# Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands

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Sperm whales, *Physeter macrocephalus*, were tracked by means of a recording depth sounder in the waters off the Galapagos Islands. At depths of less than 300 m the whales generally dived nearly vertically at 60-100 m/min. At greater depths their descents were usually slower. Between February and April 1985, they dived to about 420 m, which is approximately the depth of the oxygen minimum. In 1987, a year of warmer water temperatures, they usually dived about 70 m shallower. There was no apparent diurnal variation in dive depths. None of the whales tracked dived to the ocean floor. Whales dived for about 40 min, followed by 10 min at the surface. Sperm whales usually started to make regular clicks when 150-300 m deep. Young calves appeared not to make prolonged deep dives. Our results are generally consistent with other direct information on the diving behaviour of relatively undisturbed sperm whales, but often conflict with results obtained using sonar for sperm whales being chased by whale catchers.

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Des Cachalots macrocéphales, *Physeter macrocephalus*, ont été suivis au moyen d'un sonar (sonde enregistreuse de profondeur) dans les eaux côtières des îles Galapagos. À des profondeurs inférieures à 300 m, les cachalots plongeaient presque à la verticale à raison de 60-100 m/min. Aux profondeurs plus grandes, leur vitesse de descente était généralement plus lente. Entre février et avril 1985, les cachalots plongeaient jusqu'à 420 m, ce qui représente à peu près la profondeur où la concentration d'oxygène est minimale. En 1987, la température de l'eau était plus élevée et les animaux atteignaient environ 70 m de moins de profondeur. Il ne semblait pas y avoir de variation journalière quant à la profondeur des plongées. Aucun des cachalots suivis n'a jamais atteint le fond. Les cachalots plongeaient pour une durée d'environ 40 min, puis passaient 10 min en surface. Ils commençaient ordinairement à émettre des claquements réguliers à 150-300 m de profondeur. Les jeunes baleineaux ne semblaient pas faire de plongées profondes. Nos résultats sont généralement en accord avec les comptesrendus d'observations directes du comportement de plongée de cachalots relativement peu perturbés, mais contredisent souvent les résultats obtenus au moyen d'un sonar par des baleiniers.

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## Introduction

The sperm whale, *Physeter macrocephalus*, is thought to be one of the most ecologically significant animals in the ocean (Kanwisher and Ridgway 1983). Their major food is mesopelagic and bathypelagic squid, although other animals are taken (Clarke 1980). Much of what is known about some deep-water squid species comes from analysis of sperm whale stomach contents (Clarke 1980). Therefore, to learn about both the sperm whale and its prey, the diving behaviour of the sperm whale is of special interest.

Clarke (1980) summarizes knowledge of the depths to which sperm whales dive. Much of the evidence is either indirect or describes the behaviour of frightened or chased whales. Indirect evidence includes the amount of line paid out after a harpooned whale dove, instances of whales becoming entangled in submarine cables at various depths, and the presence of a fresh bottom-living shark in the stomach of a sperm whale killed in water more than 3000 m deep. This evidence suggested that sperm whales could dive to a few thousand metres below the surface.

Lockyer (1977) tracked sperm whales using sonar while they were being chased by a 610 gross ton catcher vessel. She collected information on 931 dives and found that most sperm whales dived to less than 400 m for less than 15 min. However, large whales dived to 1100 m for up to 1 h. Measured dive rates ranged from 0 to 600 m/min. Mano (1986), using similar methods, examined 106 dives. His results were generally similar to Lockyer's, except that the measured dive rates, averaging about 28 m/min, were considerably less than Lockyer's (1977), which had a mean of 122 m/min.

There have been a few direct measurements of the dives of relatively undisturbed whales. Backus and Schevill (1966) present a depth sounder trace presumed to be of a sperm whale at 526 m below the surface; they also mention flecks, representing sperm whale click vocalizations, on the depth sounder record. Watkins and Schevill (1977) used a four-hydrophone array to track sperm whales under water. They could not provide information on the usual depth of a feeding dive, but noted that the whales swam downwards at 33-50 m/min. Gordon (1987), tracking sperm whales off Sri Lanka with a vertically mounted depth sounder (the same one

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used in the studies described in this paper), measured a mean initial dive rate of 116 m/min, with the mean rate measured over an entire trace of 84 m/min. He found that sperm whale dives usually levelled off at between 300 and 600 m, with a maximum observed depth of 800 m. Mullins et al. (1988), using the same methods as those described in this paper, obtained two depth sounder traces from a single diving whale on the Scotian Shelf. In both cases the sperm whale dove to the ocean floor (305 and 400 m, respectively) at about 90 m/min.

