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THE DIET OF GALÁPAGOS SPERM WHALES *PHYSETER MACROCEPHALUS* AS INDICATED BY FECAL SAMPLE ANALYSIS

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ABSTRACT

Fecal samples were collected while following sperm whales (*Physeter macrocephalus*) off the Galápagos Islands, Ecuador. They contained 133 upper beaks and 164 lower beaks of cephalopods. Analysis of the lower beaks suggests that the sperm whales fed primarily on three genera of cephalopods; *Histioteuthis* (62%), *Ancistrocheirus* (16%), and *Octopoteuthis* (7%). The beak dimensions indicate that the cephalopods ranged in mantle length from 5 to 54 cm and in mass from 12 to 650 g. Fecal samples varied significantly between five study years and over different parts of the study area, but the number of beaks collected per sample did not correlate significantly with defecation rate (a measure of feeding success). Using beak material from fecal samples gives a biased estimate of sperm whale diet, reducing the frequencies of very small and very large cephalopods. However, all other available methods of assessing sperm whale diet also possess biases.

Key words: sperm whale, *Physeter*, diet, cephalopod beaks, Galápagos Islands.

The sperm whale (*Physeter macrocephalus*) is the largest and probably the most important predator of deep-water cephalopods. Estimates of the annual consumption of cephalopods by sperm whales exceed 110 million metric tons (Clarke 1977). This is larger than the annual worldwide fisheries catch by all countries combined, 83 million tons in 1990 (FAO 1990). The abundance of cephalopod predators such as tunas, seals, and toothed whales suggests that substantial populations of cephalopods exist worldwide and that these populations are of great importance in ocean ecosystems.

Scientists have encountered great difficulty in sampling populations of adult deep-water cephalopods. Samples caught at depth by human sampling devices are very different from those obtained from the stomachs of predators such as

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the sperm whale. It is likely that adult stages of mesopelagic squids are able to outmaneuver most sampling devices. Therefore, many species of cephalopods are under represented, or absent altogether, from net samples but present in abundance in the stomachs of predators caught in the same sampling area (Clarke 1977). As a result, much of the present knowledge of deep-water cephalopods has come from examination of sperm whale stomach contents obtained from the whaling industry. The ongoing moratorium on sperm whale whaling has led to the development of new methods of studying sperm whale diet. This paper examines one method, the collection of sperm whale feces at the ocean surface.

For reasons related primarily to diving physiology, it is thought that marine mammals most often defecate at the surface (Kooyman *et al.* 1981). During a study of living sperm whales off the coast of Sri Lanka, Gordon (1987) sampled sperm whale feces and was able to taxonomically identify the chitinous mouth parts or "beaks" contained in the fecal material. A similar study was carried out off the Galápagos Islands (Papastavrou 1987). Although the numbers of beaks collected in these studies are small compared to those from studies of stomach contents, it was felt that the work provided valuable information on sperm whale diet. In this paper we describe a study of fecal samples from Galápagos Islands sperm whales, discuss the biases associated with diet determination from fecal samples, and examine temporal and spatial variability in sperm whale diet.

Materials and Methods

Field methods—Sperm whales were tracked at sea from 10- and 12-m 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 a group or sequence of groups of whales closely for several days at a time. When a whale dive was accompanied by visible defecation, the boat was maneuvered over the slick left by the diving whale and as much fecal material as possible was collected using a dipnet. Defecation rates were calculated as the proportion of fluke-ups within 250 m of the boat which were accompanied by defecations (Whitehead *et al.* 1989). Only observations of diving whales were used in the calculation of defecation rate. In this way defecations made during, and possibly caused by, breaching or other energetic activities were eliminated.

Fecal samples were collected over five study years, primarily in waters to the west of the Galápagos Archipelago. Sperm whale studies were carried out in the area between February and April 1985, January and June 1987, April 1988, April and May 1989, and April 1991.

