

**Abstract.**—In this study of the feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, stomach content samples were collected from dolphins caught by an artisanal fishery operating along the central coast of Peru. Collections were made from three fishing ports, Pucusana, Ancon, and Cerro Azul, during the summers and winters of 1985 and 1986. Overall, the anchoveta, *Engraulis ringens*, the most abundant vertebrate in Peruvian coastal waters, was the principal prey of dusky dolphins with respect to each of four different measures of dietary importance. Anchoveta was also the dominant prey in both seasons of both years, and for all reproductive classes of dusky dolphins. Other prey species commonly found in dolphin stomachs were horse mackerel, *Trachurus symmetricus*, hake, *Merluccius gayi*, sardine, *Sardinops sagax*, Patagonian squid, *Loligo gahi*, and jumbo flying squid, *Dosidicus gigas*. Regressions of body size on otolith or squid beak dimensions were used to estimate lengths and weights of anchoveta and some other prey. All prey species averaged less than 30 cm in estimated length and 300 g in weight. Estimated total lengths of anchoveta consumed as prey increased between seasons in 1985 and between years, paralleling the lengths of anchoveta taken by the purse-seine fishery. However, estimated total lengths of anchoveta eaten by dusky dolphins were consistently smaller than lengths of those caught by the fishery.

# Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, in the coastal waters of central Peru

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The dusky dolphin, *Lagenorhynchus obscurus*, is common in the coastal waters of New Zealand, South America, and South Africa, but like most species of small cetacea from the Southern Hemisphere, its feeding habits are poorly described (Gaskin, 1982; Goodall and Galeazzi, 1985). The squid, *Nototodarus sloanei*, and fish have been reported as prey in New Zealand waters (Gaskin, 1972), whereas in Argentina Würsig and Würsig (1980) observed dusky dolphins feeding on southern anchovy, *Engraulis anchoita*. Prior to the present study, little was known of the feeding habits or natural history of the dusky dolphin in Peruvian waters, although large numbers of dusky dolphins were being taken in an artisanal fishery (Read et al., 1988; Van Waerebeek and Reyes, 1990).

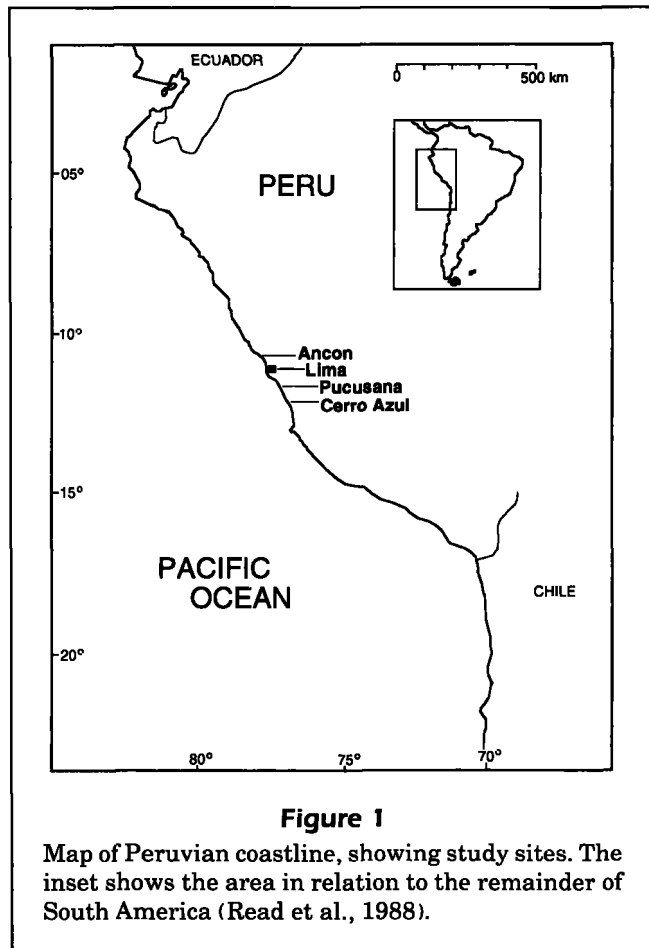
In Peru, the dusky dolphin is found in the waters of the coastal upwelling system (McKinnon, 1988), which has been extensively studied by those involved in managing the system's various fisheries (Pauly and Tsukayama, 1987; Pauly et al., 1989). The cool waters of the coastal upwelling region constitute one of the most productive areas of the world ocean (Ryther, 1969), but oceanographic conditions and the abundance and distribution of fishes can vary greatly within and between years, especially when El Niño's occur (Pauly and Tsukayama, 1987; Pauly et al., 1989).

