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DIFFERENCES IN FEEDING HABITS BETWEEN PREGNANT AND LACTATING SPOTTED DOLPHINS (*STENELLA ATTENUATA*)

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Lactating mammals have higher energy requirements than all other mature adults and may need to eat greater quantities or change to a diet richer in nutrients (Brody, 1945; Close et al., 1985; Clutton-Brock et al., 1982; Perez and Mooney, 1986; Wright, 1984). When diets of cetaceans have been examined, however, the reproductive state of the animal rarely has been taken into account. In this study, we found a dietary difference between pregnant and lactating spotted dolphins (*Stenella attenuata*).

TABLE 1.—*Specimen number, date and time of day of collection, and minimum number of fish and squid consumed by pregnant and lactating spotted dolphins in the sample. Data for these specimens are freely accessible by the indicated specimen numbers through established data repositories at the United States National Oceanographic and Atmospheric Administration, Southwest Fisheries Center, La Jolla, California.*

Pregnant						Lactating					
Specimen		Date	Time	Squid	Fish	Specimen		Date	Time	Squid	Fish
DBH	765	14 Nov. 1975	0755	101	12	WAW	549	24 May 1978	0639	24	318
DBH	767	14 Nov. 1975	0755	213	5	WAW	532	20 May 1978	0734	43	297
WAW	524	27 Apr. 1978	0820	159	2	WAW	533	20 May 1978	0734	31	202
SLG	080	6 Dec. 1984	0842	8	87	STB	024	6 Apr. 1985	1043	66	40
JXB	001	2 Nov. 1979	0850	161	6	WAW	555	7 Oct. 1978	1132	97	106
LSL	025	25 Jun. 1980	0935	31	3	WAW	565	7 Oct. 1978	1132	23	16
PEL	316	14 Jul. 1985	1046	156	1	WSL	008	29 Jan. 1978	1205	1	33
WSL	018	29 Jan. 1978	1205	1	28	CER	001	26 Nov. 1979	1327	40	6
STB	005	1 Apr. 1985	1207	0	3	SOB	014	24 Nov. 1978	1435	92	1
SOB	013	24 Nov. 1978	1435	218	0	SRM	056	16 Feb. 1980	1438	9	855
SLG	091	6 Dec. 1984	1716	49	1	SRM	057	16 Feb. 1980	1438	25	585
						MBH	023	3 Oct. 1980	1702	1	22

We examined stomach contents of 11 pregnant and 12 lactating spotted dolphins collected by scientists and technicians of the U.S. National Marine Fisheries Service and Inter-American Tropical Tuna Commission on board purse-seiners of the yellowfin tuna (*Thunnus albacares*) fishery in the eastern tropical Pacific 15°N–10°S, 130°W–87°W from 1971 to 1985. Fishermen depend on these dolphins to locate tuna, and some dolphins are killed incidentally during the fishing operation. Dolphin stomachs were collected randomly on an opportunistic basis by the technicians. The specimens were distributed throughout the range of collection geographically, monthly, and by time-of-day (Table 1).

Initial data (e.g., specimen number, date of collection, and body length) on each dolphin were collected at sea. Dolphin pregnancy was determined by inspection of the uterus either in the field (for fetuses longer than 25 cm) or in the laboratory. Lactation was determined in the field by palpation and incision of mammary glands. Tissue samples also were collected at sea. Ovaries and uteri were preserved and stored temporarily in 10% formalin; stomachs were frozen at approximately −20°C.

Stomachs were thawed at the laboratory and the bolus was removed and sieved through screens of coarse to fine mesh (6.3 mm–180 μm). Only contents from the esophageal (or first) compartment were examined in this study because the most recently ingested meal is found largely in this chamber. Prey items were separated into categories of squid and fish. Undigested fragments of squid and fish tissue were weighed. Upper and lower squid beaks were counted, and the highest count of either was considered the minimum number of individual squid ingested. Similarly, left and right otoliths were separated and counted. The highest count of either was used as the minimum number of individual fish in the stomach.

The importance of prey type was evaluated by percent number, percent mass, and percent frequency of occurrence of prey (fish or squid) combined for all individuals within a stratum (pregnant or lactating) to calculate the index of relative importance (= % frequency of occurrence [% numerical frequency + % volume or mass] of a given prey item; Pinkas et al., 1971). Also, because of the skewed distribution of prey by mass in the stomachs of a given predator group (Amundsen and Klemetsen, 1986), and because our sample size (23 dolphins) is small, we calculated a sample variance of the proportion of squid in the stomachs, pooled for pregnant and for lactating dolphins, by bootstrap analysis (Efron, 1979, 1982). Differences in the observed proportion of squid between pregnant and lactating dolphins then was tested by application of the central-limit theorem using the following equation:

$$Z = \frac{\hat{P}_P - \hat{P}_L}{\sqrt{[\hat{V}(\hat{P}_P) + \hat{V}(\hat{P}_L)]}}$$

where

$\hat{P}_P$ = the observed proportion of squid from stomachs of all pregnant dolphins,
$\hat{P}_L$ = the observed proportion of squid from stomachs of all lactating dolphins, and
$\hat{V}$ = the variance estimated from 1,000 bootstrap replicates (with replacement), with each individual dolphin treated as a unit.