Gaskin (1964) gives the average dive time of undisturbed sperm whales as about 50 min, and most of Gordon's (1987) measured dive times were between 25 and 50 min. However, Clarke (1976) reports dive times of more than 82 min, and Watkins et al. (1985) believe they observed sperm whales dive for more than 2 h.

In this paper we report on studies of the diving behaviour of relatively undisturbed sperm whales off the Galapagos Islands, Ecuador.

#### Methods

Between 1982 and 1984, the World Wildlife Fund funded a study of living sperm whales in the Indian Ocean, principally in the waters off Sri Lanka. The purpose of the study was to develop techniques for studying the behaviour, and especially the social organization, of living sperm whales (Whitehead and Gordon 1986; Gordon 1987). The research was conducted from the 10-m auxiliary sloop *Elendil/ Tulip*. Among the techniques developed were some useful for examining the diving behaviour of sperm whales. With the same sloop as used in the Indian Ocean research, we made detailed studies of the social organization of the sperm whales around the Galapagos Islands (0°N, 90°W) between 23 February and 20 April 1985 and between 3 January and 28 June 1987.

While at sea, groups of sperm whales were tracked acoustically by means of a specially built Dev-Tec directional hydrophone. The vessel was sometimes under sail but more generally manoeuvred using a rubber-mounted Volvo 2003 marine diesel engine with "sailboat drive." This engine and drive is sufficiently quiet that sperm whale sounds can be recorded from a hydrophone towed 10 m behind the vessel with the engine in forward gear. Sperm whales sighted at the surface were approached as discreetly as possible to about 70 m. We tried to position the boat behind the whales before they dived. After a sperm whale lifted its flukes at the start of a dive, we manoeuvred the boat over the slick (smooth patch of water) left by the diving whale and turned on a vertically mounted Simrad Skipper 603 recording depth sounder set to a standard gain and paper speed. On reaching the slick, we reduced the speed of the boat to 0-2 km/h and steered the boat on the last observed heading of the diving whale. Frequently, but not always, this procedure led to the appearance of a diagonal line or lines on the depth sounder record representing the diving whale, such as those shown in Fig. 1.

If no whale trace appeared on the record, or a trace was present but began to grow faint or totally disappeared, we either accelerated the boat or changed heading or both. In choosing how to manoeuvre the boat we took into account the general speeds and headings of whales recently observed and indications of vertical layering of currents, and attempted to obtain the bearing of the whale being tracked by listening for its clicks on the directional hydrophone. Most traces of sperm whales lasted 1-4 min, although we managed one trace of 11 min.

Occasionally, traces representing sperm whales were obtained when the depth sounder was turned on for a regular monitoring of scattering layers (each 3 h while at sea) or for other reasons. These opportunistically obtained traces were similar to those from whales tracked after observed dives. No such traces were ever found when sperm whales were not in the vicinity.

The recorded depth of each whale trace was measured at 1-min



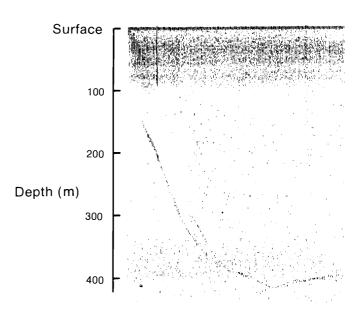


FIG. 1. Depth sounder record showing two diving sperm whales (1985). Bands of plankton are represented between 0 and 100 m and between 340 and 405 m. Flecks representing the clicks of the diving whale(s) start to appear on the trace about 1.5 min after the first appearance of a whale trace.

intervals from the beginning of its appearance on the record. These were subtracted to give ascent-descent rates, and their mean value was used as the depth corresponding to the indicated rate. Because of the loss of some data not all 1985 traces were examined for ascent-descent rates.

Depths at which the dive rate was zero (horizontal tangent to the dive trace) were measured. In this paper they are referred to as dive depths.