The objective of the present study was to characterize, in terms of both species composition and prey size, the feeding habits of the dusky dolphin in Peruvian waters. Seasonal and annual variation in feeding habits was also investigated and compared with abundance data for important prey species during the same periods. In addition, potential dietary differences among dolphins of different reproductive states were examined, as feeding habits of lactating females differ from those of nonlactating females and males in some small cetaceans (Bernard and Hohn, 1989; Recchia and Read, 1989).

## Methods

Data on feeding habits were obtained by analysis of undigested hard parts of prey, specifically fish otoliths and squid beaks, from stomach content samples collected through the fishery. Dolphins were usually captured by artisanal fishermen in gill nets set from dusk to dawn within the coastal upwelling zone (Read et al., 1988; Van Waerebeek and Reyes, 1990), but six stomach samples from a single landing by a purse seiner, in the summer of 1985, were also included.

All samples were collected at ports along the central coast of Peru, where the largest dolphin catches occurred during the present



study (Read et al., 1988). Pucusana, a small fishing town approximately 50 km south of Lima (Fig. 1) was the principal collecting site. Stomach content samples were also collected from the nearby ports of Cerro Azul and Ancon, about 70 km south and 90 km north of Pucusana, respectively (Fig. 1). Dolphin landings at any given port were highly variable (Read et al., 1988), therefore collecting efforts were concentrated at the port or ports where the most dolphins were being caught. The collecting periods were the austral summers (1 January through 31 March) and winters (1 July through 30 September) of 1985 and 1986.

### Field procedures

Standard length, measured in a straight line along the main axis of the body from the tip of the upper jaw to the notch of the flukes, was taken for each specimen upon being landed. Females were pressed above the nipples and expression of milk, indicating lactation, was noted. When dolphins were eviscerated, female reproductive tracts were removed and checked for the presence of a fetus. Ovaries were in-

spected for corpora lutea and albicantia, then preserved in 10% formalin.

Collection of stomach contents also began upon evisceration, between approximately 6 and 48 hours after capture. Each of the fore-, main, and pyloric stomachs was separately rinsed through a series of three brass sieves (Treacy and Crawford, 1981; Murie and Lavigne, 1985) of mesh diameters 4.75, 1.40, and 0.425 mm. The sieved contents were then placed in deep, water-filled plastic trays so that any remaining flesh could be skimmed off. Fish otoliths and clean squid beaks were retrieved and stored in 5–10% alcohol; squid beaks with flesh still attached were stored in either 70% alcohol or 10% formalin. The forestomach consistently contained the least digested contents and the greatest volume, so only material from that chamber was later quantified and analyzed (see also Perrin et al., 1973; Bernard and Hohn, 1989).

### Reproductive status

Reproductive status of females was classified after macroscopic examination of gonads and accessory reproductive tissues. Males were classified only as to sex. Females were defined as 1) immature, if their ovaries lacked corpora lutea and albicantia; 2) pregnant, if a fetus was visible in the uterus; 3) lactating; 4) simultaneously pregnant and lactating; or 5) resting, if corpora lutea or albicantia were present but there was neither a fetus visible in the uterus nor evidence of lactation (Perrin and Donovan, 1984). The "resting" category may have included females with small embryos not detected during field inspections, in addition to individuals actually between reproductive cycles (Perrin and Donovan, 1984). Data were incomplete for several females; therefore they were classified as "unknown females." No information on gender was available for several additional samples; their sex and reproductive status were classified as "unknown."

