Variations in the feeding success and behaviour of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions

SEAN C. SMITH AND HAL WHITEHEAD[1]
Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada

Received May 11, 1992
Accepted June 25, 1993

SMITH, S.C., and WHITEHEAD, H. 1993. Variations in the feeding success and behaviour of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. Can. J. Zool. **71**: 1991–1996.

The feeding success of sperm whales off the Galápagos Islands, Ecuador, was examined over 5 study years; 1985, 1987, 1988, 1989, and 1991. A total of 160 days were spent following sperm whales at sea. The defaecation rates of sperm whales were used as an indication of feeding success. The recorded acoustic click rates of sperm whales were used as an indication of aggregative and foraging behaviour. Significant variation in feeding success occurred temporally over periods of days, months, and years. Feeding success also varied spatially with geographic area. Feeding success was inversely related to sea surface temperature (SST). The foraging and associative behaviour of sperm whales also varied with feeding success, SST, and by year. Variations in the feeding success and behaviour of Galápagos sperm whales can likely be attributed to changing oceanographic conditions in the waters surrounding the Galápagos archipelago.

SMITH, S.C., et WHITEHEAD, H. 1993. Variations in the feeding success and behaviour of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. Can. J. Zool. **71** : 1991–1996.

Le succès alimentaire a été évalué chez des Cachalots macrocéphales au large des îles Galápagos, Équateur, au cours de cinq années, 1985, 1987, 1988, 1989 et 1991. Les cachalots ont été suivis en mer pendant 160 jours au total. Les taux de défécation des animaux ont servi d'indicateurs de leur succès alimentaire et la fréquence des signaux acoustiques d'indicateur de leur comportement de regroupement et de recherche de nourriture. Le succès alimentaire subit d'importantes variations quotidiennes, mensuelles et annuelles, il varie également en fonction de la région géographique et est fonction inverse de la température de surface de l'eau de mer (SST). Le comportement de regroupement et de recherche de nourriture varie également, en fonction du succès alimentaire, de la température SST et de l'année. Les variations du succès et du comportement alimentaires des cachalots des Galápagos sont probablement attribuables aux conditions océanographiques variables dans les eaux qui entourent l'archipel.

[Traduit par la rédaction]

Introduction

The sperm whale (*Physeter macrocephalus*) is the largest member of the Odontocete family of "toothed" whales. Estimates of the current worldwide population of sperm whales are as high as 1.9 million individuals (Rice 1989). It is known that sperm whales feed predominantly on meso- and bathypelagic cephalopods (Clarke 1966, 1980; Kawakami 1980). However, methods of effectively sampling deep-living squids have yet to be developed. The examination of sperm whale feeding behaviour and stomach contents is, in many ways, the most informative method of studying meso- and bathy-pelagic cephalopod ecology. The current moratorium on sperm whale whaling has directed feeding studies towards the living animal in its natural environment.

The distribution of sperm whales is somewhat localized. Townsend (1935) used logbook records of whaleships to chart the distribution of sperm whales. He noted that sperm whales were found in greatest concentration in the vicinity of oceanic islands. Berzin (1971) and Volkov and Moroz (1977) linked the distribution of sperm whales to areas where the upwelling of cool nutrient-rich seawater commonly occurred. Historically, whalers often used a thermometer in order to find cool surface temperatures which were indicative of good whaling areas (Ashley 1926). Upwelling regions are extremely productive, and although they comprise only 1% of the world's oceans, they account for 50% of the world total fish harvest (Ryther 1970). Thus, it is likely that sperm whales congregate in these areas because of the presence of high concentrations of cephalopods. The productivity of upwelling areas is likely to vary by season and from year to year primarily as a result of differences in the strength of the currents that drive upwelling cells. Therefore, the feeding success of predators within the upwelling ecosystem is likely also to vary.