Possible errors affecting measured dive rates and dive depths include the following. (i) The whale not being directly under the boat. As dive traces were never obtained when the boat was heeled more than 5°, and the recording depth sounder was sensitive in a cone of 33° with a vertical axis, the maximum possible proportional error in measured depth due to this cause is  $(1 - \cos((33^{\circ}/2) + 5^{\circ}))/$  $\cos((33^{\circ}/2) + 5^{\circ}) = 0.075$ . With no heel, this value is reduced to 0.043. Errors due to this cause will always lead to overestimates in depth. (ii) Waves and swell. These were rarely over 2 m high. Errors due to wave and swell height should be unbiased and are insignificant on the scale of the analysis in this paper. (iii) Speed of sound. The speed of sound in seawater used for calibrating the display of the recording depth sounder is 1450 m/s. Using the equation for the speed of sound in seawater given by Cushing (1973), and temperature and salinity values appropriate to Galapagos waters (Charles Darwin Research Station, unpublished data), we calculate that this value is an underestimate by about 3%. Thus measured depths given in this paper are probably biased to the low side by about 3%.

As errors due to variations in the speed of sound and the whales not being directly under the boat will tend to cancel one another out, we estimate that overall errors in depths given in this paper will be rarely greater than 4%.

Most of the animals sighted during the studies were females, calves, or immatures (Whitehead and Arnbom 1987), but distinctively large mature males were sometimes present.

On some occasions during the Galapagos study we were able to observe an individual whale or a small cluster (whales swimming together; see Whitehead and Arnbom 1987) of whales from their

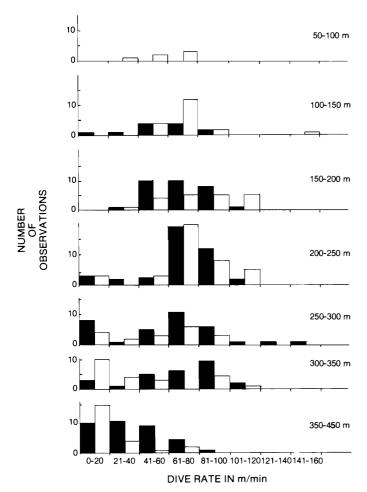


FIG. 2. Descending rates of diving sperm whales at different depths for 1985 (solid bars) and 1987 (open bars): the rate is the change in depth over each 1-min interval. The mean depth during 1-min intervals was used to allocate depths to the different histograms.

emergence at the surface until the following dive. In these cases we could measure the time at the surface. There will be biases in these data. In particular long surface times (greater than about 12 min), especially when clusters are forming and reforming, will be under-represented.

To examine the time taken by the whales to complete a "cycle," consisting of a dive plus a period at the surface, we used the interval between successive identifications of individual sperm whales from photographs of flukes, which are shown as a whale dives (Arnbom 1987). Independent information on the cycle time comes from an autocorrelation analysis of the time series of the number of fluke-ups (dives) seen in each 5-min interval during daylight. A variance stabilizing square-root transformation was applied to the counts of fluke-ups before the autocorrelation analysis. On occasions when there is some clumping in the dive times of sperm whales within a group, the autocorrelation should peak at the median cycle time.

Student's t- and F-tests were used to compare means.

## Results

# Dive rate

Because most depth sounder records were obtained after an observed dive of a whale, there are many more descending whale traces than ascending ones. At depths of less than 300 m, the whales generally dived at between 60 and 100 m/ min (Fig. 2). At greater depths their descents were usually slower. The dive rates are similar for the data from the 2

years. The maximum measured dive rate was 150 m/min at 150 m below the surface during the 1985 study. Ten ascent rates (or level traces), ranging between 0 and 30 m/min, were measured from three dives during 1985. Seventeen ascent rates (or level traces), ranging between 0 and 130 m/min, were measured from five different dives during 1987.

## Dive depth

The 1985 dive depths are remarkably consistent at about 420 m (mean of 382 m) (Fig. 3). Those from 1987 were significantly (P < 0.05) less than this (mean of 314 m). Only four of the 1987 dive depths were from the February – April period of the 1985 study, but all were less than 320 m deep. The whales were tracked in the same general geographical area, west of Isabela Island, between late February and late April in both 1985 and 1987 (Whitehead et al. 1988).

Two traces of large males were made during the Galapagos studies, one in each year. These whales dived to 260 m (1985) and 270 m (1987).