### Identification of prey and calculation of measures of relative importance

A reference collection of otoliths from common Peruvian marine fishes was made from specimens purchased at local markets and identified with Chirichigno's (1978) key. Otoliths from stomach contents were identified by comparison with this collection and collections belonging to the Instituto del Mar del Peru (IMARPE) and to P. Majluf (University of Cambridge). Squid species were identified from their beaks by using published keys (Wolff, 1984; Clarke, 1986), through reference to beaks from local squids identified and supplied by F. Cardoso (Museo de

Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), and with the assistance of S. Candela (University of Miami, Florida).

Counts and measurements of undigested hard parts of prey allowed calculation of several measures of the relative importance of each prey species. The simplest measure, "percent frequency of occurrence", was defined as 100 multiplied by the number of stomachs in which a prey species was present/the total number of stomachs in the sample, excluding empty stomachs. "Percent total numbers," was defined as 100 multiplied by the number of individuals of a species of prey/the sum of individuals for all prey species (Frost and Lowry, 1980). The number of individuals of each prey species in a sample was estimated by dividing the count of its otoliths (for fish) or squid beaks (for squid) by two (Frost and Lowry, 1980).

Lengths and weights of consumed fish were estimated by using regressions involving fish length and otolith length, or fish weight and either fish length or otolith length. Calculations for anchoveta, *Engraulis ringens*, Pacific Sardine, *Sardinops sagax*, hake, *Merluccius gayi*, and horse mackerel, *Trachurus symmetricus*, followed Chirinos and Chuman (1968), Samame (1977), McKinnon (1988), and Hawes (1983), respectively, except that length was estimated for *T. symmetricus* by using  $L=4.37 \times W^{1/3}$ , and weights of *E. ringens* and *S. sagax* were estimated by using  $W=0.007 \times L^3$  and  $W=0.015 \times L^3$ , where  $W$ =weight (g) and  $L$ =total length (cm).<sup>1</sup>

For each fish species, ten randomly selected otoliths from each stomach were measured (Murie, 1984). If fewer than ten suitable otoliths were present, all those available were utilized. Only otoliths with minimal degradation were measured. Degradation was apparent from a loss of detail, particularly the loss or reduction of spines and lobulations along the edges of the otoliths (Frost and Lowry, 1986).

Squid mantle lengths were estimated for each squid species by using linear regressions of mantle length on rostrum length and squid weights from regressions of  $\log_e$  weight on  $\log_e$  rostrum length (Wolff, 1984). Regressions were not available for patagonian squid, *Loligo gahi*, so regression equations for *Loligo opalescens*, a closely related species, were used (Wolff, 1984). For each squid species, ten randomly selected beaks were measured from each stomach, unless fewer than ten were present, in which case all were utilized.

A mean individual weight (MIW) was calculated for each prey species in each stomach and then used

in estimating the percent weight contribution of each prey species to the dusky dolphin's diet. The MIW was usually the mean of the regression-estimated weights of individuals of a given prey species in a particular stomach, unless all hard parts were too degraded to permit reliable measurement, in which case an overall MIW, the mean of all regression-estimated lengths of that species in all stomachs with measurable hard parts, was employed. For anchoveta, however, enough measurable otoliths were available from stomach samples to permit statistical analyses by year and season of capture. Overall MIW's for anchoveta were therefore calculated for each group of stomachs within which analyses revealed no significant differences (for example, the summer of 1985; see Results).

The total weight of each species of squid or fish present in each dolphin stomach was estimated by multiplying the number of individuals present by the appropriate MIW value. The percent weight of each prey species in the dusky dolphin's diet was calculated by using weights summed over all stomachs, as 100 multiplied by the total weight of each prey species/the total weight of all prey present. Species for which regression-estimates of length and weight were not available were excluded from these calculations.

The percent gross energy contribution of each species was defined as 100 multiplied by gross energy of the prey species/summed gross energy of all prey consumed, for all stomach content samples. The gross energy available from a prey species is the caloric density ( $\text{kcal} \cdot \text{g}^{-1}$ ) $\times$ weight (g) consumed. Caloric density (CD) values were obtained from the literature for each prey species, either directly from bomb-calorimetric analyses or indirectly from data on proximate composition, by using CD's for fat, carbohydrate, and protein of 9.4, 4.15, and 5.65  $\text{kcal} \cdot \text{g}^{-1}$ , respectively (Pike and Brown, 1984).