The Galápagos Islands lie astride the equator at 91° west longitude, approximately 800 km from the South American mainland. The most significant feature of the Galápagos marine environment is the presence of cold water at the surface to the west of the archipelago (Houvenaghel 1978, 1984). Galápagos upwelling is caused by an eastward flowing subsurface current which is deflected to the surface when it encounters the islands. The presence of this cold nutrient-rich water at the surface is largely responsible for the remarkable productivity of the area (Houvenaghel 1978). Upwelling in the Galápagos varies on a seasonal basis and is most extensive between June and August (Houvenaghel 1978; Papastavrou 1987). Periodically, the Galápagos are affected by the weather phenomenon known as "El Niño". El Niño events typically suppress upwelling in the region. Sea surface temperatures are elevated and productivity is decreased, greatly affecting the region's marine life (Merlen 1984; Arntz 1986; Trillmich 1991). These periodic dramatic changes in local productivity make the Galápagos an excellent region in which to study the responses of marine life to ecosystem changes. Examining the responses of sperm whales to these changes in productivity will lead to a better understanding of cephalopod ecology in particular and upwelling ecosystems in general.

In this study, two easily measured indications of sperm whale behaviour were collected; defaecation rates (a measure

[1]Author to whom correspondence should be sent at the following address: Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

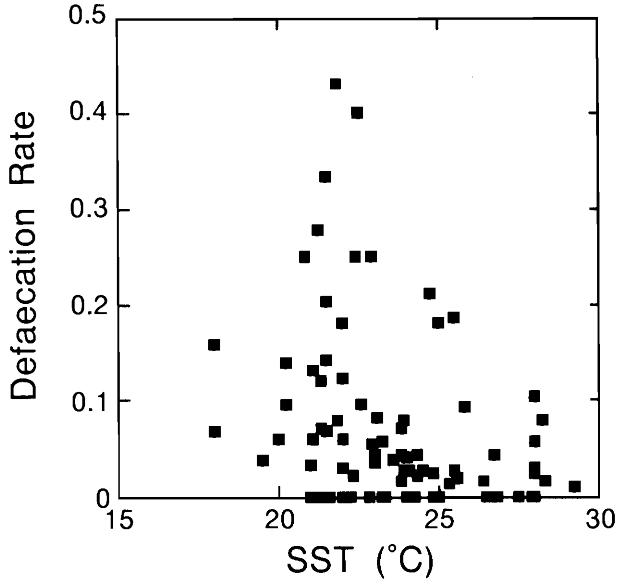

FIG. 1. Daily defaecation rate (defaecations per fluke-up) versus 06:00 SST for all data.

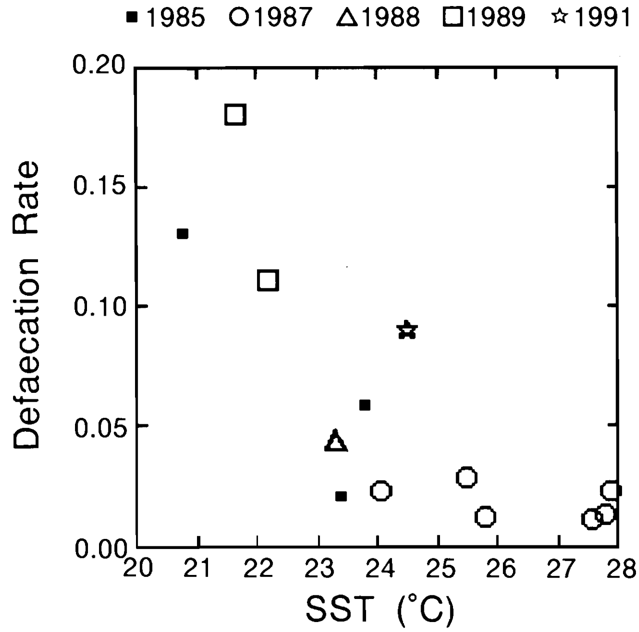

FIG. 2. Defaecation rate (defaecations per fluke-up) versus mean 06:00 SST for each month of the 5 study years.

of feeding success), and click rates (a measure of the number of foraging sperm whales in a particular area). Sperm whales usually emit acoustic clicking noises while underwater (Backus and Schevill 1966; Watkins and Schevill 1977). Acoustic clicks are probably used for hunting and communication (Gaskin 1982; Whitehead and Weilgart 1990). The click rates of sperm whales can be used as an indication of the number of whales present and their behavioural mode (Whitehead and Weilgart 1990). If underwater clicks function mainly in foraging, click rates as an indicator of the aggregative behaviour of the whales might be correlated with the day-to-day feeding success of the sperm whales and with measures of oceanic productivity such as sea surface temperature (SST). There are physiological reasons to suggest that marine mammals may defaecate only at the surface (Kooyman et al. 1981). These relate primarily to the metabolic demands of deep diving. The defaecation rate can, therefore, provide a reasonable measure of feeding success when passage time is considered, and can then be examined for changes over time and position to give an indication of variability in sperm whale feeding success.

