*). They observed that the distributional patterns of predators were strongly influenced by the distribution of krill swarms. They also found an offset of a few km between a peak in krill density and peaks in some predator densities, suggesting that each predator specializes in a different part of the swarm, or that different species of predators avoid each other, or both. Schneider & Piatt (1986) showed a positive correlation between the distribution of piscivorous seabirds (*Uria algae* and *Fratercula arctica*) and schooling fish (primarily capelin *Mallotus villosus*) over spatial scales of 2 to 6 km. In all these studies, both aggregations of prey and aggregations of predators could be observed, and the patch size measured.

Sperm whales spend about 70–75% of their time at depths of a few hundred meters (Lockyer, 1977; Gordon, 1987; Papastavrou *et al*., 1989; Watkins *et al*., 1993), and most of their diet consist of meso and bathypelagic cephalopods (Clarke, 1980; Kawakami, 1980; Clarke *et al*., 1993). Because of the ability of these deep-living squid to escape trawls and nets (Clarke, 1977; Clarke, 1985; Vecchione & Roper, 1991), and because of the difficulty of studying them using acoustic methods (Starr & Thorne, in press), much of our knowledge of these cephalopods comes from studies of the stomach contents of sperm whales (Clarke, 1985; Nemoto *et al*., 1985; Nemoto *et al*., 1988). Therefore, it is not possible to directly relate sperm whale distribution to the distribution of its main prey item, nor to directly measure the size of a patch of squid.

However, it is likely that environmental variables influence the density of squid as well as the sizes of their patches. It has been postulated that a temperature gradient of about 5°C in the upper one hundred meters and the presence of oceanic fronts are important factors contributing to the concentration of squids (Uda, 1959). Therefore, the small-scale distributions of some species of teuthophagous predators have been studied in relation to environmental factors. For instance, Hui (1985) showed that pilot whales (*Globicephala macrorhynchus*) were encountered significantly more often in areas of high relief than in areas of low relief over a spatial scale of 11 km.

Furthermore, in the absence of direct observations, habitat utilization can be inferred from feeding success. Following Whitehead *et al*. (1989), Smith & Whitehead (1993) and Whitehead (1996), we use the defecation rate (the rate of observing defecations as sperm whales dive) of a group of sperm whales as an indicator of their feeding success.

In this study we relate the movement patterns of groups of sperm whales to their feeding success in order to investigate foraging behavior, estimate the probable size of patches of prey and the distances between them. We also investigate relationships between the feeding success of a group of whales and an index of underwater relief and the volume of acoustic backscatter. Finally we describe the environmental and biological characteristics of sperm whale habitat over spatial scales of 9 to 45 km by examining changes in environmental variables while sailing away from a group of whales.

Methods

Field methods

Data were collected from a 12.5 meter, ocean-going cutter during a survey around the South Pacific in 1992–1993 (Fig. 1). Sperm whales were located by listening every half hour through an omnidirectional hydrophone for their characteristic clicks (Backus & Schevill, 1966). Weather permitting (wind strength ≤ 3 on the Beaufort Scale), sperm whales were then followed both acoustically and visually for periods ranging from a few hours to two and half days (Whitehead & Gordon, 1986). A total of 626 hours were spent in visual or acoustic contact with groups of sperm whales. The position of the boat was recorded every hour using a Trimble Transpak Global Positioning System (GPS).

When not disturbed (by human activity or predators), groups of sperm whales usually show 2 broad types of behavior as described by Whitehead & Weilgart (1991) from the results of an extensive multivariate analysis: (1) The whales dive deeply as indicated by fluke-ups and regular click trains, and are thus presumed to be foraging (called 'foraging' by Whitehead & Weilgart, 1991); (2) the whales cluster closely together at the surface, moving very slowly, often touching and rubbing one another, and sometimes emitting 'codas' (a type of vocalization which has been related to social activities, Weilgart, 1990) and thus this behavior has been called 'socializing' (Whitehead & Weilgart, 1991). For each daylight hour spent following groups of whales, we recorded whether the animals were predominantly foraging or socializing. The 'proportion of time foraging' represents therefore the proportion of daylight time during which most of the group was showing foraging behavior.

A measure of feeding success

During daylight hours when the wind strength was equal or below Force 3 on the Beaufort scale, individual sperm whales were followed very closely (~ 30 m behind), and photographs of their flukes were taken at the commencement of a deep-dive