By using published data from non-El Niño years only, CD values for anchoveta were calculated as 1.589  $\text{kcal} \cdot \text{g}^{-1}$  for the summer and 1.548  $\text{kcal} \cdot \text{g}^{-1}$  for the winter (Lam, 1968). Data were unavailable for *S. sagax*, but like *E. ringens* it is a clupeoid, and the reproductive seasons of the two species are similar (Muck et al., 1987; Pauly and Soriano, 1987), therefore *S. sagax* was assigned the same seasonal values as *E. ringens*. A value of 1.244  $\text{kcal} \cdot \text{g}^{-1}$  was calculated for *T. symmetricus* by using proximate composition values from the related *T. trachurus* (Sidwell, 1981). Similarly, a value of 1.158  $\text{kcal} \cdot \text{g}^{-1}$  for *M. gayi* was based on equivalent data from *M. productus* (Sidwell, 1981). For *Loligo gahi*, 0.968  $\text{kcal} \cdot \text{g}^{-1}$  was obtained from proximate composition data in Croxall and Prince (1982). No published values were available for *Dosidicus gigas*, so a mean ommastrephid

<sup>1</sup> Pauly, D. International Center for Living Aquatic Resources Management, Manila. Personal commun., 1985.

estimate of  $0.922 \text{ kcal}\cdot\text{g}^{-1}$  was calculated from bomb calorimetric and proximate composition data in Croxall and Prince (1982), Vlieg (1984), and Clarke et al. (1985).

### Statistical analyses

Seasonal and annual variation in the size of consumed anchoveta were analyzed with a two-way ANOVA of the mean estimated lengths of the anchoveta in each dolphin stomach, weighted by the number of otoliths measured (SAS, 1985 and 1987). Because of the unbalanced design, sums of squares and *F*-values were calculated by using the "Type III sum of squares" (SAS, 1985). Sidak adjusted *t*-tests were used for comparisons among pairs of means (Sokal and Rohlf, 1981; SAS, 1987). Log-linear analyses were conducted on frequency of occurrence data, also by using SAS (1987), and the resulting *G*-statistics were tested for significance following Sokal and Rohlf (1981).

Data from different locations were pooled for analyses of the effects of year and season on dusky dolphin feeding habits. This was appropriate because the two most distant of the three ports are separated by only about 160 km (Fig. 1), and all three ports are found along the central portion of the Peruvian coast. This region is relatively homogeneous and often treated as a single unit in analyses of oceanographic processes and fish populations (e.g. Brainard and McLain, 1987; Pena et al., 1989). It was necessary to pool data from all locations and collection periods to obtain sample sizes sufficient for analyses of prey occurrence with respect to dolphin reproductive status.

### Results

One hundred and thirty-six stomach samples contained recognizable hard parts and were used in subsequent analyses (Table 1). Six additional stomachs were empty, containing no recognizable hard parts at the time of their collection. There were no obvious patterns in the years, seasons, or locations in which the empty stomachs occurred, or the reproductive status of the individuals from which they were obtained (Table 1). Eight additional samples contained otoliths at the time of their collection, according to field notes, but lacked otoliths when examined in the laboratory several months later. These otoliths may have dissolved during storage; therefore these samples were not included in analyses.

Species included in percent weight and percent gross energy calculations—*E. ringens*, *T. symmetricus*, *M. gayi*, *S. sagax*, *L. gahi* and *D. gigas*—represented the vast majority of prey, over 98% of the total number consumed. Other species, anchoa, *Anchoa* sp., blackruff, *Serirolella violacea*, a flyingfish, *Hirundichthys* sp., and deepsea smelt, *Leuroglossus urotamus*, were found in only trace amounts in stomach contents (Table 2).

Anchoveta was the most important prey species by all measures of relative importance. It accounted for 92.5% of all dusky dolphin prey items by total numbers and was present in 97.8% of stomachs. By weight, anchoveta accounted for 83.8% of prey, and by gross energy, 87.3% (Table 2). No other prey species accounted for more than 5.1% of prey by weight, 2.5% by total numbers, or 4.0% by gross energy, or was found in more than 26.5% of the stomachs examined (Table 2).

