Variation in the Feeding Success of Sperm Whales: Temporal Scale, Spatial Scale and Relationship to Migrations
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Variation in the feeding success of sperm whales: temporal scale, spatial scale and relationship to migrations

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Summary

1. Variability in a measure of the feeding success of sperm whales, defecation rate, was calculated over temporal scales ranging from 5 h to 4 years, and spatial scales ranging from 100 to 5000 km.
2. Sperm whale feeding success was not obviously linked to any sub-annual environmental cycles, with the possible exception of time of day.
3. Variability in feeding success over temporal scales of 1–64 days, and spatial scales of 100 km, was about 60% of the long-term mean, but reached 130% of the long-term mean over time intervals of 2–4 years and distance intervals greater than 500 km.
4. During periods of days characterized by low feeding success groups of sperm whales moved greater distances.
5. Migration over ranges of about 300–1000 km allows sperm whales to maintain high biomass and low reproductive rates in an environment which, at any location, contains long, unpredictable periods of food shortage.

Key-words: *K*-selection, mesopelagic ocean, movement, *Physeter macrocephalus*, variability in food supply.

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Introduction

A consideration of scale should be central in ecology (Levin 1992). At the species level, patterns of environmental variation over a wide range of spatial and temporal scales determine population ecology and define evolutionary selective pressures. At higher levels of organization, consideration of both temporal and spatial scale is a necessity in both community and landscape ecology (Levin 1992).

Oceanographers and marine ecologists have recognized the importance of cross-scale research in studies of a diverse range of marine organisms and their environment (e.g. Stommel 1963; Haury, McGowan & Wiebe 1978; Schneider & Duffy 1985; Rose & Leggett 1990). Populations of particular species track spatial and temporal variability in their environment at some scales but not others. Tracking at temporal scales longer than the organism's lifetime and spatial scales broader than its home range is largely achieved through variations in reproduction, recruitment, mortality and migration. Environmental variability over smaller scales, which is not tracked at the population level, usually results in changes in the feeding success, nutritional status and, sometimes, the behaviour of individual organisms.

Populations of species with low reproductive rates and high mean biomass (relative to the long-term mean availability of nutrients) cannot track environmental variation through changes in reproduction or mortality, except over very long time scales. A species which maintains a high biomass, and yet evidently does not face selection pressure for high reproductive rates, must possess mechanisms for surviving and averaging environmental variation over temporal scales less than their lifetimes, and spatial scales less than their home ranges. However, scale has rarely been explicitly considered in studies of such '*K*-selected' species (e.g. Jaquet 1996).

The sperm whale, *Physeter macrocephalus* Linnaeus, is a large animal (10 t for females, 30 t for males) with an extremely low reproductive rate: mature females (> *c.* 10 years old) give birth to single offspring once every 4–5 years (Best, Canham & Macleod 1984). The currently accepted population parameters for this species (International Whaling Commission 1982) suggest a maximum potential rate of increase of less than 1% per year. The sperm whale is also successful: estimated pre-whaling numbers and biomass exceed those of any other large whale; and the sperm whale appears to dominate the upper trophic levels of the habitat in which it feeds, the mesopelagic ocean (200–1000 m deep), consuming cephalopod biomass at a rate comparable to all human marine fisheries combined (Kanwisher & Ridgway 1983; Katona & Whitehead 1988; Rice 1989). Some pre-whaling population estimates for North Pacific sperm whales are larger than the marine environment is believed to be able to maintain (Northridge 1982), strongly indicating that pre-whaling sperm whale biomass was a large proportion of the total at their trophic level in the mesopelagic ecosystem.

It is only possible for sperm whale populations to track substantial environmental variability by increasing population size through reproduction over temporal scales of several decades and longer. Considerable environmental variation over shorter time periods poses potential problems for individual sperm whales. Members of the species must have somehow largely solved these problems, as their populations seem to have maintained substantial biomass. Therefore, it is important to consider the variability in the sperm whales' environment over temporal scales of a few years and less, as well as over spatial scales within the animals' potential range of dispersal. Little is known of the dynamics of the mesopelagic ocean, with the bulk of current information on some important cephalopod species being deduced from studies of sperm whale diet (e.g. Clarke 1980). Thus, an examination of pattern and scale in the distribution and feeding success of sperm whales may give information about a relatively inaccessible ecosystem (Jaquet 1996), as well as about their own evolutionary ecology.

In past studies my colleagues and I have used the defecation rates – the rate of observing defecations as sperm whales dive – as indicators of their feeding success (Whitehead, Papastavrou & Smith 1989; Kahn, Whitehead & Dillon 1993; Smith & Whitehead 1993). This is justified for the following reasons.