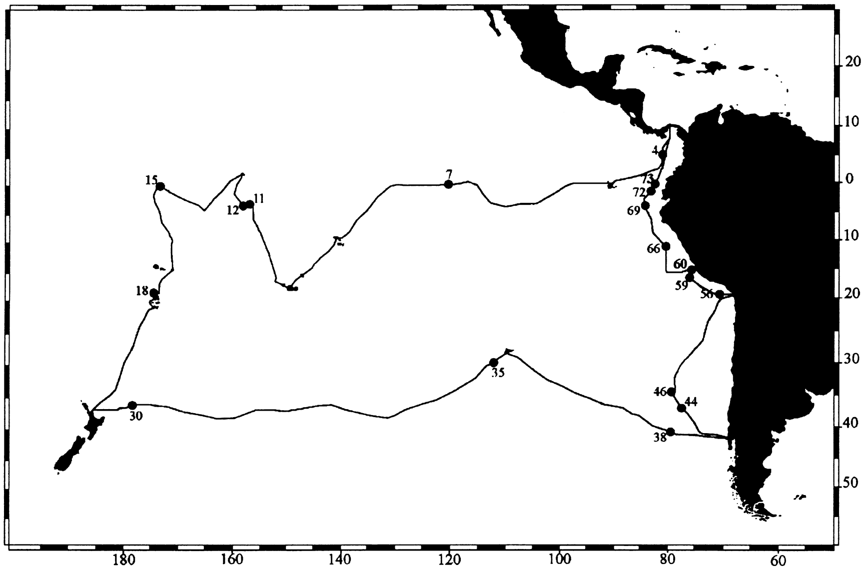


Figure 1. Track of the research vessel with positions and identity numbers of groups of female and immature sperm whales which were followed for more than 12 hours and/or for which variations in chlorophyll concentration, intensity of scattering layers and sea surface temperature were measured while sailing away from the group.

(fluke-up) to identify individuals (Arnbom, 1987). When starting a deep dive, sperm whales leave a slick (patch of flat water easily discernible for a few minutes after the beginning of the dive), allowing us to find the exact spot where the whale initiated its dive. Being so close behind the whale, the boat was usually able to be in the slick in a matter of tens of seconds after a dive, and the presence or absence of a defecation (brown patch in the water) was recorded whenever we were confident of our ability to make such a determination. The ‘defecation rate’ of a group (number of slicks with defecation/total number of slicks checked) was then calculated to give an estimation of its feeding success during the time it was tracked (Whitehead *et al.*, 1989; Smith & Whitehead, 1993; Whitehead, 1996).

The use of defecation rate as an indication of feeding success is justified for the following reasons.

—During deep dives, deep-diving mammals shut down physiological systems which are not immediately essential (Kooyman *et al.*, 1981); and therefore sperm whales are unlikely to defecate at great depths.

—Around the Galápagos Islands, Smith & Whitehead (1993) observed a strong inverse correlation between mean defecation rate and sea surface temperature (which is closely related to productivity in the area).

The defecation rate being a proportion of the number of slicks examined, for a similar defecation rate, shorter dives mean more slicks examined and thus lower feeding success. However, Papastavrou *et al.* (1989) found similar dive durations in 1985 (non El Niño year, high feeding success) and in 1987 (El Niño year, low feeding success), suggesting that dive duration is not related to extrinsic conditions.

Papers based on this technique have already been published in Marine Ecology Progress Series (Whitehead *et al.*, 1989), Journal of Animal Ecology (Whitehead, 1996), and Canadian Journal of Zoology (Smith & Whitehead, 1993). This technique has also been used in a paper recently published in Marine Mammal Sciences (Christal & Whitehead, 1997).

In our current state of knowledge about sperm whales, neither vocalizations nor respiration rate can be used as a good indicator of feeding success. Although it has been suggested that certain types of vocalizations (echolocative creaks) occur when sperm whales are closing in on prey (Gordon, 1987), creaks are also used in social settings (Whitehead & Weilgart, 1991). Moreover, Clarke *et al.* (1993) postulated that sperm whales catch much of their food by visual location of luminous shoals of small, slow swimming cephalopods. There is also no indication that respiration rate is in any way related to feeding success. Therefore, it seems that observation of defecation rates is the best currently available method of estimating feeding success of living sperm whales.

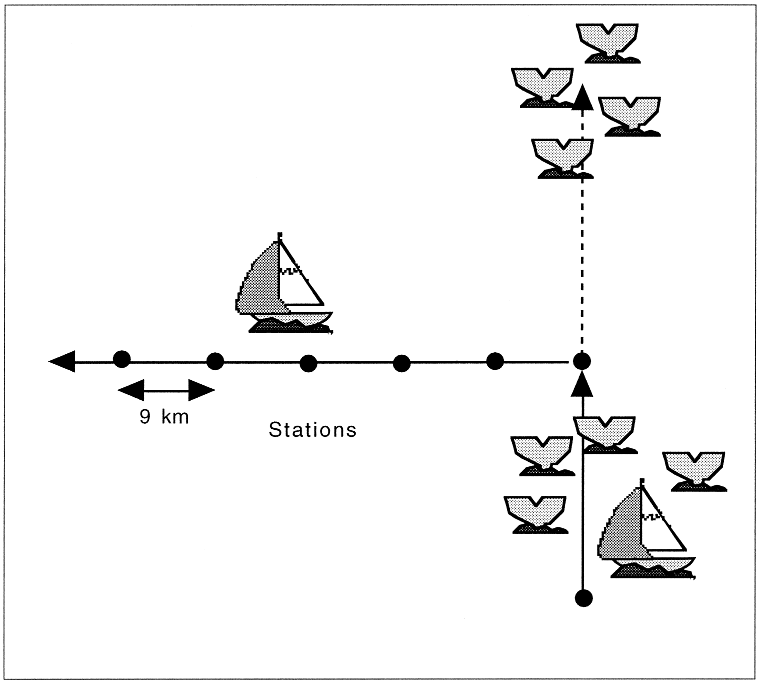


Figure 2. Small scale observations while sailing away from a group of whales. At each 'station' measurements of chlorophyll concentration, intensity of scattering layers at 3 different depths and sea surface temperature were made.