In this paper, the feeding success of sperm whales is examined on a daily, monthly, yearly, and spatial basis. The relationship between feeding success and sperm whale behaviour is explored, and links between oceanographic conditions and sperm whale feeding success and behaviour are discussed.

Materials and methods

Data were collected over a 5-yr study period from waters primarily to the west of the Galápagos archipelago. Sperm whale studies were conducted in the following periods: February–April 1985, January–June 1987, April 1988, April–May 1989, and in April of 1991. Groups of female and immature sperm whales were tracked at sea from 10 and 12 metre sailing vessels equipped with a directional hydrophone (Whitehead and Gordon 1986). The hydrophone could home in on the acoustic clicks made by sperm whales from a distance of approximately 8 km. Using this equipment it was possible to follow groups of whales closely and continuously for several days at a time. Defaecation rates were measured as the proportion of fluke-ups (flukes raised into the air at the start of a foraging dive) made by whales within 250 m of the vessel that were accompanied by defaecations (Whitehed et al. 1989) and were calculated for periods of days (06:30 to 18:30), calendar months, and years. Defaecations that occurred during breaching (leaping from the water) or other surface activities were not counted in the analysis. Material from defaecations was collected when possible so that diet could be investigated (Smith 1992). The acoustic activity of sperm whales was recorded for 5 min of every hour on the hour while in the company of whales. The recorded sounds were then played into a digital oscilloscope and the click rate in clicks per second was calculated (Whitehead and Weilgart 1990). The measured click rates were then used to calculate three measures: nightclick (the mean click rate measured between 18:30 and 06:30), dayclick (the mean click rate measured between 06:30 and 18:30) and lowclick (the proportion of the recordings with fewer than 20 clicks per second measured over the 24-h period). Click rates give an indication of the aggregative behaviour of the whales. Therefore, nightclick indicates the aggregative behaviour of whales during the period of darkness and dayclick indicates the aggregative behaviour of the whales during daylight conditions. Lowclick indicates the proportion of time whales did not forage during the 24-h period when nightclick and dayclick were measured. Nightclick, dayclick, and lowclick were compared with the defaecation rate on the following day to account for passage time. In this manner, the click rate measured over 24 h could be correlated with the defaecation rate to give an indication of the feeding success of the whales during the time period for which click rates were calculated. Laws et al. (1975) estimated maximum ingestion to excretion intervals in elephants of 21 to 28 h. This rate is undoubtedly faster in a large carnivore such as the sperm whale. Therefore, studying defaecation rates on a 24-h time scale is not unreasonable.

The sea surface temperature (SST) was measured at 06:00 daily while at sea. Thus the effects of sun warming on the ocean surface were eliminated. Upwelling activity is indicated by the presence of cold water at the surface (Houvenaghel 1978). In this study, therefore, SST is used to indicate the presence and degree of upwelling.

Results

Daily defaecation rates for all study years combined were inversely related to the 06:00 SST ($r = -0.314$, $P < 0.0025$; Fig. 1). The rate of observing faeces during each month of the entire study (Fig. 2) was negatively correlated with the mean

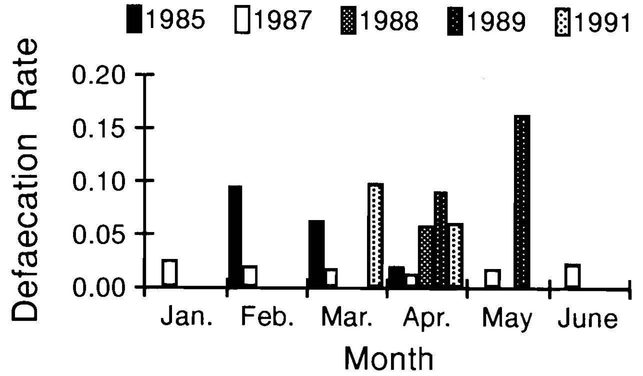

FIG. 3. Defaecation rate (defaecations per fluke-up) versus calendar month for the 5 study years.