1. During deep dives, deep-diving mammals shut down physiological systems which are not immediately essential (Kooyman, Castellini & Davis 1981). Thus, while at depth, sperm whales are unlikely to use the muscular mechanisms needed to defecate.
2. Off the Galápagos, mean defecation rates are well correlated with sea surface temperatures, which are very closely related to productivity (Smith & Whitehead 1993).
3. The majority of observed defecations are coincident with the commencement of dives. Thus, the rate at which defecations are produced at the start of dives is probably very closely related to the overall defecation rate.
4. In our principal study area off the Galápagos Islands, as well as in the mainland Ecuador study area 1100 km away, the species composition of sperm whale diet as deduced from faecal samples shows only minor temporal or spatial variation, being principally composed of small (< 1 kg) deep-water squids, especially histioteuthids (Smith 1992). Thus, differences in defecation rates are more likely to be related to changes in the amount of food consumed rather than its composition.

In this study, I examine variability in the defecation rates of female and immature sperm whales over scales covering 5 h–4 years and 100–5000 km. The results are used as an indicator of the scales of variability in the mesopelagic ocean and the ecological pressures facing the slowly reproducing sperm whale.

Methods

FIELD STUDIES

Data for the analysis of temporal scale in defecation rates were collected during studies each lasting 1–6 months in 1985, 1987, 1989, 1991 and 1995 of a population of about 4000 female and immature sperm whales (Whitehead, Waters & Lyrholm 1992) off the Galápagos Islands, Ecuador (0°S, 91°W) (Fig. 1, Table 1). The timing of these studies allows variation in feeding rate to be studied over periods of 5 h, 1–64 days, 2 years and 4 years as well as over spatial scales of 111 km. To examine larger spatial scales, defecation rates were measured during 16 encounters with sperm whales (each lasting 1–3 days) at various distances from one another during a 1992–93 survey of the South Pacific (Fig. 1, Table 1). Additionally, the 1991 Galápagos data were compared with those from a study off mainland Ecuador (1100 km away) 1 month earlier in 1991.

During these studies we tracked groups of sperm whales, each consisting of about 20 females and immatures, acoustically and visually, for periods of days at a time (Whitehead & Gordon 1986). In daylight hours the whales were approached from behind so that we could photograph their tail-flukes. The tail-flukes are raised into the air as the whale dives – an activity known as the 'fluke-up.' These photographs were used to identify individual sperm whales (Arnbom 1987), and so to examine population biology using mark–recapture methods (Whitehead *et al.* 1992). As each identification photograph was taken we noted whether a defecation (brown patch in the water) was, or was not, observed from the whale as it dived, or whether we were unable to tell. The proportion of fluke-ups at which we were potentially able to observe a defecation, and did observe a defecation, is called the defecation rate, and is taken to be an indication of the feeding success of the whales in the previous 24 h or so (Whitehead *et al.* 1989).

During the 1985–91 studies the position of the vessel was determined using a Tracor Transtar SATNAV satellite navigator (positions accurate to about 0·5 km

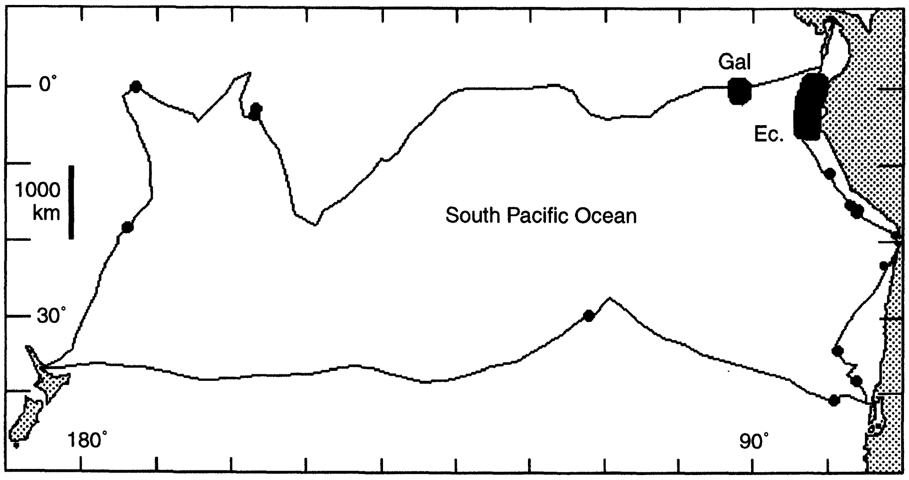

Fig. 1. Locations of data collection in the South Pacific Ocean. The Galápagos (Gal.) and mainland Ecuador (Ec.) study areas are shaded. The route of the 1992–93 survey is shown by the thin line, and the locations at which defecation rate data were collected are marked by filled circles.

approximately every 1·5 h). From 1992 to 1995, continuous position information (accurate to about 0·2 km) was available from a Trimble Transpak GPS system, with latitudes and longitudes being recorded every hour or whenever a fluke photograph was taken.