Stomach fullness studies, conducted during commercial whaling, showed no evidence for any special feeding period (Clarke, 1980). Many species of deep-living squid, including most species sperm whales are feeding on, do not undertake diurnal vertical migrations to the surface layers, but only a slight vertical shift in distribution (Roper and Young, 1975). Therefore, it seems likely that sperm whale foraging behavior would not differ much between day and night and that the absence of observations during night time (when it is impossible to see defecations) did not introduce too strong a bias in our analyses.

Defecation rates were calculated for groups only when 15 or more slicks were checked. Previous studies have shown a mean defecation rate of about 10% (Whitehead, 1996), and thus, 15 slicks was roughly the minimum which had to be checked in order to obtain a reasonably reliable difference between a low feeding success (0 slicks with defecations/15 slicks checked) and a high feeding success (2–4 slicks with defecations/15 slicks checked). The defecation rate of a group was calculated over the total number of hours that each group was followed (usually about 30 hours, but up to 66 hours).

The lack of data on the time lag between ingestion and excretion in sperm whales presents a problem when attempting to determine feeding success from defecation rates. Studies of stomach contents (notably Clarke, 1980) suggested that digestion of cephalopod flesh takes place within hours of capture by the whale. Therefore, defecation rate is likely to give an indication of the feeding success during the past 12 h (Smith & Whitehead, 1993). In the present study, as the data were averaged over roughly 30 hours, it is possible to use defecation rate as a measure of feeding success even though the exact time for the food to go through the entire gut is not known.

Environmental measures

Environmental variables were recorded when a group was first encountered, then once per day at 15:00 local time, and once more before leaving the group. Whenever possible, environmental variables were also recorded every 9 km until 45 km while sailing away from a group, on a heading roughly perpendicular to their general heading (Fig. 2). Chlorophyll concentration ('Chlorophyllconc') was estimated by a spectral radiometer (McLean & Lewis, 1991) for most of the survey, and by a Secchi

Table 1. Description of the variables calculated for each group of whales. The variables in bold were also calculated from data obtained while sailing away from a group

Variables	Description	Units
Velocity	Total distance traveled by a group while followed divided by the number of hours it was tracked	km/h
Straightdistance-12	Distance between position where tracking was initiated and position 12 hours later	km
Realdistance-12	Distance traveled during 12 hours	km
Zigzag	Total distance traveled by a group between the position when first encountered and the position when left divided by the straight-line distance between these 2 positions	—
Proportion of time foraging	Proportion of daylight time during which most of the group is showing 'foraging behavior'	percentage
Defacation rate	Number of slicks with defecation divided by total number of slicks examined	—
Chlorophyllconc	Chlorophyll concentration	mg/m^3
Intensity of SL0–50 m	Maximum intensity of the surface scattering layer (0–50 m)	subjective scale from 0.0 to 4.0
Intensity of SL50–300 m	Maximum intensity of the medium scattering layer (50–300 m)	subjective scale from 0.0 to 4.0
Intensity of SL300–600 m	Maximum intensity of the deep scattering layer (300–600 m)	subjective scale from 0.0 to 4.0
Backscatter-total	Total amount of acoustic backscatter between 0 and 600 m	—
SST	Sea surface temperature	°C
C.I.	Contour index, defined using Hui's (1979) formula, *C.I.* = 100 X[(maxdepth–mindepth)/maxdepth]	—

disk when sailing away from a group. During half of the survey, chlorophyll concentration was recorded simultaneously by a spectral radiometer and a Secchi disk to assess the validity of the Secchi disk measurements. Secchi depth (in meters) was converted to chlorophyll concentration using the following formula: $\mathrm{Chl} = 920 Z_{sd}{}^{-2.6}$, where Z_{sd} is the Secchi depth in meters (Lewis *et al*., 1988). Sea surface temperature ('SST') was recorded every 3 hours. The intensities of sub-surface scattering layers were recorded at three different depths (between 0 and 50 m; 50 m and 300 m; 300 m and 600 m) with a Furuno CH 16 sonar (frequency: 60 KHz) using a subjective scale ranging from 0 to 4 (0 = blue water, 4 = very intense scattering layer). 'Intensity of SL0-50 m' represented the intensity of the scattering layer between 0 to 50 m (~depth of the euphotic zone); 'Intensity of SL50–300 m' represented the intensity of the scattering layer between 50 to 300 m; and 'Intensity of SL300–600 m' represented the intensity of the scattering layer between 300 to 600 m (approximate depth range at which sperm whales normally feed, Papastavrou *et al*., 1989).