TABLE 1. Defaecation rates in sampling areas A through E (Fig. 5) for each study year

Area	1985	1987	1988	1989	1991
A	—	0.038	—	0.111	0.074
B	0.027	0.022	—	0.103	0.020
C	0.054	0.012	0.063	0.318	0.063
D	0.038	0.012	0.034	—	—
E	0.042	—	0.100	—	—

TABLE 2. Results of testing for significant variation in defaecation rates versus area for each year of the Galápagos study

Year	No. of areas included in analysis	Likelihood ratio G	df	P-value
1985	4	2.34	3	0.506
1987	4	6.19	3	0.103
1988	3	0.88	2	0.644
1989	3	22.99	2	0.000
1991	3	4.06	2	0.131

NOTE: df, degrees of freedom.

06:00 SST for a particular month. This relationship was highly significant ($r = -0.766$, $P < 0.001$). There did not appear to be any consistent relationship between defaecation rate and calendar month (Fig. 3). The lowest defaecation rates occurred in April of 1987 and the highest rates in May of 1989. Differences in the feeding success by year (Fig. 4) were highly significant (Kruskal–Wallis one-way analysis of variance, $P < 0.001$). Defaecation rates were higher in 1985 and 1989 and lowest in 1987.

The general area where whales were tracked off the Galápagos was divided into squares of 12 400 km^2 in area (3600 square nautical miles, Fig. 5). The defaecation rate in each area and in each year of the study was tabulated (Table 1). Differences in defaecation rates by area were tested by year using a G test (Table 2). In 1989 there were significant differences in the defaecation rate by area (Fig. 5). In particular, the defaecation rate in area C to the west of the archipelago was 3 times higher than in other areas in 1989. Most of the research activity took place to the west and north of the archipelago.

The mean daily click rates of sperm whales were plotted against the defaecation rate for the following day (Fig. 6). The

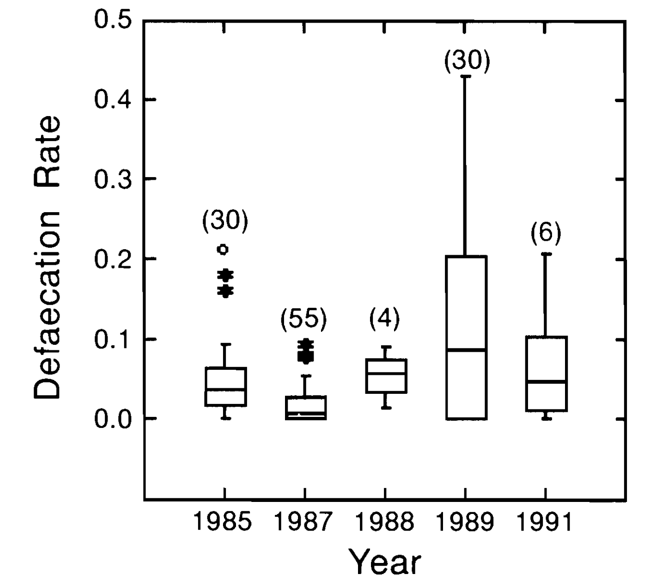

FIG. 4. Boxplot of daily defaecation rates (defaecations per fluke-up) versus year. Sample sizes are indicated in parentheses. The median value is indicated by the horizontal line, interquartile range by the box margins, and the range of adjacent values by the limit lines. Outside values are designated with an * and far outside values are designated with an **o**.