CYCLICAL PATTERNS IN FEEDING SUCCESS

Defecation rates were calculated for phases of three environmental cycles: lunar (days after full-moon, in 5-day periods), diurnal (local standard time in h), and tidal (hours after high tide, in 2-h periods). The patterns of change in defecation rate with these cycles for the four major Galápagos studies (in 1985, 1987, 1989 and 1995) were compared using Kendall's nonparametric coefficient of concordance (W). A significant value of the coefficient of concordance (taken as $P < 0{\cdot}05$) would indicate that there were consistent patterns in the defecation rate with the phase of the environmental cycle for the three study years.

TEMPORAL AND SPATIAL VARIATION IN FEEDING SUCCESS

Our observations are from a binary process (defecation seen/not seen at fluke-up). Binomial theory was used to estimate the coefficient of variation (CV) between pairs of defecation rates calculated from data separated by a particular time or distance (Appendix I). The CV is an indicator of how, relative to the overall mean, feeding success changed over the given temporal or spatial scale, by waiting x days, or travelling y kilometres.

For each time interval d, the Galápagos data were concatenated to give defecation rates for periods of d days (or hours), and pairs of adjacent intervals were compared (as described in Appendix I). The spatial analysis, over three spatial scales, was a little more complex.

1. The position of the boat during each hour of the Galápagos study was estimated and data were concatenated for each stay in a 1°latitude × 1°longitude square less than 3 days in length. Defecation rates for squares adjacent in space and time were compared (as described in Appendix I) to give an estimated CV over distances of about 111 km (the distance between the centres of adjacent squares).

2. The 1992–93 South Pacific data were concatenated for encounters less than 100 km apart, and defecation rates for concatenations less than 1000 km apart were compared in calculating a CV (mean distance between concatenations 545 km).

3. Similarly, encounters within 1000 km were concatenated and pairs of encounters less than 10 000 km apart were compared (mean distance between con-

Table 1. Field studies

Area	Dates	Fluke-ups observed	Defecation rate
Galápagos	23 Feb – 20 Apr 1985	740	0·062
Galápagos	3 Jan – 28 Jun 1987	1325	0·021
Galápagos	13 Apr – 21 May 1989	617	0·156
Galápagos	30 Mar – 14 Apr 1991	126	0·087
Galápagos	27 Apr – 3 Jun 1995	681	0·211
Mainland Ecuador	30 Jan – 12 Mar 1991	498	0·058
South Pacific	11 Sep 1992 – 28 Apr 1993	454	0·121

catenations 4920 km). The comparison between the defecation rates during the 1991 Galápagos and mainland Ecuador studies was also included in this estimate.

MOVEMENTS

To examine temporal differences in migration rates from the core area around the Galápagos Islands where we collect our data, I modified a likelihood mark–recapture model of the Galápagos population which uses the photographic identifications of individuals (Whitehead *et al.* 1992). The original model allows migration into and out of the core area from a wider population, and estimates immigration and emigration rates. In the revised model, different rates of emigration from the core area were assumed for 1987, a year of particularly poor feeding success (Fig. 4), compared with 1985, 1989 and 1991 combined (data were too few to compare all years separately, and the 1995 identification data have yet to be analysed).

Over a shorter temporal scale, movement patterns were examined using the distance moved in km between 06.00 and 18.00 h on days for which there was no break in whale tracking, and greater than 30 fluke-ups were examined for the presence of faeces (to give a reasonably precise defecation rate).

THREE CAUTIONS

1. It is a necessary feature of a study such as this that each analysis over a particular temporal scale uses data collected over a certain spatial scale, and vice versa. Based on the movement patterns of the research vessel during the studies, the estimated size of the confounding spatial scale (the average distance between the mean positions of the research vessel during two adjacent intervals) is listed for analyses of temporal scale in Table 2, and vice versa.

2. Particular groups of 20 or so sperm whales were followed over periods of about 6 h–5 days. Therefore, if feeding success is group specific, *CV*, as calculated here, and used as an indicator of the change in feeding success experienced by a group over certain spatial and temporal scales, may be biassed upwards over periods of about 2 days or more. Due to the large population size, repeat follows of particular groups were infrequent over any time scale greater than a few days.

3. In the temporal analysis the gaps between adjacent intervals over which no data were collected vary with interval (Table 2). They range between about 9% of the interval for periods of 5 h and 17% of the interval for intervals of 64 days to 90% of the interval for intervals of 2 years. These differences may cause a small positive relative bias in *CV* for intervals with large gaps, especially over 2 years.