Beak identifications—The beaks found in fecal samples were sorted initially into types having a similar morphological appearance. The lower beaks were then identified to the genus and sometimes species level using keys presented in Clarke (1986). Identification was greatly aided by comparative work carried

Figure 1. Beak *Histioteuthis* sp. Scale bar = 10 mm.

out at the Smithsonian Institute, Washington, DC, and by comparison with reference material from M. R. Clarke. In addition, material was sent to N. Voss (University of Miami) and to F. G. Hochberg (Museum of Natural History, Santa Barbara, California) for further confirmation. The lower beak rostral lengths, or lower beak hood lengths of octopods (LRL) were measured to the nearest 0.5 mm using vernier calipers or a graticulated microscope. The wet weight in grams of the cephalopod material was then estimated from LRL beak measurements using regression equations presented in Clarke (1986). Upper beaks were not considered in this paper as they have fewer identifiable features and taxonomic keys are limited.

Results

One hundred and sixty-four lower beaks were identified from 60 samples collected on 35 different days over the five study years. As we were usually tracking about 20 sperm whales on a particular day, and the total population being studied was about 4,000 sperm whales (Whitehead *et al.* 1992), there are unlikely to be many duplicate samples from the same animal, and few individual sperm whales will have contributed more than five identified beaks to the collection.

Four species of cephalopods made up 85% by number of all samples. Of these, an unidentified species of histioteuthid (Fig. 1) constituted 52%. *Histioteuthis hoylei* made up 10% and the ancistrocheirid cephalopod *Ancistrocheirus lesueurii* contributed 16% to the total (Table 1). *Octopoteuthis deletron* made up an additional 7%. The four species *Pholidoteuthis boschmai, Liocranchia* sp.,

Table 1. Species composition (%) of cephalopod beaks collected from Galápagos sperm whales in different years. Number of beaks given in parentheses.

Species	1985	1987	1988	1989	1991	Total
Histioteuthis sp.	73 (54)	26 (4)	29 (5)	42 (21)	14 (1)	52 (85)
A. lesueurii	9 (7)	13 (2)	29 (5)	20 (10)	29 (2)	16 (26)
H. hoylei	7 (5)	20 (3)	6 (1)	8 (4)	43 (3)	10 (16)
O. deletron	1 (1)	6 (1)	23 (4)	8 (4)	14 (1)	7 (11)
Other spp.	10 (8)	35 (5)	13 (2)	22 (11)	—	15 (26)
Totals	(75)	(15)	(17)	(50)	(7)	(164)

Discoteuthis sp., and the pelagic octopod *Haliphron atlanticus* were of lesser abundance in the samples and contributed a total of 15%.

The estimated wet weight in kilograms and the lower rostral length (LRL) range of the three most abundant well-identified species found in this study were compared with the same three species from a stomach-contents study by Clarke *et al.* (1976) of sperm whales caught off Peru and Chile (Table 2). These results indicate that the beaks collected from our fecal samples were generally smaller than beaks found in the sperm whale stomachs.

Beaks of the unidentified histioteuthid squid collected in this study closely resembled beaks of *Histioteuthis heteropsis.* However, the lack of appropriate comparative material (specifically a beak from a whole identified specimen from the region) prevents a positive identification. The beaks from this study had a mean LRL of 4.3 mm and were somewhat larger than beaks of *H. heteropsis* collected in the Pacific.

A contingency-table test on the four most common species encountered showed significant differences between years in the proportions of different species ($\chi^2 = 36.03$, df = 12, $P < 0.001$). The number of beaks collected per sample was not significantly correlated with the mean monthly defecation rate for the major species or for the four lesser species combined (Spearman correlations, $P > 0.05$).

Differences in species composition of the samples over the sampling area were examined by dividing the Galápagos sampling region into five one-degree square areas (Fig. 2). The proportion of samples containing a particular species was determined for each area. There were significant differences in the occur-

Table 2. Comparison of lower rostral length (LRL in cm) and estimated mean weight (g) of cephalopod species in this study and from study of beaks in stomach contents by Clarke *et al.* (1976).