A measure of the total amount of backscatter ('Backscatter-total') was calculated as the intensity of the surface scattering layer multiplied by its thickness, plus the intensity of the medium scattering layer multiplied by its thickness, plus the intensity of the deep scattering layer multiplied by its thickness. A contour index ('C.I.') was calculated using the charts 'Bathymetry of the North/South Pacific, Scripps Institution of Oceanography and Institute of Marine Resources, 1970'. Due to the resolution of the bathymetric charts across the South Pacific, 70 km was the smallest radius which could be used to calculate a meaningful contour index. More detailed bathymetric charts do not exist over such a large spatial scale (The South Pacific Ocean) and are only available for coastal areas. The track of a group of whales was plotted on the charts, and the maximum and the minimum depths in a radius of 70 km were used to calculate the 'C.I.' according to Hui's (1979) formula:

$$\text{'C.I.'} = 100 \times [(\text{maxdepth-mindepth})/\text{maxdepth}].$$

Data analyses

For each group that was followed for more than 12 consecutive hours, all the variables listed in Table 1 were calculated. The 'velocity' represented the speed of a group of whales and was calculated as the total distance traveled by a group divided by the number of hours it was tracked. The straight-line distance traveled by a group in 12 hours while being

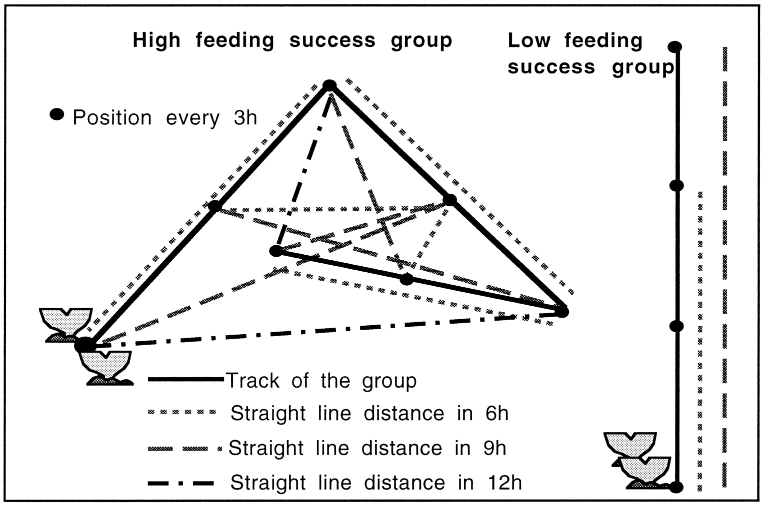


Figure 3. Examples showing 2 groups, one with high feeding success zigzagging over an area, and one with low feeding success traveling in a straight-line. Each of the dash-lines represent a straight-line distance traveled in respectively 6 h, 9 h and 12 h. Then, the mean straight-line distance cover in 6 h by a group was calculated as the average of all the 6 h segments.

followed by the research vessel was expressed by 'Straightdistance-12'; the total distance traveled by the group in 12 hours (including all zigzags) was expressed by 'Realdistance-12'. The variable 'zigzag' ('Realdistance-12' divided by 'Straightdistance-12') gives an indication of the directness of the movements of a group of sperm whales during the time it was followed. A high value (>>1) means that the group was mainly moving back and forth over an area while a value of 1 means that the group was traveling in a straight line.

To investigate the relationship between the feeding success and the movement of a group, a Spearman coefficient of correlation was calculated between 'zigzag' and 'defecation rate'. A positive correlation would result if the whales moved back and forth over an area at times when feeding success was high, but traveled consistently in one direction when feeding success was low.

The spatial and temporal scales of sperm whale movement patterns were investigated by calculating for each group the straight-line distance traveled in each 3-hour interval, then the straight-line distance traveled in each 6-hour interval, then in each 9-hour interval and so on (Fig. 3). For each group, the mean straight-line distance traveled in 3 hours was calculated by summing the straight-line distances traveled in all 3-hour intervals and dividing this sum by the number of intervals. The mean straight-line distance traveled in 6-hour intervals, 9-hour intervals, etc., were calculated in a similar way. If a group was moving back and forth over a certain area, the mean straight-line distance covered by the group in any time interval cannot be larger than the largest diameter of the area. On the other hand, if a group was moving in straight-line, the straight-line distance covered by the group will keep increasing with increasing time intervals (Fig. 3). For each group, the mean straight-line distance was plotted against time interval in hours.

To examine whether the mean swimming speed ('velocity') of a group was related to its feeding success and/or to movement patterns, Spearman coefficients of correlation were calculated between 'velocity' and 'defecation rate' and between 'velocity' and 'zigzag'. Also, to examine whether the proportion of time a group spent foraging was related to feeding success or movement patterns, Spearman correlations were calculated between 'proportion of time foraging' and 'defecation rate' and between 'proportion of time foraging' and 'zigzag'. To investigate how feeding success was related to productivity and environmental variables, Spearman coefficients of correlation were calculated between 'defecation rate' and 'backscatter-total' and between 'defecation rate' and 'C.I.'.