Results

OVERALL DEFECATION RATE

During our studies off the Galápagos Islands, the sperm whales defecated at a mean rate of 0·102/fluke-up (averaged over studies – Table 1). Sperm whales off the Galápagos forage about 76% of the time (Whitehead & Weilgart 1991) and, while foraging, consecutive fluke-ups are about 50 min apart (Papastavrou, Smith & Whitehead 1989). When not foraging they rarely fluke-up (Whitehead & Weilgart 1991), but may defecate, although non-fluke-up defecations are not considered in this paper. Thus, the rate of defecations during fluke-ups is about

Table 2. Estimates of *CV* in defecation rates

Temporal scale *d* (days)	Mean gap between adjacent intervals (days)	Confounding spatial scale (km)	No. of pairs of comparisons *m*	Jackknife *CV* (SE) *CV*
0·21	0·02	*c.* 10	91	0·00 (0·47)
1	0·5	*c.* 50	106	0·80 (0·29)
2	0·6	*c.* 75	59	0·77 (0·43)
4	1·7	*c.* 100	34	0·17 (1·04)
8	4·0	*c.* 150	27	1·22 (0·42)
16	7·1	*c.* 150	18	0·61 (0·18)
32	8·6	*c.* 150	11	0·50 (0·23)
64	10·7	*c.* 150	6	0·45 (0·22)
730	652	*c.* 175	3	1·21 (0·45)
1460	1063	*c.* 175	2	1·48 (0·61)

Spatial scale *d* (km)	Confounding temporal scale (days)	No. of pairs of comparisons *m*	Jackknife *CV* (SE) *CV*
111	*c.* 3	68	0·84 (0·34)
545	*c.* 10	12	1·29 (0·65)
4920	*c.* 80	17	1·05 (0·5)

$0·102 \times 0·76 \times 60/50 = 0·093$ defecations h^{-1}. Assuming that defecation rates are similar at night to those that we observed during the day (see Whitehead & Weilgart 1991), this suggests that each individual makes an average of about 2·2 defecations with a fluke-up in 24 h.

CYCLICAL DEFECATION RATES

There was no significant consistent variation in defecation rate with lunar cycle ($W = 0·050$, $P = 0·94$) or tidal cycle ($W = 0·293$, $P = 0·32$) between the Galápagos study years. The test for a consistent diurnal cycle was significant ($W = 0·602$, $P = 0·01$). As shown in Fig. 2, there were consistently low defecation rates during the early morning and late evening (06.00–08.00 h, 16.00–18.00 h local time). However, these could be an artefact of the difficulties of seeing defecations with low solar elevation, as off the Galápagos, on the equator, the sun rises at ≈ 06.00 and sets at 18.00 h local time year-round. Studies were carried out in more than 1 year during 6 calendar months (February–June). There was no apparent consistent relationship between defecation rate and calendar month (Smith & Whitehead 1993). Thus, our data suggest that the feeding success of the sperm whales off the Galápagos Islands is not substantially related to the phase of any sub-annual environmental cycle, with the possible exception of daytime.

TEMPORAL VARIATION

The temporal *CV* in defecation rates is tabulated in Table 2 and plotted against time interval in Fig. 3. No *CV*s are plotted for time intervals less than 5 h: as each whale only defecated with a fluke-up once every 11 h or so (see above), the probability of a defecation at any time should indicate the feeding success of the animal integrated over a period of at least a few hours, some hours previously. Thus, the group defecation rate indicates the feeding rate of the group integrated over a period of several hours, some hours previously. Calculated *CV*s for intervals less than 5 h were very low, as was the value for a 5-h interval which is plotted. Group defecation rates seem to show little variation over periods of a few hours.

The variation in defecation rates for intervals of 1day is a little less than the mean defecation rate ($CV = 0·80$), and the *CV* generally falls with increasing time interval for periods up to at least 2 months. The peak at 8 days is, I believe, most probably a statistical artefact, although the relatively large gap between adjacent 8-day intervals (Table 2) and the coincidence with the mean duration of stay in Galápagos waters (see below) may have contributed. The Galápagos defecation rates have high *CV*s for intervals of 2 and 4 years (Fig. 3). The estimated variability in feeding success over these time intervals is about 1·3 times the mean. The pattern of variability in feeding success of the sperm whales off the Galápagos Islands over scales from months to years are illustrated in Fig. 4: feeding success was high during the 1989, 1991 and especially the 1995 studies, fell dramatically over 3 months in 1985, and was consistently low during the 6 months of the 1987 study. This high between-year variability is not restricted to the Galápagos. Off mainland Ecuador, where we have data from 1991 and 1993 (as part of the South Pacific survey), the *CV* in defecation rates over this 2-year interval was 1·42.