Table 1

Distribution of stomach content samples containing otoliths or squid beaks, or both, collected from dusky dolphins, *Lagenorhynchus obscurus*, by year, season, and dolphin reproductive status. Numbers in parentheses represent number of empty stomachs containing neither otoliths nor squid beaks.

Year	Season	Location	Reproductive status <sup>1</sup>							Total
			ImmF's	RestF's	PregF's	LactF's	UnknF's	Males	Unkn's	
1985	Summer	Pucusana	4	0	0	1	0	10	0	15
1985	Winter	Pucusana	0	0	0	1	0	0	0	1
1985	Winter	Ancon	4	7	0	8(1)	4	19(1)	0	42(2)
1986	Summer	Pucusana	1	1	3	5	0	10	0	20
1986	Summer	Cerro Azul	0	0	5	1	0	4(1)	0	10(1)
1986	Winter	Pucusana	4	5	4(1)	5	0	12(1)	4	34(2)
1986	Winter	Cerro Azul	1	2	6	1	0	4(1)	0	14(1)

<sup>1</sup> ImmF's=immature females; RestF's=resting females; PregF's=pregnant females; LactF's=lactating females (including simultaneously pregnant and lactating females; two were collected, one at Ancon in the winter of 1985, one at Pucusana in the summer of 1986); UnknF's=females of unknown reproductive status; Males=all males; Unkn's=individuals of unknown sex.

By weight, anchoveta accounted for more than half of all prey consumed in every collection period and its lowest frequency of occurrence was 93.3% (Table 3). The percent weight of *T. symmetricus* in dusky dolphin diets was always low, ranging from 0% in the winter of 1985 to a maximum of 14.5% in the summer of 1986, but frequency of occurrence was more variable, ranging from 0% to 53.3% (Table 3). In a log-linear analysis, the three-way interaction between year, season, and frequency of occurrence of *T. symmetricus* in stomachs was not statistically significant ( $G=1.91$ ,  $df=1$ ,  $P>0.10$ ), nor was the interaction between season and frequency of occurrence significant ( $G=2.26$ ,  $df=1$ ,  $P>0.10$ ). The large increase in frequency of occurrence of this prey from 1985 to 1986, however, resulted in a highly significant interaction between frequency of occurrence and year ( $G=37.76$ ,  $df=1$ ,  $P<0.001$ ). The only other prey found sufficiently often in stomachs for statistical testing of frequency, but not so often that insufficient variation was present (as for anchoveta), was *L. gahi*, for which log-linear analysis yielded a significant three-way interaction between frequency of occurrence, year, and season of collection ( $G=13.44$ ,  $df=1$ ,  $P<0.001$ ). Thus neither season nor year exerted a clear, independent effect on consumption of *L. gahi*, although there was considerable variation among collecting periods (Table 3).

Reproductive status did not have any obvious effect on dusky dolphin feeding habits (Table 4). The frequencies of occurrence of *T. symmetricus* and *L. gahi* did not differ significantly between either lactating females and pooled nonlactating mature females ( $G=0.39$ ,  $df=1$ ,  $P>0.5$ ;  $G=1.06$ ,  $df=1$ ,  $P>0.3$ , respectively for each prey species) or between lactating females and all other individuals pooled ( $G=0.29$ ,  $df=1$ ,  $P>0.5$ ;  $G=0.17$ ,  $df=1$ ,  $P>0.5$ , respectively). Anchoveta were consumed by both sexes almost without exception (Table 4).

Table 2

Relative importance of prey species of the dusky dolphin, *Lagenorhynchus obscurus*, from the coastal waters of central Peru in the summers and winters of 1985 and 1986 ( $n=136$  stomachs, 9,137 individual fish and squid). Percent weight and percent gross energy were calculated by using only the six most important prey species.