	This study		Clarke *et al.* 1976	
Species	Range LRL	Mean weight	Range LRL	Mean weight
H. hoylei	0.5–0.8	0.351	0.5–1.3	1.145
O. deletron	0.7–1.5	0.144	0.3–1.2	0.211
A. lesueurii	0.4–0.6	0.418	0.4–0.9	0.603

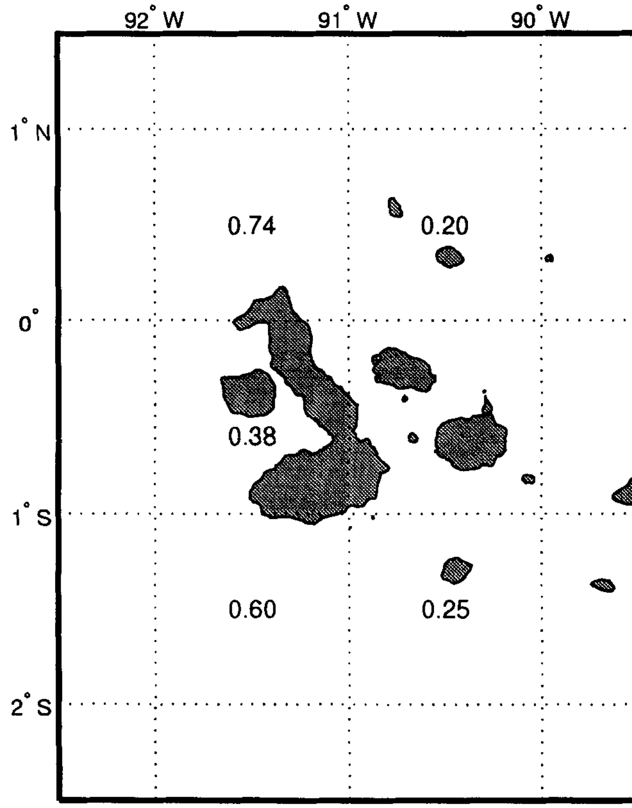

Figure 2. Western Galápagos Islands showing proportions of fecal samples containing identified beaks from *Histioteuthis* sp. in each of five one-degree squares.

rence of *Histioteuthis* sp. with area (χ^2 = 10.51, df = 4, P < 0.05). *Histioteuthis* sp. was found most frequently in samples collected to the west of the Galápagos Archipelago (Fig. 2). The occurrence of other species in the samples did not vary significantly (P > 0.05) between areas.

Discussion

The diet of sperm whales from this study is similar to results from most other studies of sperm whale diet in the Pacific Ocean (Table 3). Our data agree especially closely with the results of Clarke *et al.* (1976), who examined beaks from the stomachs of sperm whales landed in Peru and Chile, and Clarke and Young (1998) who examined stomachs of two sperm whales stranded in Hawaii. However, our results contrast greatly with those of a study of flesh remains from sperm whale stomachs carried out by Clarke *et al.* (1988), also working on whales caught off Peru and Chile. Clarke *et al.* (1988) concluded that sperm whales in their study were feeding virtually exclusively on the

Table 3. Comparison of results of six studies of sperm whale diet in southern and eastern Pacific Ocean.