Finally, to investigate whether there were consistent changes in environmental variables at different distances from groups, and so to give further indications of the possible sizes of prey patches, the values of some environmental variables ('Chlorophyllconc', 'Intensity of SL 0-50', 'Intensity of SL 50-300', 'Intensity of SL 300-600', 'SST') were

Table 2. Summary of statistics for all variables recorded while following groups of sperm whales

Variable	N. of cases	Min.	Max.	Mean	S.D.	Units
Velocity	16	2.5	5.2	4.1	0.7	km/h
Straightdistance-12	16	13.6	48.9	33.1	12.9	km
Realdistance-12	16	29.6	62.3	49.4	8.7	km
Zigzag	16	1.12	3.7	1.74	0.80	—
Proportion of time foraging	11	11	90	57.0	27.2	%
Defecation rate	11	0	0.325	0.084	0.09	—
Chlorophyllconc	16	0.1	3.24	0.51	0.7	mg/m^3
Intensity of SL0–50 m	16	0	4	2.34	1.39	—
Intensity of SL50–300 m	16	1	4	3.11	1.02	—
Intensity of SL300–600 m	16	0	4	1.96	1.49	—
Backscatter-total	16	150	1440	753.3	421.1	—
SST	16	17.2	28.8	24.5	3.3	°C
C.I.	16	0	93	51.9	32.8	—

recorded just before leaving a group of whales and then every 9 km until 45 km on a heading roughly perpendicular to the heading of the whales (Fig. 2). For each variable and for each group, the difference between the values at each station (9, . . . ,45 km) and the values just before leaving a group were calculated. Then, for each station, the mean value and the standard deviation of all the differences was calculated for each variable. The environmental data were collected for 17 groups, but measurements of chlorophyll concentration were recorded only for 10 groups, and scattering layer characteristics for 12 groups.

Results

Sixteen groups of female and immature sperm whales were followed for more than 12 hours (Fig. 1); the maximum tracking time was 67 hours and the mean was 32 hours. The summary statistics of the variables recorded while following groups are presented in Table 2.

The mean 'velocity' (4.1 km/h, S.D.=0.7) was very consistent between groups. The total distance traveled through the water in 12 hours ('Realdistance-12', mean=49.4 km, S.D.=8.7) was more consistent between groups of sperm whales than the distance covered in a straight line during 12 h ('Straightdistance-12', mean=33.1 km, S.D.=12.9). 'Defecation rate' was significantly correlated with 'zigzag' index ($r_s=0.729$, $P<0.05$), suggesting that, as hypothesized, sperm whales are feeding more when they are going back and forth over an area than when they are moving in a straight line.

For each group, the mean straight-line distance traveled during periods of 3 hours to 66 hours is plotted on Fig.4. Fig 4A shows that, when the feeding success was low (<0.06 defecations/fluke-up), groups of sperm whales tended to travel in a rather straight line without zigzagging, as indicated by the straight-line relationship between distance moved and time interval. The slope of these relationships is very similar among all these groups, suggesting a very similar mode of travel. None of the curves approach an asymptote indicating that none of the groups started backtracking while being followed. Therefore, as these groups traveled between 100 and 240 km, this suggests that the distance between 'good quality' prey patches, where it might pay sperm whale's to backtrack, may be in the order of at least 100 km. Fig. 4C shows the relationship between distance traveled and time intervals for the groups having a high feeding success (>0.11 defecations/fluke-up). For 3 of the groups (#11, #72, #73) the curves leveled after 25 to 40 km, suggesting that the groups are moving back and forth over an area with a maximum span of 40 km. As these groups have a high feeding success, it is likely that these areas correspond to patches of prey. Group #59 showed the same behavior as the groups with low feeding success suggesting exceptions to the general rule of zigzagging with high feeding success and straight-line movement with low feeding success. The curves representing the groups with moderate feeding success (between 0.06 and 0.08 defecations/fluke-up) are found in between the ones representing groups with low feeding success and the ones representing groups with high feeding success (Fig. 4B) suggesting a continuity in foraging behavior.

To help visualization, the track of a few groups of sperm whales were plotted on Fig. 5 and 6. These figures do not capture the small scale movements of the groups (less than about 10 km and less than 3

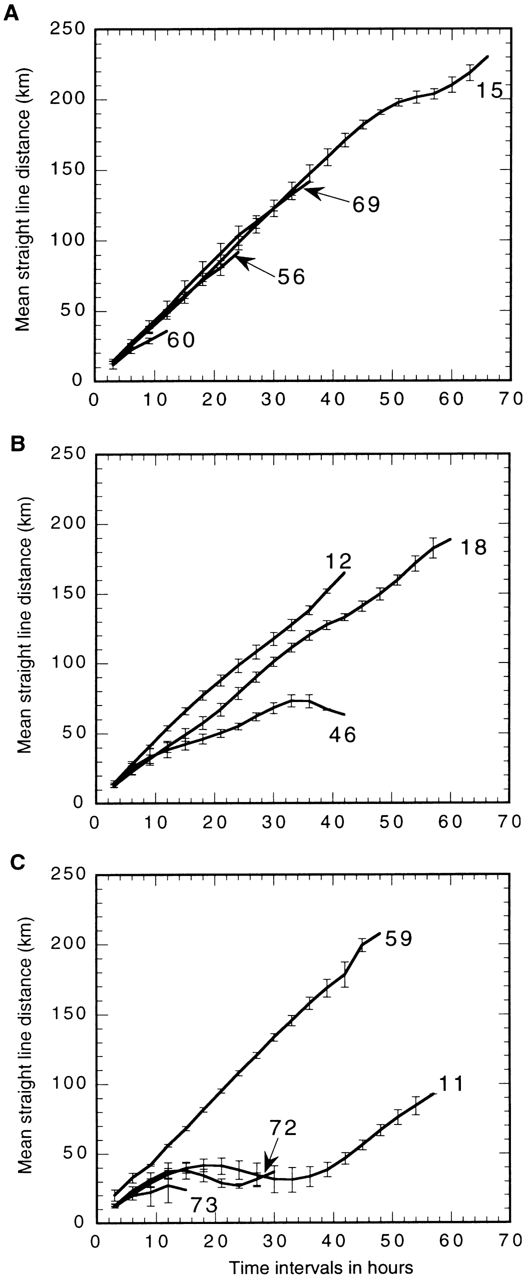


Figure 4. Mean straight-line distance traveled by each sperm whale group versus time interval. (A) groups with low feeding success (0%–5.4%); (B) groups with moderate feeding success (6.1%–8%); (C) groups with high feeding success (11.4%–32.5%). The numbers at the end of each curve represent the identity number of the groups (as in Fig. 1).