The *CV*s plotted in Fig. 3 are not independent of one another since they are all calculated from the same data. Thus, the plotted standard errors in Fig. 3 overemphasize differences between *CV*s for different time intervals. Variation in defecation rates between 1985 and 1991 biennial studies was significantly

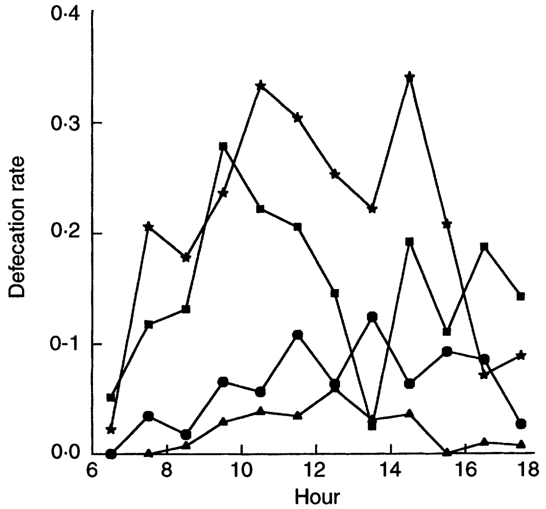

Fig. 2. Diurnal defecation rates (per fluke-up) during daylight hours during 1985 (●), 1987 (▲), 1989 (■), and 1995 (*) studies.

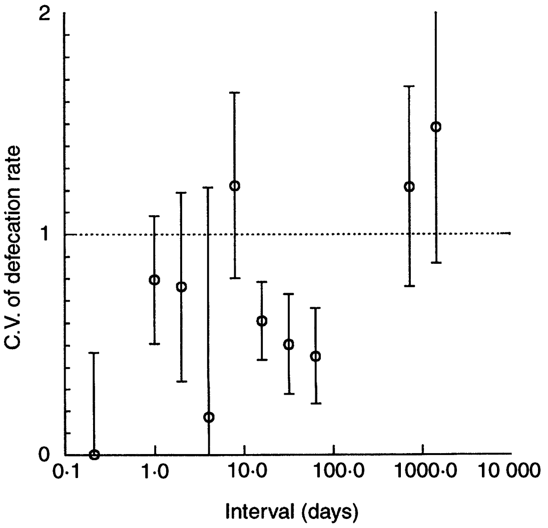

Fig. 3. Estimated coefficients of variation (*CV*) in defecation rates (per fluke-up) of female and immature sperm whales off the Galápagos Islands with time interval. Bars show estimated standard errors.

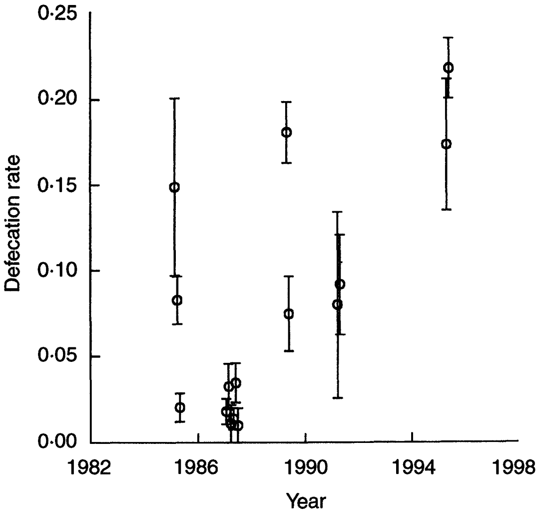

Fig. 4. Mean defecation rates (per fluke-up) with date for 32-day periods. Bars show estimated standard errors.

greater than for 32-day periods within studies (ANOVA, $F_{3,9} = 8\cdot34$, $P = 0\cdot006$, arcsine-square root transformation used to normalize binomial data).

SPATIAL VARIATION

Spatial variability in defecation rates is tabulated in Table 2, and plotted against distance in Fig. 5. Over distances of about 100 km the variation in feeding success is similar to the variation over periods of a few days, rather less than the mean (Fig. 3). However, over several hundred, or thousand, kilometres the variation in feeding success is larger, about 1·2 times the mean and similar to that over time periods of 2–4 years.

MIGRATION RATES

Emigration rates from our study area around the Galápagos Islands were substantially higher in 1987, 0·92 month^{-1} (giving a mean stay of 2·6 days), than in the other years, 0·84 month^{-1} (giving a mean stay of 5·7 days). The estimated 1987 emigration rate, 0·92 month^{-1}, was higher than that estimated from 21/22 simulations of a population without a differential migration in 1987 (simulations as in Whitehead *et al.* 1992). However, an additional 23 simulated populations produced unreasonable parameter estimates (e.g. migration rates less than zero or greater than one) when a separate 1987 emigration rate was added to the estimation model, so the significance of the difference in emigration rates between years must be considered cautiously.