Prey species	% Frequency of occurrence	% Total numbers <sup>1</sup>	% Weight	% Gross energy
<i>Engraulis ringens</i>	97.8	92.5	83.8	87.3
<i>Trachurus symmetricus</i>	26.5	2.5	3.5	2.9
<i>Merluccius gayi</i>	8.1	0.6	5.1	4.0
<i>Sardinops sagax</i>	4.4	0.2	2.2	2.3
<i>Loligo gahi</i>	19.1	2.2	3.7	2.4
<i>Dosidicus gigas</i>	11.0	0.4	1.6	1.0
<i>Anchoa</i> sp.	1.5	0.1	—	—
<i>Seriotelella violacea</i>	1.5	0.0	—	—
<i>Hirundichthys</i> sp.	0.7	0.0	—	—
<i>Leuroglossus urotramus</i>	0.7	0.5	—	—
Unknowns <sup>2</sup>	9.6	1.1	—	—

<sup>1</sup> Percent total numbers values were sometimes very low, e.g. 0.01% or only 0.0% to an accuracy of one decimal place, even when a prey species was present in more than one stomach and its percent frequency of occurrence was greater than 1%.

<sup>2</sup> There appeared to be at least eight species of fish represented among the otoliths which could not be identified.

Table 3

Relative dietary contribution of prey species commonly eaten by the dusky dolphin, *Lagenorhynchus obscurus*, for each combination of year and season.

Prey species	% Total weight (% Frequency of occurrence)			
	Summer 1985 ( $n=15$ ) <sup>1</sup>	Winter 1985 ( $n=43$ )	Summer 1986 ( $n=30$ )	Winter 1986 ( $n=48$ )
<i>E. ringens</i>	76.6 (100.0)	86.4 (97.7)	66.0 (93.3)	91.4 (100.0)
<i>T. symmetricus</i>	0.2 (6.7**)	0.0 (0.0**)	14.5 (53.3**)	3.4 (39.6**)
<i>M. gayi</i>	22.0 (13.3)	3.1 (9.3)	6.9 (16.7)	0.0 (0.0)
<i>S. sagax</i>	1.0 (6.7)	0.4 (2.3)	0.9 (3.3)	4.9 (6.3)
<i>L. gahi</i>	0.1 (6.7**)	9.6 (34.9**)	2.3 (26.7**)	0.2 (4.2**)
<i>D. gigas</i>	0.0 (0.0)	0.5 (20.9)	9.4 (16.7)	0.1 (2.1)

<sup>1</sup>  $n$ =Number of dusky dolphins from which stomach content samples were collected.

\*\*=Significant differences present at  $P<0.001$ .

### Prey size

All dusky dolphin prey species for which lengths and weights could be estimated averaged less than 30 cm (mantle length for the squids, fork length for *M. gayi*, and total length for all others) and 300 g. The

Table 4

Percent composition by weight and frequency of occurrence of prey found in stomach contents of dusky dolphins, *Lagenorhynchus obscurus*, classified by reproductive status. All collection periods are pooled (summers and winters of 1985 and 1986).

Reproductive status <sup>1</sup>	n	% Weight <sup>2</sup> (% Frequency of occurrence)					
		<i>E. ringens</i>	<i>T. symmetricus</i>	<i>M. gayi</i>	<i>S. sagax</i>	<i>L. gahi</i>	<i>D. gigas</i>
Imm. Fem.'s	14	74.3 (92.9)	4.6 (14.3)	7.3 (14.3)	0.0 (0.0)	12.9 (21.4)	0.8 (28.6)
Rest. Fem.'s	15	82.6 (100.0)	0.9 (26.7)	0.0 (0.0)	15.9 (6.7)	0.6 (6.7)	0.0 (0.0)
Preg. Fem.'s	18	85.7 (100.0)	0.7 (33.3)	0.9 (5.6)	3.0 (11.1)	0.8 (16.7)	8.9 (16.7)
Lact. Fem.'s	22	87.1 (100.0)	0.7 (22.7)	8.3 (13.6)	0.6 (4.5)	3.0 (22.7)	0.4 (13.6)
Males	59	81.8 (96.6)	7.5 (30.5)	5.9 (8.5)	0.4 (1.7)	4.0 (22.0)	0.4 (6.8)

<sup>1</sup> Imm. Fem.'s=immature females; Rest. Fem.'s=resting females; Preg. Fem.'s=pregnant females; Lact. Fem.'s=lactating females, including those simultaneously pregnant and lactating; Males=all males; individuals of unknown reproductive status omitted.