hours) as the boat was constantly moving between visible whales (at the surface) and as foraging whales are usually spread over several km. Fig 5 shows three groups which were followed for about 60 hours: number 15, number 18 and number 11 with respectively low, medium and high feeding success. Group number 15 (low feeding success) and number 18 (medium feeding success) were traveling in a rather straight line (straighter for number 15 than for number 18) and group number 11 (high feeding success) had a smaller range with more zigzagging. Fig. 6 show two groups which were followed for about 34 hours: number 69 (low feeding success) and number 72 (high feeding success). The trends observed in this figure are similar to those in Fig. 5, a rather straight line for a group with low feeding success and smaller distances traveled with more zigzagging for a group with high feeding success.

The mean speed through the water ('velocity') was not significantly correlated to either 'defecation rate' or 'zigzag' ($r_s=0.3$, $P>0.05$ and $r_s=0.0$, $P>0.05$ respectively). The coefficients of correlation between 'proportion of time foraging' and both 'defecation rate' ($r_s=0.505$, $P>0.05$) and 'zigzag' ($r_s=0.424$, $P>0.05$) were not significant either, but their higher values suggested that the whales were perhaps spending more time foraging when they had a high feeding success than when they had a low feeding success.

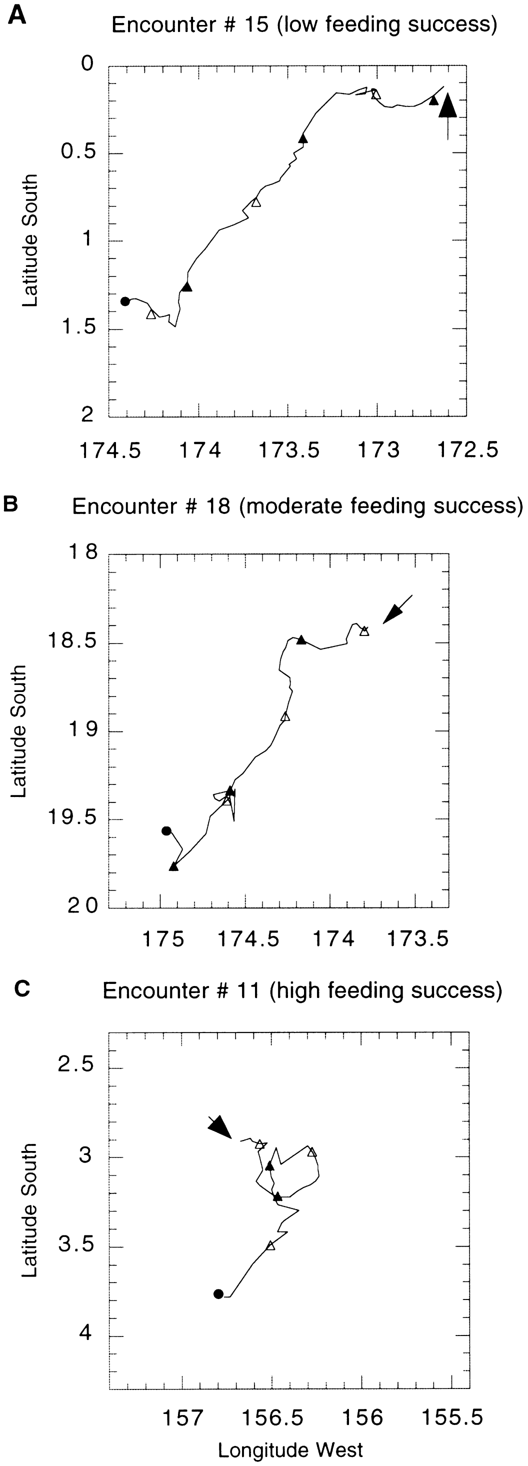
'Defecation rate' was not related to either 'backscatter-total' ($r_s=-0.118$, $P>0.05$), nor to the 'contour index' ($r_s=-0.137$, $P>0.05$).

There was no consistent pattern in the differences between the values of each environmental variable at the time of departure from a group and at distances up to 45 km away from the group (Fig. 7). Moreover, the standard deviation was always very high in comparison to the mean difference.

Finally, the groups were divided into 2 sets according to their feeding success, separating the groups which may have been feeding over a patch of prey from the ones which may have been traveling between patches. The first set contained 8 groups having a rather high feeding success (8%–32%), while the second set comprised 9 groups having a comparatively low feeding success (0%–6.3%). Similar analyses to those described above were carried out for the 2 sets. However, as there was still no pattern for the groups having a high feeding success, and as the graphs representing just groups with high or with low feeding success were very similar to the ones presented on Fig. 7, they are not shown here.