The depths of dive showed little evidence of a diurnal cycle (Fig. 3). In addition to the dive depths shown in Fig. 3, several whales were tracked diving to greater than 300 m at night, but their traces did not level out (e.g., Fig. 7).

The sea floor was never represented on the depth sounder during the dive traces collected in these studies, although, using the same methods and equipment, Gordon (1987) and Mullins et al. (1988), clearly show sperm whales diving to the ocean floor. In the areas where the dive traces reported in this paper were obtained, the ocean is generally 2000-4000 m deep.

## Surface time and dive time

Surface times of 67 individuals (from 41 clusters) were measured during the Galapagos studies (Fig. 4). Most surface times were between 5 min 30 s and 12 min 30 s, with medians of 9 min 40 s for 1985 and 9 min 20 s for 1987. There was no significant variation in the surface time with the number of whales in a cluster (P > 0.05). Two clusters that included mature males had surface times of 16 min 5 s and 11 min 10 s.

The distribution of times (less than 120 min) between adjacent identifications of individuals from their flukes has one prominent mode at 5 min, for whales photographed while making short dives or lobtailing (thrashing flukes on water surface), and another at approximately 40-65 min (Fig. 5). A third, less pronounced, mode at about 100 min probably principally represents two dive cycles with the flukes not being identified at the start of the middle dive. Nineteen cycle times were measured for mature males. Their distribution appears similar to that for the females and immatures.

Autocorrelation analysis of the time series of fluke-ups (Fig. 6) showed that bursts of fluke-ups tended to follow one another at periods of 40-55 min, suggesting a cycle time of about this length.

In both analyses cycle times appear to have been slightly longer in 1985, although this tendency was not statistically significant for the autocorrelations.

Thus the general dive cycle for the sperm whales off the Galapagos consisted of approximately 10 min at the surface, followed by a dive of about 40 min.

## Sperm whale clicks on the depth sounder

Flecks, representing clicks of the diving whales, appeared on the depth sounder record when whales were 150-300 m below the surface during the 1985 Galapagos study (Fig. 7).

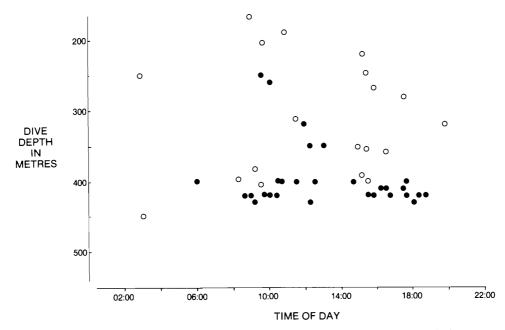


FIG. 3. Dive depth with time of day for 1985 (solid circles) and 1987 (open circles).

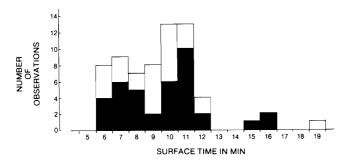


FIG. 4. Measured surface times of sperm whales in 1985 (solid bars) and 1987 (open bars) to nearest minute.

#### Dives of calves

First-year calves, distinguishable from other sperm whales by their considerably smaller size, were very rarely seen to show their flukes or otherwise to seem to start steep dives. Calves appeared to usually swim at or close to the surface. Remoras, *Escheneidae* spp., were seen attached to sperm whale calves but not to adults. During our studies off the Galapagos, and earlier work off Sri Lanka, remoras attached themselves to a number of other marine organisms such as blue whales, *Balaenoptera musculus* (Alling 1985), and whale sharks, *Rhincodon typus* (Arnbom and Papastavrou 1988). It is possible that remoras cannot cope with the rapid changes of pressure associated with the deep diving of adult sperm whales and their presence may thus indicate that calves do not usually make prolonged deep dives.

## Discussion

## Effect of research vessel on diving behaviour

In the studies described in this paper every effort was made not to influence the behaviour of the whales. Occasionally if our boat approached too fast or too close, the whales increased speed briefly, dived for about 1-3 min, or changed heading. However, these instances were rare. The dive rates and depths of the whales were similar whether they were being tracked under sail or power, and whether the trace was obtained after a fluke-up or opportunistically. We believe it unlikely that the presence of the boat influenced the sperm whales' diving behaviour except very occasionally. Although it is possible that the presence of the research vessel may have caused the whales to dive earlier than they would normally have done, such instances were probably rare as whales followed closely (<100 m) for just the last minute before the fluke-up had similar surface times to those followed closely for more than 5 min, as well as those not approached within 100 m.