<sup>2</sup> May not total 100 in each row due to rounding.

most common prey species, *E. ringens*, *T. symmetricus*, and *L. gahi*, averaged less than 20 cm and 100 g (Table 5).

The regression-estimated lengths of consumed anchoveta varied significantly with year, season, and the interaction between year and season ( $F=416.06$ ,  $62.56$ , and  $35.42$ , respectively;  $df=1$ ,  $67$ ,  $P<0.0001$ ; Table 6). In comparisons between pairs of means, anchoveta were found to be significantly larger in the summer and the winter of 1986 than in either the summer or the winter of 1985 (Table 6). In 1985, otolith lengths were significantly different between summer and winter, but not in 1986 (Table 6).

Mean total lengths of anchoveta from fishery samples (for each combination of year and season) were positively correlated with mean regression-estimated lengths of anchoveta consumed by dusky dolphins ( $r=0.98$ ,  $df=2$ ,  $P<0.05$ ; Table 6). Mean estimates of total length for anchoveta consumed by dusky dolphins were consistently 1.4–2.0 cm smaller than mean total lengths of anchoveta taken by the fishery, however (paired  $t$ -test,  $t=12.4$ ,  $df=3$ ,  $P<0.01$ ).

## Discussion

The prey of the dusky dolphin in Peruvian coastal

Table 5

Mean lengths (cm) and weights (g), as estimated from regressions on otolith length/radius and squid beak rostrum length, of fish and squid species commonly found in the stomachs of the dusky dolphin, *Lagenorhynchus obscurus*, landed along the central Peruvian coast in 1985 and 1986.

Prey species	Estimated mean length (SE)		Estimated mean weight (SE)	
	No. of hard parts <sup>1</sup>	(No. of stomachs) <sup>5</sup>	No. of hard parts <sup>1</sup>	(No. of stomachs) <sup>5</sup>
<i>E. ringens</i> <sup>1</sup>	13.4	(0.14)	17.3	(0.49)
	593	(71)	593	(71)
<i>S. sagax</i> <sup>1</sup>	25.1	(0.32)	237.0	(8.67)
	4	(2)	4	(2)
<i>M. gayi</i> <sup>2</sup>	25.2	(4.62)	198.0	(104.0)
	18	(5)	18	(5)
<i>T. symmetricus</i> <sup>1</sup>	11.5	(1.16)	25.6	(8.67)
	34	(13)	34	(13)
<i>L. gahi</i> <sup>3</sup>	13.0	(0.27)	33.3	(1.23)
	97	(26)	97	(26)
<i>D. gigas</i> <sup>3</sup>	13.4	(1.00)	72.7	(16.4)
	34	(15)	34	(15)

<sup>1</sup> Total length.

<sup>2</sup> Fork length.

<sup>3</sup> Mantle length.

<sup>4</sup> Number of hard parts measured.

<sup>5</sup> Number of stomachs from which samples were taken.

waters can be characterized as schooling, small to medium size, pelagic or semi-pelagic species (*M. gayi* is usually demersal but sometimes forms large pelagic schools [Mejía and Jordán, 1979]). Anchoveta was typical and was unequivocally the most important prey species in 1985–86. It was most important by all measures of consumption and constituted almost 90% of the dusky dolphin's diet by percent gross

**Table 6**

Mean estimated total lengths of anchoveta, *Engraulis ringens*, consumed by dusky dolphins, *Lagenorhynchus obscurus*, in central Peruvian coastal waters in 1985 and 1986, compared to mean lengths of anchoveta taken in the purse-seine fishery.

Collection source	Summer 1985	Winter 1985	Summer 1986	Winter 1986
<b>Stomachs of dusky dolphins</b>				
Mean estimated total length of anchoveta <sup>1</sup> (SE)	11.5 <sup>a</sup> (0.14)	12.9 <sup>b</sup> (0.09)	14.1 <sup>c</sup> (0.10)	14.3 <sup>c</sup> (0.07)
Number of otoliths measured	112	150	103	228
Number of stomachs from which otoliths were collected	12	18	14	27
<b>Purse-seine fishery</b>				
Mean total length of anchoveta <sup>2</sup>	13.5	14.6	15.5	16.3

<sup>1</sup> Based upon measurements of otoliths in dusky dolphin stomachs.