Groups of sperm whales generally moved only short distances between 06.00 and 18.00 h when defecation rates were high (Fig. 6): with daily defecation rates greater than 0·16 per fluke-up, distances between positions at 06.00 and 18.00 h were always less than 16 km, whereas when daily defecation rates were less than 0·1 these distances were generally greater than 20 km, and movements of greater than 40 km during daylight were only found when defecation rates were less than 0·03. The inverse relationship between daily movement and defecation rate was strong (Spearman's $r_s = -0\cdot58$, $n = 37$), significant ($P < 0\cdot01$), consistent among all years ($r_s(1985) = -0\cdot72$, $n(1985) = 14$; $r_s(1987) = -0\cdot11$, $n(1987) = 14$; $r_s(1989) = -0\cdot78$, $n(1989) = 9$; $r_s(1991) = -1\cdot00$, $n(1991) = 2$; $r_s(1995) = -0\cdot43$, $n(1995) = 7$; see Fig. 6), and still present with the addition of those days with less precise defecation rates ($r_s = -0\cdot35$, $P < 0\cdot01$, $n = 70$, including days with > 10 fluke-ups examined).

Such relationships could exist if there were periods

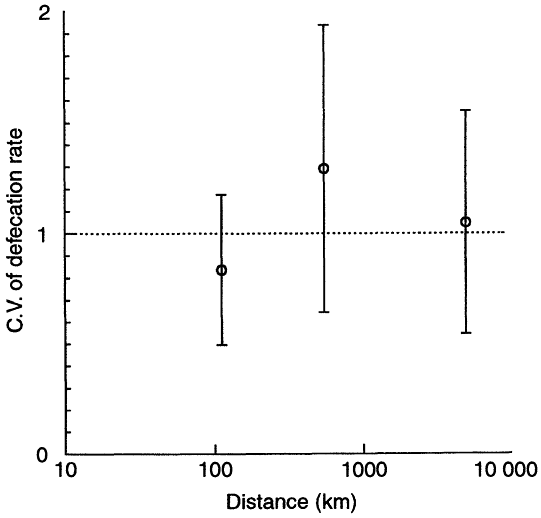

Fig. 5. Estimated coefficients of variation (*CV*) in defecation rates (per fluke-up) of female and immature sperm whales in the South Pacific with distance. Bars show estimated standard errors.

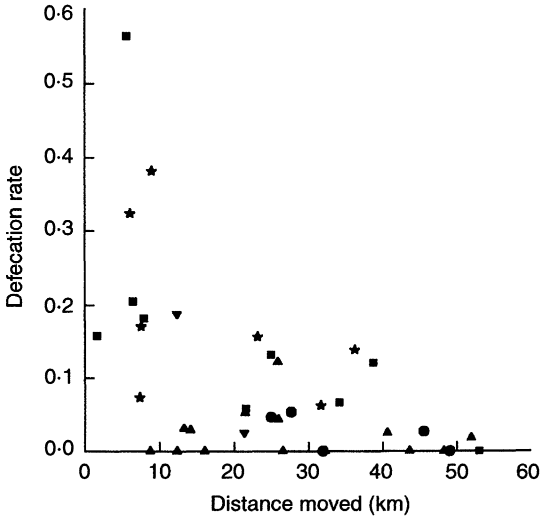

Fig. 6. Daily defecation rates (per fluke-up) plotted against distance between 06.00 and 18.00 h positions for 1985 (●), 1987 (▲), 1989 (■), 1991 (▼) and 1995 (*) studies for those days in which greater than 30 fluke-ups were examined.

of a day or so in which animals moved fast but foraged little, and others when they foraged but moved slowly. However, defecation rates were calculated only from observations at the start of foraging dives, and when calendar months were used as units, the overall defecation rate was also negatively related to the mean distance travelled during daylight hours ($r_s = -0{\cdot}53$, $P < 0{\cdot}05$, $n = 13$). There was also little correlation ($r = 0{\cdot}183$, $P = 0{\cdot}26$, $n = 39$) between the distance travelled during daylight on any day and mean estimated instantaneous speed of whales through the water (on those days in 1985 and 1987 when > 30 instantaneous speeds through the water were estimated). Thus, it appears that the inverse relationship between defecation rate and distance moved in daylight was not a consequence of differences in foraging intensity between days but rather the result of groups moving more consistently in particular directions when feeding success was low, and doubling back on their tracks when it was high.

Discussion

VARIABILITY IN FEEDING SUCCESS

Of the estimates of temporal variability of feeding success, the most prominent is the large variation over scales of 2–4 years: sperm whale feeding success was very different in periods a few months long separated by two or more years (Fig. 4). Off the Galápagos, there are substantial periods (at least 6 months in 1987; Fig. 4) during which sperm whales seem to be retrieving very little sustenance from the environment. The same seems to be true in other ocean areas. Soviet studies found variations in the fullness of sperm whale stomachs in different years within an area (Berzin 1971). Berzin believed these variations were due to different ecological conditions, especially variation in food supplies.