Watkins and Schevill (1975) note that sperm whales reacted obviously to acoustic pings in the 6- to 13-kHz range by stopping clicking or swimming away from the pinger. No such reactions were noted to our depth sounder which pinged at the much higher frequency of 50 kHz.

#### Rate of dive

It is clear from the ease with which we managed to track diving sperm whales on a vertically mounted depth sounder with a 33° cone that sperm whales frequently dive nearly vertically. But many, and probably most, dives were not absolutely vertical: often only one of two to three whales diving in the same place at the same time would appear on the depth sounder. Although sometimes we tracked whales with the boat stationary or with it moving at a known constant rate, layering of ocean currents prevents us making a more detailed statement than that sperm whales often dive almost straight down.

The vertical descent rates measured in this study, usually 60-100 m/min, are slightly greater than the general estimated horizontal speeds of the whales at the surface during the 1985 Galapagos studies (mean 57 m/min, SD 25 m/min; Whitehead 1989). The maximum measured descent rate, 150 m/min, is very similar to the maximum observed sustained (over more than 5 min) horizontal speed of sperm whales during this study (170 m/min).

The dive rates measured in this paper are in close agreement with those obtained for sperm whales by Gordon (1987) and

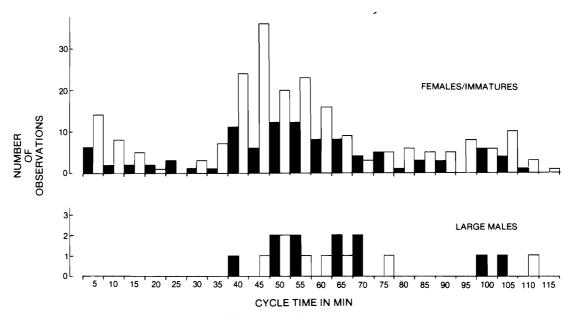


FIG. 5. Intervals between identifications of particular individuals from fluke photographs, as an indication of dive cycle durations, for 1985 (solid bars) and 1987 (open bars).

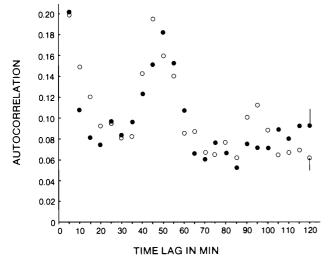


FIG. 6. Autocorrelations in the incidence of fluke-ups recorded for each 5-min interval for 1985 (solid circles) and 1987 (open circles). Bars on the symbols representing a lag of 120 min indicate standard errors, which are nearly constant across the diagram for each year. Sample sizes ranged between 3389 and 4125 pairs of intervals for 1985 and between 5422 and 6710 for 1987.

Mullins et al. (1988), and rather larger than those measured by Watkins and Schevill (1977), whose whales seemed to remain near the surface. They are, however, generally smaller and much less variable than the values reported by Lockyer (1977).

Lockyer (1977) justifies her maximum descent rate of 760 m/min by quoting Berzin (1971), who gives the maximum burst speed of a sperm whale as 617 m/min, and suggesting that the extra 143 m/min are contributed by changes in buoyancy and the force of gravity. Papastavrou (1987) shows that these forces are insignificant and that therefore either the whale must have been swimming at 760 m/min or there were

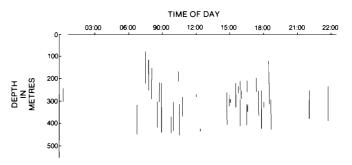


FIG. 7. Depths at which diving sperm whales made clicks that were visible on the depth sounder output with time of day for the 1985 study.

errors in the measurement. Lockyer, who calculated dive rates from whole dives, worked out standard deviations of dive rates for dives of different depths. These varied between 38 and 102 m/min. In contrast the largest standard deviation in dive rate at any depth in the Galapagos studies was 43 m/min. These major differences are likely due to the errors inherent in Lockyer's use of a nonvertically mounted transducer (any boat heel or error in measurement of vertical angle will have major consequences on estimated whale depths) and the fact that her whales were being chased. We therefore agree with Lockyer's (1977) own qualification that her results might not be representative of the normal diving behaviour of sperm whales.