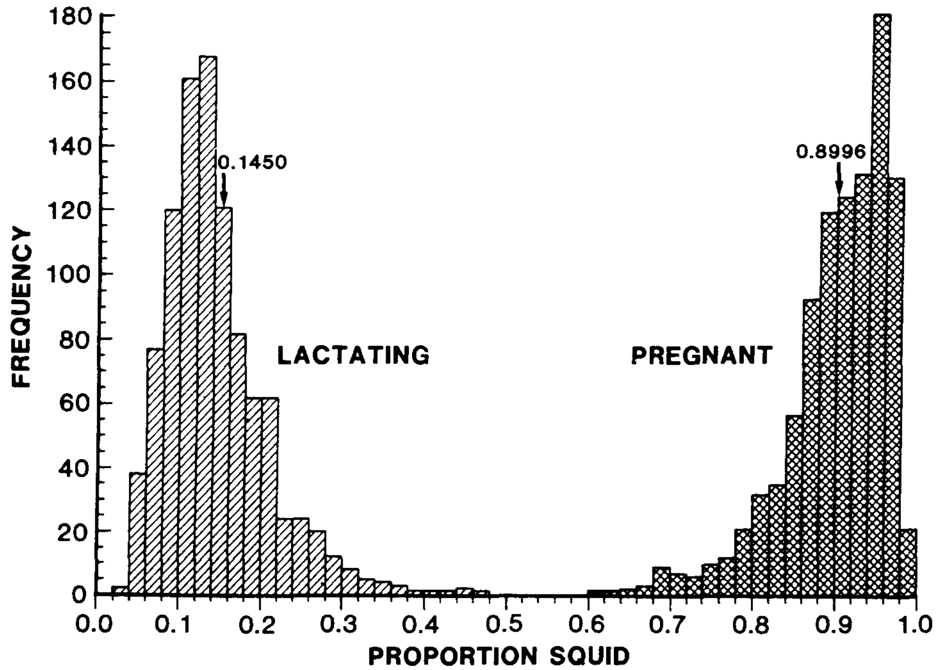

FIG. 1.—Frequency distributions for the mean proportion of squid in 11 pregnant and 12 lactating spotted dolphin stomachs calculated from 1,000 bootstrap replicate samples. The black box represents the one point of overlap between the mean proportions.

We used the nonparametric Mann-Whitney test to test for differences in stomach fullness (determined by dividing the mass of prey by stomach mass + prey mass; Fiedler and Bernard, 1987) between the two strata, and to test for differences in proportion of squid in stomachs of females collected before and after 1200 h (local time) within a stratum.

Fish and squid were the primary prey found in stomachs. The only crustaceans and mollusks found were a few isopods and pteropods, likely secondary prey. Most often only hard parts of prey remained, such as squid beaks and fish otoliths. The most frequently observed fish family was Exocoetidae, epipelagic flying fishes. There were some flotsam fishes (Nomeidae), followed by a few mesopelagic lantern fish (Myctophidae). The squid family most often represented was Ommastrephidae.

Both methods for evaluating prey importance showed that the diet of pregnant spotted dolphins differed greatly from that of lactating dolphins (Table 1). Pregnant dolphins consumed more squid by mass and proportion than did lactating dolphins. Conversely, lactating dolphins consumed more fish by mass and proportion than did pregnant dolphins. The index of relative importance for squid consumed by pregnant females was 7 times that of fish; the index for fish consumed by lactating females was approximately 8 times that for squid. Proportions of squid and of fish in the stomachs of pregnant and lactating dolphins were significantly different ($P < 0.0001$) using estimates of sample variance obtained from bootstrap techniques, resulting in rejection of the null hypothesis of no difference (Fig. 1).

There was some evidence ($0.05 < P < 0.10$) of a difference in stomach fullness between the two groups of females. The estimated difference is large (mean fullness of pregnant dolphin stomachs = 0.23, SD = 0.20; mean fullness of lactating dolphin stomachs = 0.47, SD = 0.40) considering our small sample size. This difference was not related to time-of-day effects. There was no significant difference in time of day on proportion of squid beaks found in the stomachs of females within a group (mean proportion of squid in pregnant females collected before noon = 0.83, SD = 0.33, and after noon = 0.50, SD = 0.56; mean proportion in lactating females before noon = 0.34, SD = 0.25, and after noon = 0.33, SD = 0.47).

Stomach-content data generally have been analyzed using contingency-table tests or the index of relative importance measure; the latter is an index of prey importance and not a statistical test. Crow (1982) recommended use of contingency-table analysis as a means of separating predator feeding modes. Commonly, prey items within a stomach are pooled, as if each prey item were an individual sample. Use of this approach is invalid because it requires the assumption that the prey items in the stomach of an individual are independent, that is, if an individual (dolphin in this case) takes a squid at one moment, the probability of taking a squid or fish at the next moment is totally unaffected. This probably is not the case for predators feeding predominantly on nocturnal, vertically migrating squid and epipelagic flying fish. The test is valid only if one prey item is selected at random from each predator. We have used the bootstrap method for obtaining a robust estimate of sample variance, enabling us to test statistically for differences in feeding habits between the two groups.