SCALES OF VARIATION IN THE MESOPELAGIC OCEAN

Off the Galápagos the low-frequency temporal variation relates closely to oceanographic conditions, with a strong negative correlation ($r = -0{\cdot}77$) between monthly defecation rates and sea-surface temperature (Smith & Whitehead 1993). In warm 'El-Niño' type conditions (1987) the whales had little feeding success. In contrast when mean sea temperatures cooled below 22 °C mean monthly defecation rates rose consistently above 0·10 per fluke-up (Smith & Whitehead 1993). Such cool temperatures off the Galápagos are linked to the strength of the Humboldt Current flowing north-west from Peru, and upwelling of the east-flowing Equatorial, or 'Cromwell,' Undercurrent around the islands (Houvenaghel 1978).

In the California Current, low-frequency, inter-annual features, including those produced by 'El-Niño' events, are the most prominent components of temporal variability in physical processes, as well as in zooplankton volume (McGowan 1990). These long-lived phenomena dominate physical and biological variability throughout the surface water masses of the eastern tropical and temperate Pacific (e.g. Arntz 1986), and must be important ecologically and evolutionarily (McGowan & Walker 1993). The analysis in this paper suggests that the general oceanic pattern of greater variability at longer wavelengths, 'red-noise,' (Steele 1985) also holds at depths of several hundred metres, with temporal variability in the mesopelagic ocean being dominated by features with wavelengths of months to years (Fig. 3). However, the spatial coherence of such phenomena may be largely limited to scales of a few hundred kilometres and less (Fig. 5).

SCALES OF EXPERIENCE FOR SPERM WHALES

Confronted with prolonged lack of food, such as that which the Galápagos sperm whales appear to face during Niño-type conditions, organisms may die, fast or move. If these variations in food supply over large temporal scales produced periodic substantial mortality in sperm whales, their biomass would be below that supportable by the environment in average conditions, and higher reproductive rates would be selected for. That sperm whales seem to maintain high biomass levels and particularly low reproductive rates suggests that the long periods of low food availability do not result in substantial additional mortality.

The sperm whale is a large animal, and has the potential to fast for long time periods. Brodie (1975, 1977) and Lockyer (1987) have examined the hypothesis that food storage is a vital part of the natural history of large whales. Specifically they suggest that the baleen whales store lipids (principally in their blubber layers) as a major part of their strategy for living in an environment with extreme seasonal and latitudinal changes in food abundance and sea temperature. The sperm whale is also faced with variability in its food supply, but, in contrast to the baleen whales, there is no obvious predictable seasonal or other cyclicity (at least off the Galápagos). How useful is the sperm whale's blubber layer in waiting out such periods? Thompson (1928) found remarkable inter-annual variation in the fatness of sperm whales at Scottish whaling stations, suggesting some partial fasting in response to poor feeding conditions. According to calculations based on the best information currently available (Appendix II), a female sperm whale could survive about 3 months on the lipids stored in its blubber. The estimate of annual energetic requirements used in Appendix II is only approximate (Lockyer 1981), and an additional few weeks might be added for energy stores in other parts of the carcass. However, these calculations strongly suggest that sperm whales cannot fast through the long periods of low food abundance that exist in their environment.

The lack of coherence in environmental variability over spatial scales of about 500 km and more (Fig. 5) suggests a more appropriate strategy for sperm whales when faced with food shortages: migration. Female sperm whales move at about 4 km h^{-1} (Whitehead 1989) and so could travel 500 km in 5–6 days or so (also suggested by 12 h movements of 40–55 km during some periods of low feeding success, Fig. 6). They do make such migrations: the mean distance between marking and capture of 22 female sperm whales in the southern hemisphere was 690 km (Best 1979); photographically identified Galápagos females travel the 1100 km or so to the waters off mainland Ecuador, but rarely much further (Dufault & Whitehead 1993, 1995); and during the 1982–83 'super' El-Niño, Peruvian sperm whalers found concentrations of sperm whales 600 km south of their usual grounds (Ramirez & Urquizo 1985). On smaller temporal and spatial scales the sperm whales migrate from areas where there is low food abundance. Off the Galápagos, distance moved during the 12 daylight hours was strongly inversely related to feeding success (Fig. 6). And in 1987, when food was particularly scarce (Fig. 4), emigration from a core area around the islands appeared to be about twice the usual rate.