Discussion

Despite the small sample size (16 groups), some clear patterns emerged from our analysis of the



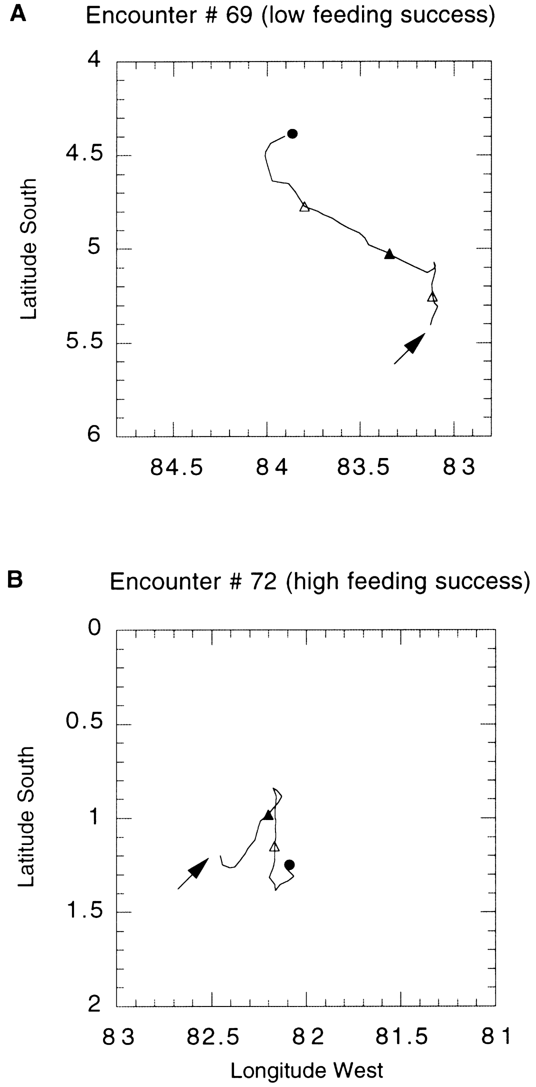


Figure 6. Track of 2 groups (having respectively low and high feeding success) followed during approximately 34 hours. The arrow represents the starting point of each encounter and the black circle the position at which the group of whales was left; open triangles represent the approximate time of sunrise while close triangles the approximate time of sunset.

Figure 5. Track of 3 groups (having respectively low, moderate and high feeding success) followed during approximately 60 hours. The arrow represents the starting point of each encounter and the black circle the position at which the group of whales was left; open triangles represent the approximate time of sunrise while close triangles the approximate time of sunset.