The dive rates given by Mano (1986), who examined the behaviour of sperm whales during whaling operations, are much less than those from any other studies: his mean measured descent rate was 28.1 m/min, and the great majority of his measured rates were less than 31 m/min. This apparent discrepancy could be due to the fact that Mano's whales were principally moving horizontally while underwater in response to the whalers: their modal "instantaneous speed" was 4 kn (123 m/min).

There are a few measured dive rates of wild, relatively undisturbed marine mammals in the literature: using time – depth recorders, Kooyman et al. (1976) measured rates of about 70 m/min for northern fur seals, *Callorhinus ursinus*, and Le Boeuf et al. (1988) found that female elephant seals, *Mirounga angustirostris*, dived at a mean rate of 118 m/min; humpback whales, *Megaptera novaeangliae*, tracked using a depth sounder dived at a mean rate of 48 m/min and a maximum rate of 131 m/min off Newfoundland (Whitehead 1981), and at about 115 m/min off Alaska (Dolphin 1987).

In general, the sperm whales observed during our studies seemed to dive reasonably vertically to a particular depth where their traces levelled out.

## Depth of dive

Sperm whales feed mainly on mesopelagic and bathypelagic squid (Clarke 1980). Thus the dive depths of sperm whales are closely related to their feeding ecology. Analysis of faecal samples by M. Clarke (personal communication in Papastavrou 1987) has shown that the Galapagos sperm whales mainly ate histioteuthid squids in 1985. Histioteuthids were also the principal food in 1987 (S. Smith and E. Hochberg, unpublished data).

Comparing our results with those of other studies suggests considerable variation in the dive depths of sperm whales. Although we have no evidence of dive depths greater than 500 m from the Galapagos, our depth sounder has a maximum range of 1100 m, and may be inefficient at picking up whales near this limit. Thus it is possible that some whales were diving to the depths of thousands of metres reported in the literature (Clarke 1976, 1980). However, the same equipment was used to track whales to 800 m off Sri Lanka (Gordon 1987), and the general levelling of traces at 300-400 m suggests that few dives went deeper than that. The whales that we tracked did not dive to the ocean floor, unlike sperm whales in some other regions (Heezen 1957; Gordon 1987; Mullins et al. 1988).

Sperm whales started producing regularly spaced clicks only after they had descended a few hundred metres (Fig. 7), in agreement with Gordon's (1987) results from Sri Lanka. Although Watkins (1980) disagrees, Backus and Schevill (1966), Gordon (1987), and Weilgart and Whitehead (1988) think that these clicks may be used as general searching echolocation, and thus may be considered an indication that the whale is in an area where suitable food may be present.

The 1985 level traces were remarkably closely clustered around 420 m. In 1987, the whales dived to significantly shallower depths. The 1985 modal dive depth of 420 m coincides with the thin oxygen minimum layer in the Galapagos area (Wyrtki 1967). There are three obvious reasons why sperm whales should dive to the oxygen minimum layer. First, the oxygen minimum layer may be the result of a concentration of respiring animals, on some of which the sperm whales are feeding. Second, the lack of oxygen might render the prey squid more sluggish and vulnerable to the whales. Third, the squid may aggregate in this region to avoid predation: the lack of dissolved oxygen might slow down or deter fish or other squid predators. Sperm whales, bearing air at the surface, would not be affected by the lack of oxygen.

The differences in the depths of dive in 1985 and 1987 may be due to the different environmental conditions of the two years. In 1985 waters were cool around the Galapagos (mean 06:00 sea surface temperature 23.7°C in March), whereas in 1987, an El Niño type year, they were much warmer (27.5°C in March). This quite substantial climatic difference may have led to a raising of the oxygen minimum layer (although El Niño seems to lower the oxygen minimum off Peru; Arntz 1986), or may have affected the depth distribution of the sperm whales' prey in some other way.

Our data show no diurnal variation in the dive depths of sperm whales, which suggests that their prey do not make substantial diurnal vertical migrations. Matsushita (1955) proposes that sperm whales feed mainly at night when the squid rise to the surface. This seems incorrect, at least in our study area. Both Okutani and Nemoto (1964) and Clarke (1980) found no evidence for diurnal variation in sperm whale feeding.