In order to improve their use of this lack of coherence in variability over scales of several hundred kilometres sperm whales should not only migrate, but know the relative likelihood of success of different migratory directions. Long-term experience and memory may be important in directing such migrations, and thus female sperm whales will benefit from living in permanent social units (Whitehead, Waters & Lyrholm 1991), which will usually contain older animals with much experience. Elephants (Elephantidae) show remarkable parallels with sperm whales in many aspects of their biology, including large size, low reproductive rates, long life-spans, similar social organizations, large biomass and wide ranges (Best 1979; Weilgart, Whitehead & Payne 1996). Eisenberg, McKay & Jainudeen (1971) have suggested that elephants benefit from the information pool available within their social groups about ephemeral resources. The same may be true for female sperm whales. The benefits of this information pool in a variable environment could select for, and maintain, long-term social bonds.

Conclusion

Sperm whales maintain high biomass and very low reproductive rates in an environment which shows great variability over time scales of one or more years. As the environmental variation has little coherence over scales of about 300 km and more, sperm whales are able to use migration as their principal strategy for surviving in an uncertain habitat.

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Appendix I

ESTIMATING VARIABILITY FROM BINOMIAL DATA

For any time (or distance) interval, d, being analysed, the data can be categorized into m pairs of measured defecation rates: x_i defecations observed in n_i fluke-ups at time t_i, and x_i' defecations observed in n_i' fluke-ups at time $t_i + d$; $i = 1, \dots, m$.

If μ_i is the true mean defecation rate at time t_i, then I assume that x_i is binomially distributed with mean $n_i.\mu_i$. The variance in defecation rates over time interval d is:

$$\sigma^2(d) = \sum_{i=1}^{m} (\mu_i - \mu_i')^2/m$$

$$= \Sigma(\mu_i^2 - 2\mu_i\mu_i' + \mu_i'^2)/m \qquad \text{eqn A1}$$

Now, from binomial theory:

$$\mathrm{Ex}(x_i) = n_i\mu_i$$

and

$$\mathrm{Ex}\,(x_i^2) = n_i\mu_i(1-\mu_i) + n_i^2\mu_i^2$$

So:

$$\mu_i = \mathrm{Ex}(x_i)/n_i$$

and

$$\mu_i^2 = (\mathrm{Ex}\,(x_i^2) - n_i\mu_i)/(n_i^2 - n_i) = \mathrm{Ex}\,(x_i(x_i-1))/n_i(n_i-1)$$

Equation A1 now becomes:

$$\sigma^2(d) = \{\Sigma(\mathrm{Ex}\,[x_i(x_i-1)]/[n_i(n_i-1)]$$

$$-2[\mathrm{Ex}\,(x_i)/n_i]\,[\mathrm{Ex}\,(x_i')/n_i']$$

$$+\mathrm{Ex}\,[x_i'(x_i'-1)]/[n_i'(n_i'-1)]\}m$$

which, as x_i and x_i' are independent, is:

$$\sigma^2(d) = \mathrm{Ex}\,[\Sigma x_i(x_i-1)/n_i(n_i-1)-2x_i x_i'/(n_i n_i')$$

$$+x_i'(x_i'-1)/n_i'(n_i'-1)]/m$$

Thus, $s^2(d) = \Sigma[x_i(x_i-1)/n_i(n_i-1)-2x_ix_i'/(n_in_i') + x_i'.(x_i'-1)/n_i'(n_i'-1)]/m$ is an unbiased estimator of $\sigma^2(d)$ (the lack of bias in this estimator was checked through simulation), and we can use $s(d)$ as an estimator of the root-mean-square difference in feeding success over interval d. Dividing $s(d)$ by the long-term mean (mean of the means of the different studies = 0·102 defecations per fluke) gives an estimate of the coefficient of variation (*CV*) of defecation rates over interval d. This is somewhat different from the standard statistical definition of a coefficient of variation, but it has the same biological connotation.

Standard errors for $s(d)$ and thus *CV* were calculated using the Jackknife procedure, omitting each observed defecation rate in turn from the analysis (Sokal & Rohlf 1981).

Appendix II

ENERGY STORAGE IN SPERM WHALES

In order to estimate the energy that can be stored in the blubber of a mature female sperm whale, I assume:

Mass of female	10 t = 10^7 g (Rice 1989)
Mass of blubber	33% (Lockyer 1981)
Lipids in blubber	60% (Brodie 1977)
Calorific value of lipids	9·45 kcal g^{-1} (Brody 1945)
Energetic requirements of 10 t sperm whale	8·0 × 10^7 kcal $year^{-1}$ (Lockyer 1981)

With these assumptions, the lipid stores in blubber can maintain a mature female for about $10^7 \times 0{\cdot}33 \times 0{\cdot}60 \times 9{\cdot}45/8{\cdot}0 \times 10^7 = 0{\cdot}23$ years.