Reference	Location	Method	Results	
Clarke *et al.* (1976)	Peru and Chile	Examined beaks from whaler-caught sperm whales (1,000 beaks)	% by # of beaks	
			Histioteuthis A	50
			Chiroteuthis	16
			Octopoteuthis	9
			Other spp.	25
Mikhalev *et al.* (1981)	Southern Hemisphere	Examined flesh contents from whaler-caught sperm whales (>15,000 stomachs)	% of species	
			Histioteuthids	29
			Taningia	22
			Architeuthis	8
			Other spp.	41
Clarke *et al.* (1988)	Peru and Chile	Examined flesh remains from whaler-caught sperm whales (2,403 stomachs)	% of species	
			D. gigas	99
			A. lesueurii	0.4
			Histioteuthids	0.1
			Other spp.	0.05
Fiscus *et al.* (1989)	California	Examined beaks and flesh from whaler-caught sperm whales (157 stomachs)	% by family	
			Gonatids	31
			Onychoteuthids	25
			Histioteuthids	16
			Other spp.	28
Clarke and Young (1998)	Hawaii	Examined beaks from the stomachs of two stranded sperm whales (292 beaks)	% by number	
			H. hoylei	45
			M. fisheri	13
			O. bartrami	8
			M. famelica	8
			Other spp.	26

Table 3. Continued.

Reference	Location	Method	Results	
This study	Galápagos Islands	Beaks from sperm whale fecal samples (164 beaks)	% of species	
			Histioteuthids	62
			A. lesueurii	16
			Octopoteuthids	7
			Other spp.	15

Table 4. Significance of potential biases in different methods of studying sperm whale diet (authors' opinion). O = unimportant, X = slightly important, XX = important, XXX = very important.

	Method:		
Bias:	Fecal samples	Stomach contents	Flesh remains
Large beaks sink	XXX	O	O
Very small beaks are missed	XX	X	O
Differential defecation of beaks	X	XX	O
Differential vomiting of beaks	X	XX	O
Loss of squid head during ingestion	X	X	X
Differential digestion rates of flesh	O	O	XXX
"Prey of prey"	X	X	O

large ommastrephid squid *Dosidicus gigas,* which was not represented in our samples.

Sampling bias—There are several inherent biases in the use of beaks from fecal samples as indicators of diet; larger beaks tend to sink before they can be collected (because of their lower surface-to-volume ratio), very small beaks may be missed or pass through the net mesh, and beaks of a particular size and/or morphology may be defecated (rather than being retained in the stomach or vomited) more readily than others. For instance, Clarke (1980) noted that stomach samples often contain more upper beaks than lower beaks. Papastavrou (1987) and this study found more lower than upper beaks, although these differences were not statistically significant. During our research it took approximately one minute to reach the slick of a diving whale, so that small lower beaks would be more likely to be collected than upper or large beaks. Because of the relatively small number of beaks collected during this and other fecal studies of sperm whales, a comprehensive key to upper beak morphology would greatly enhance the amount of information available per sample.

Sperm whales are thought to vomit squid beaks when the accumulation in the stomach becomes excessive (Clarke 1980). Possibly, beaks of a particular size or morphology are vomited more readily than others. Differential vomiting and defecation of beaks has particular significance in studies of beaks from sperm whale stomachs (Table 4). It has been suggested by Clarke *et al.* (1988) that in larger squids the head is sometimes lost during feeding so that large squid beaks are under represented in sperm whale stomachs. This being true, the loss of the buccal mass (containing the beak) and the tentacles would bias all diet studies more or less equally (Table 4).