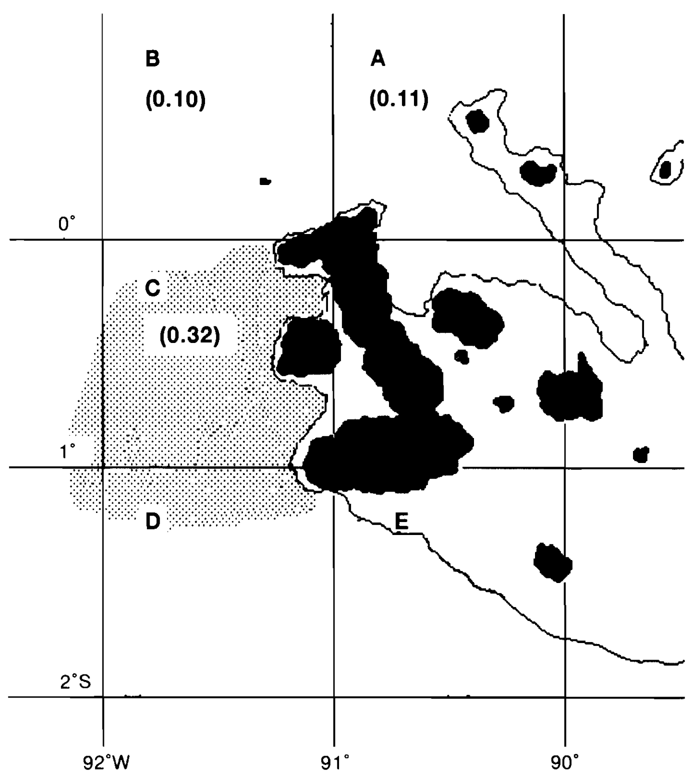

FIG. 5. Chart of the Galápagos region showing the defaecation rate (defaecations per fluke-up) in 1989 and the areas in which it was measured. General area of upwelling activity is indicated by shading (after Houvenaghel 1978).

data points did not appear to be normally distributed and so nonparametric Spearman correlations were used to test for significance. Dayclick was significantly correlated with defaeca-

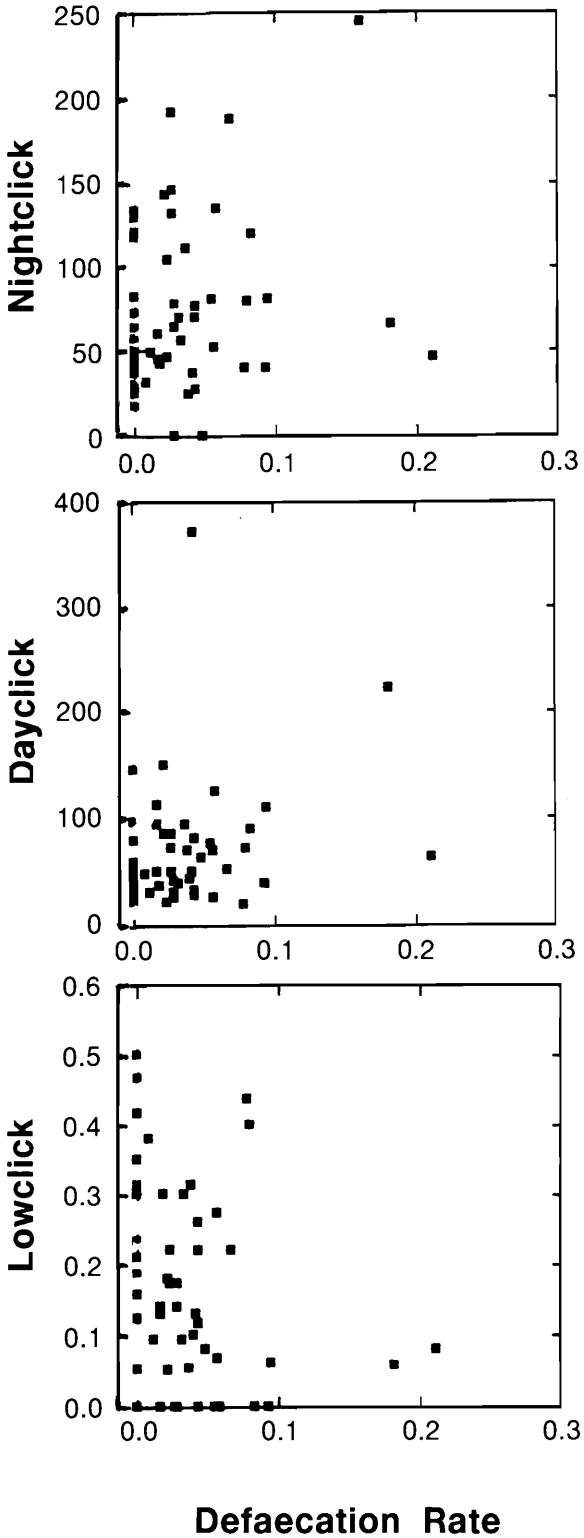

FIG. 6. The click rate in clicks per second versus the defaecation rate (defaecations per fluke-up) for nightclick, dayclick, and lowclick.