<sup>2</sup> Mean total length of anchoveta taken in the fishery, calculated from data in Pauly and Palomares (1989); SE's and N's unavailable.

<sup>a,b,c</sup> Means with different letters in the superscript differed significantly (Sidak adjusted *t*-tests;  $t \geq 8.41$ ,  $P < 0.001$  in all cases) while those with the same letter did not ( $t = 1.42$ ,  $P > 0.5$ ).

energy, usually considered the best measure of relative prey importance (Lavigne et al., 1982). Few data are available on feeding habits for other regions, but in Argentina dusky dolphins also fed on a species of anchovy (Würsig and Würsig, 1980).

There were no consistent seasonal patterns in prey consumption in the present study. Rather, anchoveta was the most important prey species in both seasons of both years, probably owing, in part, to its relatively high abundance throughout the study period (Pauly and Palomares, 1989). Consumption of *T. symmetricus* was more variable and opportunistic. In 1985 *T. symmetricus* was almost absent from stomach samples, but it was a major prey item in 1986 when unusually large numbers of juveniles, similar in size to other important dusky dolphin prey, were observed in the coastal waters of central and northern Peru (IMARPE et al., 1986). Other species, particularly *L. gahi*, varied greatly among collection periods in their importance as prey, but did not exhibit consistent seasonal or annual patterns.

In examining the effects of season, year, and other variables on diet, only frequency of occurrence was analyzed statistically because analyses of other measures of prey importance involve excessive violations of the assumptions underlying most statistical tests (Recchia and Read, 1989). Percent-weight estimates were used for qualitative comparisons among collection periods and reproductive classes, rather than percent gross energy values, because the latter were very gross approximations.

Anchoveta was the main prey of all reproductive classes of dusky dolphins. In contrast, in the eastern tropical Pacific most spotted dolphins, *Stenella attenuata*, eat mainly ommastrephid squids whereas

lactating females eat principally fish (Bernard and Hohn, 1989). The greater energy and water requirements of lactating females may force them to feed on fish, which contain more energy and water per unit weight than squid or, alternatively, the presence of a calf may prevent females from feeding at the depths at which squid occur (Bernard and Hohn, 1989). In Peru, lactating dusky dolphins were apparently able to satisfy their energy and water requirements, as did other females, males and juveniles, by feeding on the abundant, high energy anchoveta (Lam, 1968).

Like the fishermen, fur seals, and seabirds of the Peruvian coast, dusky dolphins were somewhat opportunistic in their feeding in respect to the sizes of the anchoveta they preyed upon, taking more of the more abundant size classes (Muck and Pauly, 1987; Majluf, 1989). Anchoveta consumed by dusky dolphins were consistently 1.4–2.0 cm smaller, however, than those taken in the fishery, perhaps because of the fishery's bias towards larger anchoveta (Palomares et al., 1987). Alternatively, the slight degradation present in some of the otoliths from which anchoveta sizes were estimated may have resulted in underestimation of total lengths (Recchia and Read, 1989). The observed discrepancy may also be due to variation in the relationship between otolith size and body size, which can differ among years because of variation in growth rates of fish (McKinnon, 1988; Reznick et al., 1989; Secor and Dean, 1989; Campana, 1990).

Relative consumption of fishes with small otoliths, such as anchoveta, may have been underestimated. Large otoliths and squid beaks are less easily dissolved by stomach acids than are smaller otoliths (Hawes, 1983; Bigg and Fawcett, 1985; da Silva and

Neilson, 1985; Recchia and Read, 1989) and squid beaks are less easily passed through the digestive tract than are otoliths (Hawes, 1983; Bigg and Fawcett, 1985). This potential bias tends to strengthen the principal finding of this study: anchoveta was by far the most important prey species of all reproductive classes of Peruvian dusky dolphins in the summers and winters of 1985–86.

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