Dosidicus gigas *and the "prey of prey" hypothesis*—Clarke *et al.* (1988) examined the flesh remains from sperm whale stomachs from the same region as Clarke *et al.* (1976) and concluded that the whales off Chile and Peru were feeding almost exclusively on the large ommastrephid squid *Dosidicus gigas.* Clarke *et al.* (1988) accounted for this discrepancy by suggesting that predation by *D. gigas* on smaller cephalopod species such as histioteuthids could bias the results of studies relying solely on beaks. While the discerning of "prey of prey" is a potential problem inherent in many stomach content and fecal material studies, we feel that the importance of *D. gigas* in this case has been overestimated by Clarke *et al.* (1988). It has been shown by Clarke (1980) that smaller and gelatinous cephalopods are more quickly digested in the sperm whale stomach than larger more muscular forms. Clarke *et al.* (1993) examined the stomachs of 17 sperm whales caught off the Azores. The authors felt confident that the whales were sampling cephalopods ranging in size from 100 to 100,000 g. It seems likely, given the information provided by Clarke (1980) and Clarke *et al.* (1993), that a large muscular ommastrephid squid such as *D. gigas* would be digested much more slowly than the gelatinous and relatively small histioteuthids. Whales examined by Clarke *et al.* (1988) were landed at shore-based whaling stations and had post-mortem times of at least several hours. They examined some 50 whales with post-mortem times of at least 48 h. None of these whales contained identifiable remains of cephalopods less than 1.0 m in length. Post-mortem digestion notwithstanding, the presence of some flesh remains of *Histioteuthis* sp. and of *A. lesueurii* in the whale stomachs examined by Clarke *et al.* (1988) casts doubt on the extent of the contribution of predation by *D. gigas* to the beak load in a particular whale's stomach. It is more likely that sperm whales in the Southeast Pacific feed opportunistically on many species of cephalopod including *D. gigas* when and where they are most abundant. As stated by Clarke *et al.* (1988) "in no other ocean of the world do sperm whales have a virtually monospecific diet." These reservations were echoed by the International Whaling Commission Scientific Committee Sperm Whale Subcommittee (1987) whose "members noted that feeding results of Clarke *et al.* (1988) were atypical . . . smaller species will be digested more quickly and this percentage may not be an accurate representation of the diet composition."

Variation in the diet of Galápagos sperm whales—Sperm whales off the Galápagos Islands feed primarily in an upwelling system created by the Equatorial Undercurrent. Upwellings are often characterized by significantly lowered sea surface temperature. The strength of the Equatorial Undercurrent varies and is affected especially by periodic El Niño meteorological events. During an El Niño event, warm surface water suppresses the upwelling and ocean productivity is generally reduced (Merlen 1984, Arntz 1986). During this study minor El Niño events occurred in 1987 and 1991. These events were associated with changes in the defecation rates (Smith and Whitehead 1993) and in the species composition of the cephalopod beaks collected (Table 1). In particular, sperm whales in 1987 appeared to direct their feeding towards more species than in other years and they dove to shallower depths in 1987 than in 1985 (Papastavrou *et al.* 1989). These differences may be caused by a change in the availability of certain species as a result of changing oceanographic conditions. The defecation rate (a measure of feeding success) showed marked differences between years and was highest in 1985 and in 1989, the coolest years of the study (Smith and Whitehead 1993). The percentage contribution of histioteuthids in samples was high in 1985 (Table 1). These results may suggest that this histioteuthid species favors conditions of lowered sea surface temperature associated with upwelling centers. There were significant differences in the occurrence of *Histioteuthis* sp. among sampling regions. In particular, *Histioteuthis* sp. occurred in a high proportion of samples from areas to the west of the Galápagos Islands where the strongest upwelling occurs (Houvenaghel 1978). In 1987 and in 1991, whales were virtually absent from upwelling regions to the west of the islands (Whitehead *et al.* 1989, and unpublished results) and *Histioteuthis* sp. were less abundant in samples from these years (Table 1). Of the cephalopod species encountered in Galápagos fecal samples, histioteuthids are likely among the slowest swimming, as they have short bodies, and their mantles have reduced musculature and capacity compared to most other squids. Therefore, sperm whales may feed mainly on histioteuthids simply because they are usually more abundant and/or require less energy output to capture. In addition, strong currents such as the Equatorial Undercurrent may passively carry slow-swimming histioteuthids to the Galápagos region. Our results on the diet (this study) and overall feeding success (Smith and Whitehead 1993) of Galápagos sperm whales suggest that in El Niño years changes in the thermal structure of the water column and the slacking of the Equatorial Undercurrent may cause changes in the abundance, distribution, and species composition of cephalopods.

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