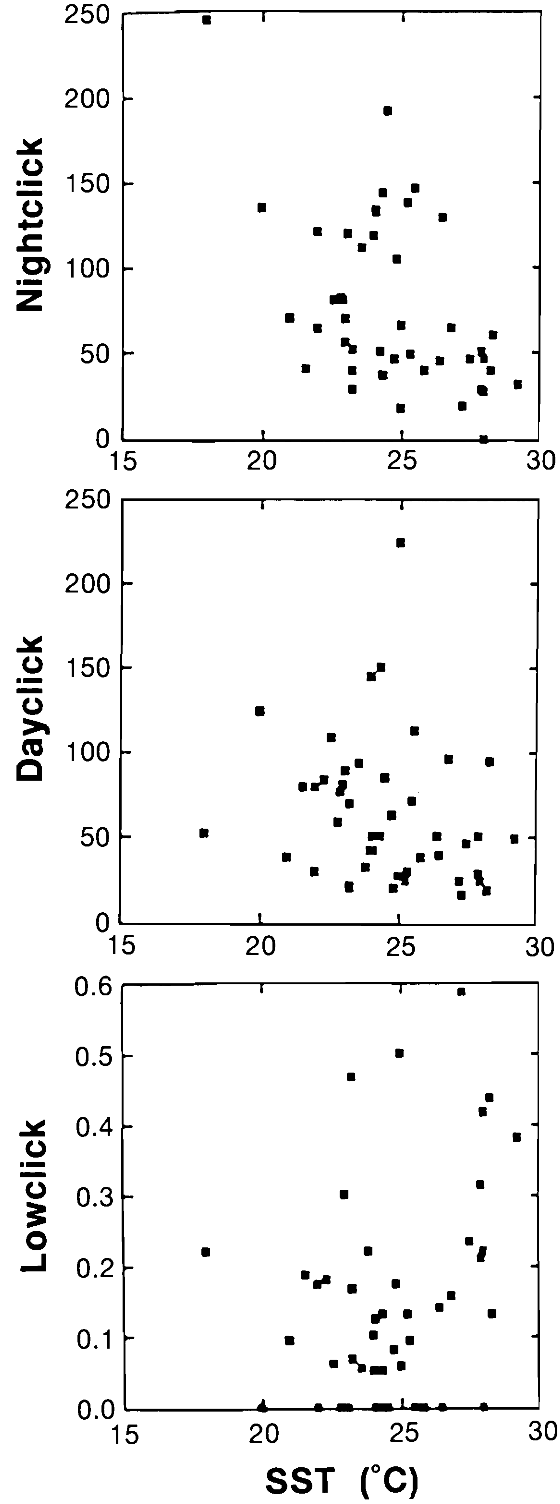

FIG. 7. Click rate in clicks per second versus the 06:00 SST for nightclick, dayclick, and lowclick.

tion rate (r = 0.225, P < 0.05). When dayclick rates were high, defaecation rates were also high. Correlations of defaecation rate with nightclick and lowclick were not significant. Daily click rates were also plotted against the daily 06:00 SST (Fig. 7). Significant correlations occurred between nightclick and SST (r = −0.510, P < 0.001) and lowclick and SST (r = 0.326, P < 0.05). In general, when SST was low, nightclick was high and when SST was low, lowclick was also low. High nightclick and dayclick rates indicate that a large number of whales were foraging at depth. High lowclick rates indicate that whales were not foraging but more likely socializing at the surface. The results suggest, therefore, that during periods of strong upwelling, when feeding success was highest, sperm whales were more aggregated and spent proportionally more time foraging than socializing.

Discussion

Year-to-year variations in the feeding success of Galápagos sperm whales may be attributed primarily to local oceanographic changes brought about by a large scale event (El Niño). El Niño affected the Galápagos in 1987 and resulted in low feeding success for sperm whales there (Figs. 2 and 4). Seasonal (monthly) temperature changes in the Galápagos are primarily the result of ocean current changes and appear to also affect sperm whale feeding success. Shorter term day-by-day variations may have more to do with the type of prey encountered during opportunistic foraging excursions. Galápagos sperm whales utilize several cephalopod species as prey (Papastavrou 1987; Smith 1992). These species undoubtedly vary in terms of swimming speed and maneuverability. For instance Histioteuthids, which comprise the majority of the Galápagos sperm whales' diet, are gelatinous and slow swimming, whereas Octopoteuthids, also represented in the Galápagos sperm whales' diet, are muscular and probably swifter. Clarke (1980) noted that larger whales fed on larger and different species of cephalopods than smaller whales, presumably because of differences in vertical prey distribution. If prey of various species exist in a patchy distribution at various depths (Whitehead 1989), changes in feeding success from day to day might be expected. The lack of data on the ingestion to excretion rates of sperm whales presents a problem when attempting to determine feeding success over a 24-h period. Indications from stomach content studies (notably Clarke 1980) are that digestion of cephalopod flesh takes place within hours of capture by the whale. Therefore, a turnover time of 24 h may not be unreasonable.