Other studies of the diving behaviour of wild air-breathing animals have been made by attaching time-depth recorders to temporarily captured birds and mammals. Most, such as the northern fur seal, seem to use only depths less than about 200 m (Kooyman et al. 1976). However, a few species seem to dive to depths similar to those we have found the sperm whales using. These include elephant seals generally diving to depths of 350-650 m (Le Boeuf et al. 1986) and Weddell seals, Leptonychotes wedelli, many of which dive to 300-400 m (Kooyman 1966). As in our studies, Condit and Le Boeuf (1984) found no diurnal variation in the dive depths of elephant seals, although Le Boeuf et al. (1988) later presented data showing them diving about 70 m shallower at night. Elephant seals are also predators of squid. Thus, there seem to be stocks of cephalopods at depths of roughly 400 m which are valuable to a few large marine mammal species and which make only small vertical migrations.

### Dive times

The techniques we use to measure surface times, the duration of the dive cycle, and hence, by subtraction, dive times, are good indicators of modal behaviour, but are biased against extremes. The usual dive cycle off the Galapagos, dives of about 40 min alternating with about 10 min at the surface, are similar to those reported from other studies (Gaskin 1964; Clarke 1976; Gordon 1987; Mullins et al. 1988). Sperm whales may make much longer dives, such as the 2-h dive reported by Watkins et al. (1985), but such dives were infrequent off the Galapagos. The sperm whales off the Galapagos occasionally showed much shorter dive times in the range of those measured by Lockyer (1977) and Mano (1986), but the results presented by those authors are probably strongly biased by the non-natural conditions of the studies. The only time off the Galapagos that we observed sperm whales making consistently short dives was when they were fleeing after an attack by killer whales, Orcinus orca, (Arnbom et al. 1987): for 5.5 h a compact cluster of sperm whales swam in one direction making dives of 10-21 min with surface periods of 7-12 min.

# Diving of males and calves

Our limited data suggest that large males have similar (although possibly generally shallower) diving behaviour to females while on the tropical breeding grounds. Clarke (1980) shows differences in the diets of adult male and female sperm whales, and speculates that these may be partially due to differences in diving behaviour. It would be very interesting to know how the diet of a large male differs from that of the females he is accompanying on the tropical breeding grounds, but more data are needed.

Our observations, like those of Best (1979) and Gordon (1987), suggest that young sperm whale calves do not often make deep or prolonged dives. Gordon (1987) describes an instance off Sri Lanka in which two adults and two calves were observed to dive together and were tracked on the recording depth sounder. At 290 and 320 m the traces of two individuals left the others and headed for the surface. Soon afterwards two calves were observed together on the surface without any adults. However, Lockyer (1977) describes an instance when a 4.3-m calf, probably less than 1 year old (Ohsum 1977), accompanying a 10.6-m whale was observed to dive to 670 m for 16.5 min. This may have been an unnatural response to chasing.

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- ALLING, A. 1985. Remoras and blue whales: a commensal or mutual interaction? J. Am. Cetacean Soc. 19: 16–19.
- ARNBOM, T. 1987. Individual identification of sperm whales. Int. Whaling Comm. Rep. Comm. **37**: 201–204.
- ARNBOM, T., and PAPASTAVROU, V. 1988. Fish in association with whale sharks *Rhincodon typus* near the Galapagos Islands. Not. Galápagos, **46**: 13-15.
- ARNBOM, T., PAPASTAVROU, V., WEILGART, L. S., and WHITE-HEAD, H. 1987. Sperm whales react to an attack by killer whales. J. Mammal. **68**: 450-453.
- ARNTZ, W. E. 1986. The two faces of El Niño 1982–83. Meeresforschung, **31**: 1–46.
- BACKUS, R. H., and SCHEVILL, W. E. 1966. *Physeter* clicks. *In* Whales, dolphins, and porpoises. *Edited by* K. S. Norris. University of California Press, Berkeley. pp. 510-528.
- BERZIN, A. A. 1971. The sperm whale. Pacific Science Research Institute of Fisheries and Oceanography, Moscow. (Translation from Russian by Israel Program for Scientific Translations, No. 600707, Jerusalem, 1972.)
- BEST, P. B. 1979. Social organization in 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.
- CLARKE, M. R. 1976. Observations on sperm whale diving. J. Mar. Biol. Assoc. U.K. 56: 809-810.