Perrin et al. (1973) examined stomach contents of 140 spotted dolphins collected in six net hauls of a tuna seiner from the same regions of the eastern Pacific as our samples. We were able to ascertain that the sex ratio from the first and second hauls was approximately 1:1 ($n = 57$) and only four females were lactating. The first haul was made before 1200 h, the second after 1200 h (in April 1968; W. F. Perrin, pers. comm.). Thus, their feeding habits may reflect those of the general population in this area. The dominant food item (in percent frequency, number, and occurrence) was squid for both hauls.

Barring major changes in feeding habits of spotted dolphins since 1968, our results indicate that feeding habits of pregnant females are similar to those of the population in general. Lactating females, which we found to consume mostly flying fish, seem to have altered their diet from the norm.

Lactating dolphins can satisfy the higher metabolic demand of producing milk either by increasing the quantity eaten or by selecting food of higher caloric value. In captivity, lactating bottlenose dolphins (*Tursiops truncatus*) consume more food than those not lactating, whereas pregnant dolphins do not appear to consume more food until just before parturition (S. H. Ridgway, pers. comm.).

The stomach-fullness test indicates that lactating spotted dolphins may have been eating more than pregnant ones. However, results of this test may be influenced by the interaction between time of day of sample collection and diurnal feeding habits, and by rate of digestion of prey. Lactating dolphins selected flying fish throughout the day and night, whereas pregnant dolphins consumed fewer flying fish than did lactating dolphins during day and night. Greater stomach fullness in lactating dolphins at least partially reflects their selection of a prey item available during the day, when samples are collected. Rate of digestion also influences the stomach-fullness results, but in the opposite direction. In both fish and mammals, a meal is digested faster when soon followed by another meal (Persson, 1984; Robbins, 1983). By eating flying fish, lactating dolphins may eat more frequently, thereby increasing their digestion rate over that of pregnant dolphins and possibly decreasing differences in stomach fullness.

The high, constant energetic cost of producing milk may necessitate that lactating females eat often. Although large whales are able to sustain a calf through several months without feeding (Lockyer, 1985), tropical dolphins have thin blubber (ca. 0.5 cm) thus, small energy reserves. In addition, their lactation period lasts 3–4 times longer than that of large whales (as long as 1.5 years; Myrick et al., 1986).

Lactating spotted dolphins may benefit from increased caloric or nutritional intake per gram of food by switching to fish. Fish and squid eaten by dolphins in the eastern tropical Pacific are different in caloric value (per 100 g muscle mass: $\bar{X} = 420$ kilojoules for fish and $\bar{X} = 290$–330 kilojoules for squid). Fish commonly eaten by dolphins in the North Pacific also have higher muscular lipid and energy values than squid from the same area (Sidwell et al., 1974). On the basis of the proximate composition of raw muscle in a flying fish (*Exocoetus volitans*) and an ommastrephid squid (*Ommastrephes bartrami*), flying fish is higher in protein and fat than squid, whereas squid is higher in water content (flying fish, $\bar{X}$ protein $= 21.2\%$ of wet mass, $\bar{X}$ fat $= 0.9\%$, and $\bar{X}$ water content $= 74.7\%$, from Sidwell, 1981; squid, $\bar{X}$ protein $= 17.6\%$ of wet mass, $\bar{X}$ fat $= 0.34\%$, and $\bar{X}$ water content $= 79.8\%$, from Croxall and Prince, 1982). Flying fish also have slightly more calcium and phosphorus, important for milk production (Sidwell, 1981).

Lactating females may consume more fish than squid to maintain water balance. The electrolytic balance is different between squid and fish. Squid are essentially isotonic with seawater, therefore, higher in Na^{+} and Cl^{-} than fish. By switching to a diet of flying fish, lactating dolphins help prevent additional water loss (Ridgway, 1972).

The behavioral restrictions imposed by a nursing calf may influence feeding habits of its mother. Most spotted dolphins in Perrin et al.'s (1973) study were feeding at greater depths than the tuna, thus avoiding direct competition. A female that dives deep to feed on squid may leave its calf vulnerable at the surface or reduce its own foraging success because the calf would not be able to dive for as long or as deeply. These restrictions would decrease the female's ability to catch squid at a time when its energetic requirements have increased. The alternative is for it to feed at or near the surface.

The behavioral restrictions and nutritional demands imposed by an altricial calf that nurses for >1.5 years are considerable. If the advantages of changing diet during lactation were primarily behavioral, we question whether maternal nutritional requirements could be satisfied because the main prey item for the rest of the population is squid. If the advantages were primarily nutritional, we question why the rest of the population also does not eat mostly flying fish when this food source can sustain a lactating female, unless it is to avoid competition with associated yellowfin tuna. Perhaps flying fish occur in less-dense schools, thus are less amenable to predation by large schools of predators. The actual reason that lactating spotted dolphins consume primarily flying fish may be a combination of several of these factors.

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