The overall feeding success of sperm whales in the Galápagos appears highly dependant on the strength of the upwelling current to the west of the Islands, where the majority of the studies took place. There is a strong relationship between the temperature of the water and sperm whale feeding success (Fig. 1). Admittedly, it is difficult to determine overall whale distribution or SST in a particular region when working from a small vessel. However, the density of marine life (including whales) in this area compared with the rest of the region indicates an increase in productivity and satellite photographs (Feldman et al. 1984) show phytoplankton blooms and lowered SST to the west of the islands. In 1989, defaecation rates of whales were significantly higher in area C (Fig. 5). The link between upwelling strength and sperm whale feeding success becomes apparent in years when El Niño suppresses upwelling. This occurred most dramatically in 1987 and resulted in significantly lower defaecation rates for Galápagos sperm whales (Figs. 2 and 4).

The manner in which increased productivity due to upwelling in a specific area leads to an increase in cephalopod biomass remains conjectural. Whitehead et al. (1989) proposed three possible mechanisms for the effect variations in upwelling might have on sperm whale feeding success. One of these hypotheses suggests that more passive cephalopod species, such as Histioteuthids, are carried to the Galápagos on the Equatorial undercurrent responsible for the upwelling. Therefore, when upwelling fails, the biomass of these cephalopod species is reduced. This hypothesis is supported by changes in species composition (notably a drop in the percentage of Histioteuthids in the diet) found during El Niño years (Smith 1992). It is also possible that when upwelling fails, cephalopod distribution changes so that sperm whales must cover more area in search of prey (Whitehead et al. 1989). In the El Niño year of 1987, sperm whales were more scattered both vertically (Papastavrou et al. 1989) and geographically (Smith 1992). A reviewer has suggested that when SSTs are high the squid may generally be found in deeper waters, making them energetically more costly to catch. A further hypothesis relates the decrease in cephalopod populations to an overall decrease in energy flow through the pelagic ecosystem. If this were the primary cause of decreases in the number of squid available to sperm whales, we might expect a time lag between the change in SST and squid biomass. However, the response of sperm whale feeding success to changing SST is rapid, occurring over a period of weeks (Fig. 2). Therefore, it may be that an explanation for decreased cephalopod abundance based solely on trophic energy transfer is insufficient (Whitehead et al. 1989).

Links between upwelling (indicated by lowered SST) and the day-to-day foraging behaviour of sperm whales are also apparent. The proportion of time whales spent in behaviour other than foraging (lowclick) was directly related to the SST (Fig. 7). When SST was low, whales were most often in the foraging mode of behaviour (Whitehead and Weilgart 1990). When nighttime click rates were high, SST was again low, indicating high densities of foraging sperm whales (Fig. 7). In addition, when daytime densities of foraging sperm whales (dayclick) were high, feeding success was also high (Fig. 6).

It appears then that the number of whales foraging for food and their success at finding it is related to upwelling as reflected by SST. Therefore, upwelling appears to benefit the whales in the short term as well as in the long term, and these benefits are reflected by greater feeding success in areas and conditions where upwelling prevails.

Acknowledgements

Special thanks to those who collected data while at sea, T. Arnbom, M. Barbeau, A. Brooks, M. Dillon, A. Faucher, L. Fawcett, C. Hendrickson, N. Jaquet, B. Lambert, K. Lohr, K. Lynch, G. Merlen, V. Papastavrou, H. Reyes, K. Richard, R. Smith, C. Smythe, J. Staniforth, S. Staniforth, S. Waters, and L. Weilgart. These studies were were funded by M. Clark, F.C.P. Whitehead, the Green Island Foundation, Connecticut Cetacean Society, The Natural Science and Engineering Research Council of Canada, and the International Whaling Commission. World Wildlife Fund/I.U.C.N. donated equipment. The Charles Darwin Research Station and the Galápagos National Park Service provided considerable support. Thanks to R. O'Dor, R.E. Scheibling, D.E. Sergeant, and two anonymous reviewers for their helpful suggestions on the manuscript.