CONDIT, L., and Le BOEUF, B. J. 1984. Feeding habits and feeding areas of the northern elephant seal. J. Mammal. 65: 281-290.

- CUSHING, D. H. 1973. The detection of fish. Pergamon Press, Oxford.
- DOLPHIN, W. F. 1987. Ventilation and dive patterns of humpback whales, *Megaptera novaeangliae*, on their Alaskan feeding grounds. Can. J. Zool. **65**: 83-90.
- GASKIN, D. E. 1964. Recent observations in New Zealand waters on some aspects of behaviour of the sperm whale (*Physeter macrocephalus*). Tuatara, **12**: 106–114.
- GORDON, J. C. D. 1987. Behaviour and ecology of sperm whales off Sri Lanka. Ph.D. thesis, University of Cambridge, Cambridge.
- HEEZEN, B. C. 1957. Whales tangled in deep sea cables. Deep-Sea Res. 4: 105-115.
- KANWISHER, J. W., and RIDGWAY, S. H. 1983. The physiological ecology of whales and porpoises. Sci. Am. 286: 102-111.
- KOOYMAN, G. L. 1966. Maximum diving capacities of the Weddell seal, *Leptonychotes wedelli*. Science (Washington, D.C.), **151**: 1553-1554.
- KOOYMAN, G. L., GENTRY, R. L., and URQUHART, D. L. 1976. Northern fur seal diving behaviour: a new approach to its study. Science (Washington, D.C.), **193**: 411-412.
- LE BOEUF, B. J., COSTA, D. P., HUNTLEY, A. C., KOOYMAN, G. L., and DAVIS, R. W. 1986. Patterns of dives in northern elephant seals, *Mirounga angustirostris*. J. Zool. **208**: 1-7.
- LE BOEUF, B. J., COSTA, D. P., HUNTLEY, A. C., and FELDKAMP, S. D. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. Can. J. Zool. **66**: 446-458.
- LOCKYER, C. 1977. Observations on the diving behavior of the sperm whale, *Physeter catodon*. In A voyage of discovery. *Edited by* M. Angel. Pergamon Press, Oxford. pp. 591-609.
- MANO, S. 1986. The behavior of sperm whales in schools observed from an operating whaler. Bull. Fac. Fish. Nagasaki Univ. 60: 1-35.
- MATSUSHITA, T. 1955. Daily rhythmic activity of the sperm whale in the Antarctic Ocean. Bull. Jpn. Soc. Sci. Fish. 47: 723-733.
- 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.
- OHSUMI, S. 1977. Age-length key for the male sperm whale in the North Pacific and comparison of growth curves. Int. Whaling Comm. Rep. Comm. 27: 295-300.
- OKUTANI, T., and NEMOTO, T. 1964. Squids as the food of sperm whales in the Bering Sea and Alaskan Gulf. Sci. Rep. Whales Res. Inst. Tokyo, **18**: 111-122.
- PAPASTAVROU, V. 1987. Feeding ecology of sperm whales *Physeter* macrocephalus in the Galapagos Islands. M.Sc. thesis, University of Bristol, Bristol.
- 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. 1975. Sperm whales react to pingers. Deep-Sea Res. 22: 123-129.
- 1977. Spatial distribution of sperm whales (*Physeter catodon*) underwater. Deep-Sea Res. 24: 693–699.
- WATKINS, W. A., MOORE, K. E., and TYACK, P. 1985. Sperm whale acoustic behavior in the south east Caribbean. Cetology, **49**: 1–15.
- WEILGART, L. S., and WHITEHEAD, H. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). Can. J. Zool. 66: 1931-1937.
- WHITEHEAD, H. P. 1981. The behaviour and ecology of the humpback whale in the northwest Atlantic. Ph.D. thesis, University of Cambridge, Cambridge.
- 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 GORDON, J. 1986. Methods of obtaining data for assessing and modelling sperm whale populations which do not depend on catches. Int. Whaling Comm. Rep. Comm. Spec. Issue, 8: 149-166.
- WHITEHEAD, H., WEILGART, L. S., and WATERS, S. 1988. Seasonality of sperm whales off the Galapagos Islands, Ecuador. Int. Whaling Comm. Sci. Comm. Doc. No. SC/40/Sp 2.
- WYRTKI, K. 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1: 117-147.