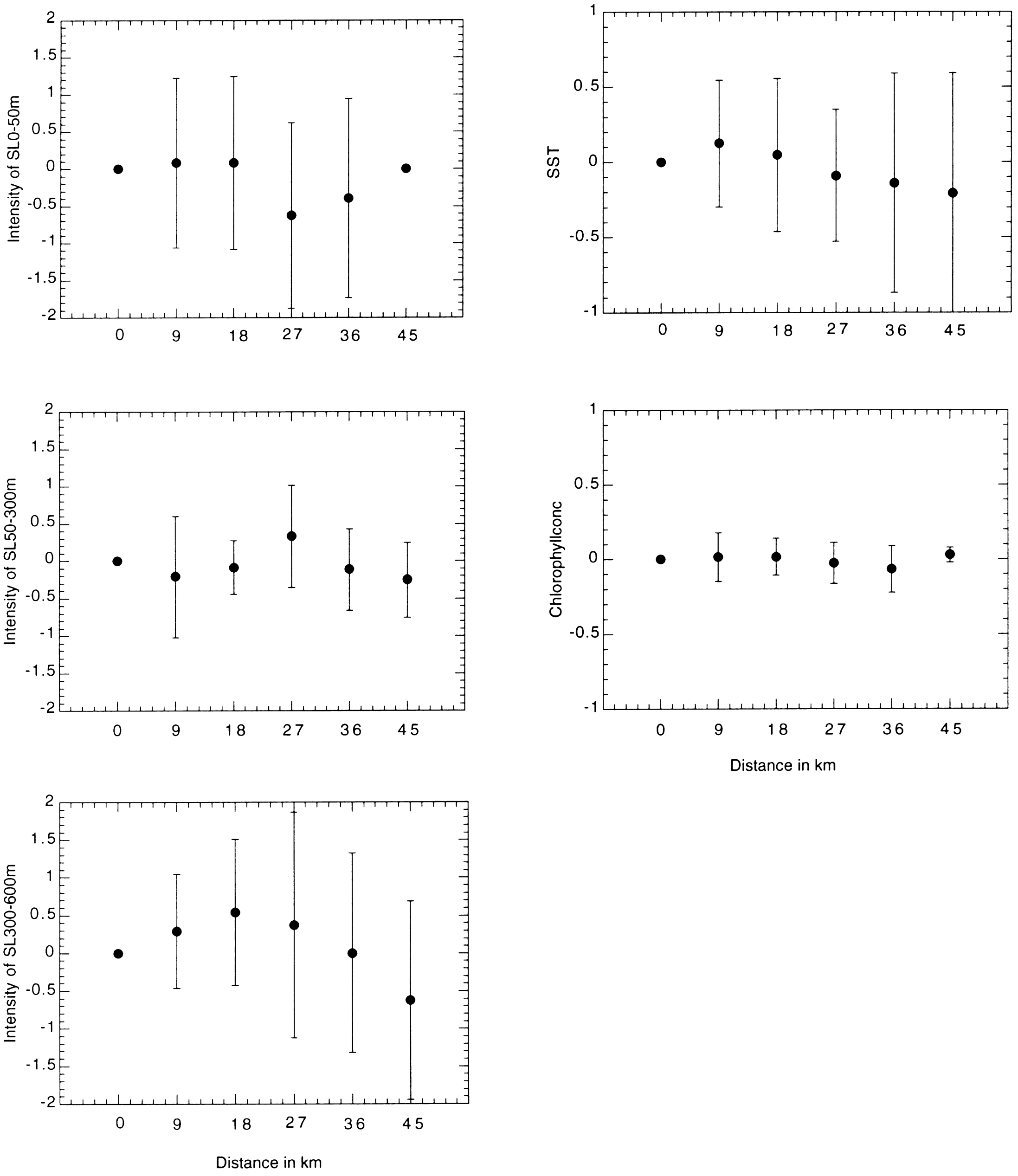


Figure 7. Variation in sea surface temperature (SST), chlorophyll concentration (Chlorophyllconc) and intensity of scattering layers at 3 different depths (Intensity of SL0–50 m, Intensity of SL50–300 m, Intensity of SL300–600 m) while sailing away from groups of whales. Each dot represents the mean difference between the value at this ‘station’ and the value measured just before leaving the group; the vertical bars represent standard deviations.

movements of groups of sperm whales over periods of a few hours to a few days. Independently of their feeding success or the amount of time that they spent foraging, the groups traveled through the water at about 4.1 km/h. This mean speed is consistent with other estimates for groups of sperm whales in different areas: 3.4 km/h (Papastavrou *et al.*, 1989, for Galápagos Islands), 4.6 km/h

(Gordon, 1987, for Sri Lanka). This speed presumably represents an optimum largely determined by energetic factors.

However, over periods of a few hours movement patterns differed substantially between groups with high and low feeding success. Groups with low feeding success moved in a rather straight line, while those with high feeding success usually zigzagged over areas about 40 km across. This is consistent with the results of an analysis of the movement patterns of groups of sperm whales off the Galápagos Islands (Whitehead, 1996). Off the Galápagos, groups with defecation rates greater than 15% moved less than 12 km in a 12 hour period, whereas groups which moved 15– 55 km all had defecation rates lower than 15%. There were only small differences in other aspects of behavior between groups with high and low feeding success. For example, the proportion of time a group of sperm whales spent foraging was not significantly different whether the group had a high or a low feeding success. Therefore, it seems that movement patterns are determined by feeding success (i.e. the whales move away from an area where there is little food) rather than feeding success being determined by movement patterns (as could be found if foraging and migratory behavior were distinct).

As inferred from the movements of the whales, the prey of the South Pacific sperm whales may occur in patches of the order of 25–40 km across (Fig. 4–6). The tracks of groups which traveled over 150 km in straight lines (Fig. 4–6) suggest that some prey patches may be well dispersed and hard to find, or sufficiently small that doubling back through them would not be profitable. There is consistency in the shape and in the slope of the curves relating distances traveled to time intervals for the groups having a low feeding success (Fig. 4A), suggesting that when traveling between prey patches, the behavior and movement of the whales is similar among groups.

With prey patches of the order of 25–40 km across, the lack of consistent variation in environmental measures at distances from 9 to 45 km from groups of whales was not unexpected. Data from this survey show that some of the same environmental measures, especially those from acoustic scattering layers and bottom topography, were strongly correlated with sperm whale distribution over spatial scales of 590 and 1120 km (Jaquet & Whitehead, 1996). Over these scales the correlation increased with increasing spatial scale, so we might have predicted that correlations over scales of 9–45 km would be small.

More surprising was the lack of relationships between the feeding success of the groups and any of our environmental measurements, but this could be due to the small sample size (n = 11), as only a strong and consistent relationship would have been detected with this study. Furthermore, a spatial lag of more than 10–100 km, and/or a time lag of more than 2 days between a peak in chlorophyll or zooplankton concentration and a peak in squid density, might have masked any relationship. However, the result could also suggest that, over a spatial scale of 10 to 100 km, some of the patches of squid that sperm whales feed on are found in rather unproductive waters. Several species of squid are known to spawn in warm, but nutritionally poor, waters (Mann & Lazier, 1991; O'Dor, 1992), and Clarke (1980) has suggested that sperm whales feed on spawning grounds, thus taking advantage of a high biomass of dying squid.

Additional information on the small-scale movements of sperm whales underwater should be available from Time Depth Recorder-type tags (e.g. Watkins *et al.*, 1993) or acoustic methods (e.g. Watkins & Shevill, 1977) before long. However, quantifying feeding success over small time scales will probably continue to be a problem, as will the location and definition of patches of mesopelagic and bathypelagic squid.

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