Arntz, W.E. 1986. The two faces of El Niño 1982–83. Meeresforschung, **31**: 1–46.

Ashley, C.W. 1926. The Yankee whaler. Halycon House, New York.

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 Scientific Research Institute of Fisheries and Oceanography, Moscow. [Translated from the Russian by Israel Program for Scientific Translations, No. 600707, Jerusalem, 1972.]

Clarke, M.R. 1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol. **4**: 91–300.

Clarke, M.R. 1980. Cephalopods in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. Discovery Rep. No. 37. pp. 1–324.

Feldman, G.C., Clarke, D., and Halpern, D. 1984. Satellite color observations of the phytoplankton distribution in the eastern equatorial Pacific Ocean during the 1982–83 El Niño. Science, (Washington, D.C.), **226**: 1069–1071.

Gaskin, D.E. 1982. The ecology of whales and dolphins. Heinemann, Portsmouth, New Hampshire.

Houvenaghel, G.T. 1978. Oceanographic conditions in the Galápagos archipelago and their relationship with life on the islands. *In* Upwelling ecosystems. *Edited by* R. Boje and M. Tomczak, Springer Verlag, New York. pp. 181–200.

Houvenaghel, G.T. 1984. Oceanographic setting of the Galápagos Islands. *In* Galápagos. *Edited by* R. Perry. Pergamon Press, Oxford. pp. 43–54.

Kawakami, T. 1980. A review of sperm whale food. Sci. Rep. Whales Res. Inst. (Tokyo), **32**: 199–218.

Kooyman, G.L., Castellini, M.A., and Davis, R.W. 1981. Physiology of diving marine mammals. Annu. Rev. Physiol. **43**: 343–356.

Laws, R.M., Parker, I.S.C., and Johnstone, R.C.B. 1975. Elephants and their habitats. Clarendon Press, Oxford.

Merlen, G. 1984. The 1982–83 El Niño: some of its consequences for Galápagos wildlife. Oryx, **18**: 210–214.

Papastavrou, V. 1987. Feeding ecology of sperm whales (*Physeter macrocephalus*) in the Galápagos Islands. M.Sc. thesis. University of Bristol, Bristol.

Papastavrou, V., Smith, S.C., and Whitehead, H. 1989. Diving behaviour of the sperm whale (*Physeter macrocephalus*) off the Galapagos Islands. Can. J. Zool. **67**: 839–846.

Rice, D.W. 1989. Sperm whale *Physeter macrocephalus* Linnaeus, 1758. *In* Handbook of marine mammals. Vol. 4. River dolphins and the larger toothed whales. *Edited by* S.H. Ridgway and R. Harrison. Academic Press, London. pp. 177–233.

Ryther, J.H. 1970. Photosynthesis and fish production in the sea: the production of organic matter and its conversion to higher forms of life vary throughout the world ocean. Science (Washington, D.C.), **222**: 1195–1202.

Smith, S.C. 1992. Sperm whales and mesopelagic cephalopods in the waters of the Galápagos Islands, Ecuador. M.Sc. thesis, Dalhousie University, Halifax.

Townsend, C.H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica (N.Y.), **19**: 1–50.

Trillmich, F. 1991. Pinnipeds and El Niño: responses to environmental stress. Springer-Verlag, Berlin.

Volkov, A.F., and Moroz, I.F. 1977. Oceanological conditions of the distribution of cetacea in the eastern tropical part of the Pacific Ocean. Int. Whaling Comm. Rep. Comm. **27**: 186–188.

Watkins, W.A., and Schevill, W.E. 1977. Spatial distribution of sperm whales (*Physeter catodon*) underwater. Deep-Sea Res. **24**: 693–699.

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

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 No. 8. pp. 149–166.

Whitehead, H., and Weilgart, L. 1990. Click rates from sperm whales. J. Acoust. Soc. Am. **87**: 1798–1806.

Whitehead, H., Papastavrou, V., and Smith, S.C. 1989. Feeding success of sperm whales and sea-surface temperature off the Galápagos Islands. Mar. Ecol. Prog. Ser. **53**: 201–203.