Prey occurrence in pantropical spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific

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Abstract.–Identified prey of pantropical spotted dolphins, *Stenella attenuata*, include 56 species of fish and 36 species of cephalopods. Species identifications were made from fish otoliths and cephalopod beaks recovered from 428 stomachs collected throughout the eastern tropical Pacific between 1989 and 1991. The most frequently found fish were lanternfish (family Myctophidae) at 40%, and the most frequently found cephalopods were flying squids (family Ommastrephidae) at 65%. The dominance of these primarily mesopelagic prey species and a significantly higher stomach fullness index for stomachs collected during the morning hours (χ^2=112.99, df=6, P<0.0001) suggest that pantropical spotted dolphins feed at night when many mesopelagic species migrate toward the surface. Significant differences in prey composition by season and geographic region indicate that pantropical spotted dolphins are flexible in their diet and may be opportunistic feeders. Comparison of the diets of pregnant and lactating female dolphins revealed that lactating females increase both the proportion of squid in their diet and quantity of food consumed.

Manuscript accepted 6 September 1996.
Fishery Bulletin 95:334–348 (1997).

Previously published analyses of the prey of pantropical spotted dolphins in the eastern tropical Pacific (ETP) have reported that many species are consumed and that the species composition and importance varies. Three previous studies reported that epipelagic species are the dominant prey and included species belonging to the families Ommastrephidae (flying squid), Onychoteuthidae (hooked squid), and Exocoetidae (flying fish) (Fitch and Brownell, 1968; Perrin et al., 1973; Bernard and Hohn, 1989). However, mesopelagic species in the families Myctophidae (lantern fish) and Enoploteuthidae (enope squid) were also identified in high numbers (Fitch and Brownell, 1968; Perrin et al., 1973). A more recent study by Roberts (1994) examined only cephalopod prey and found that primarily mesopelagic squid species in the family Ommastrephidae were dominant. Another study reported on the prey of a spotted dolphin caught off Hawaii. The prey were predominantly mesopelagic species belonging to the families Myctophidae and Enoploteuthidae (Shomura and Hida, 1965). All these studies were based on either a small number of samples or samples that were collected from a restricted area of the Pacific Ocean and, therefore, may be limited in their represention of the prey of pantropical spotted dolphins.

In this paper, we describe the prey of pantropical spotted dolphins collected throughout their range in the ETP. We calculate the percent number and percent frequency of occurrence for each prey species identified to quantify the relative importance of prey species. Variability in the diet due to geographic region, oceanographic season, and, for females, due to reproductive condition are examined. We also present the size distribution of prey consumed for species for which data were available in order to convert otolith and beak measurements to prey size.

Methods

Stomachs were collected from 428 pantropical spotted dolphins in 103 net sets by biological technicians placed aboard U.S. tuna purse-seine vessels fishing in the ETP between 1989 and 1991 (Fig. 1; see Jefferson et al., 1994, for collection procedures).

Only the contents in the esophageal (fore) stomach were examined for our analyses because this stomach compartment contains the most recent meal and thus the most identifiable remains (Harrison et al., 1967). The forestomach of each specimen was weighed full and empty to the nearest 0.1 g with a Mettler PC4400 balance. The contents were sorted and recovered by

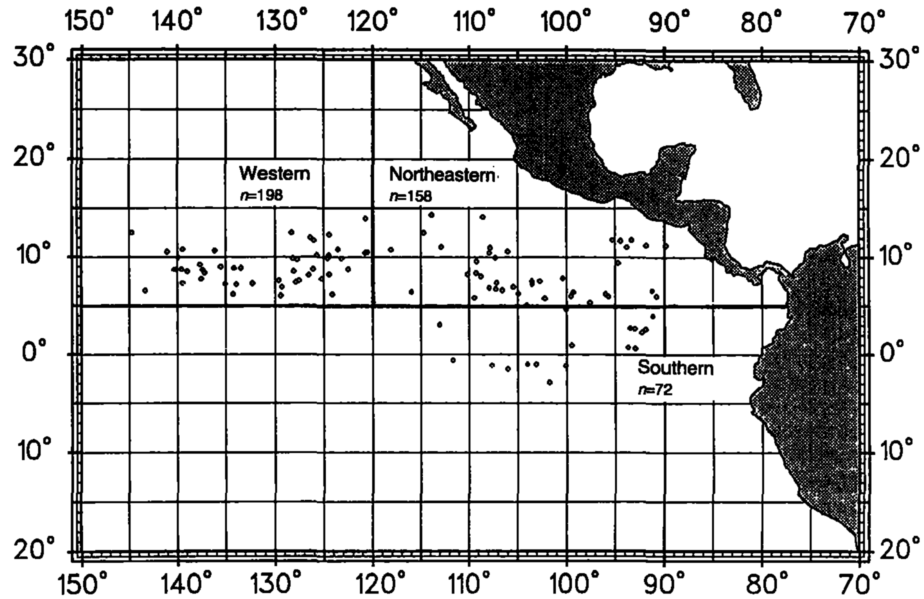

Figure 1

Distribution of net-sets (n=103) from which 428 pantropical spotted dolphin stomachs were collected between 1989 and 1991. For analysis of geographic variability in prey composition, the sample was divided into areas which correspond to recognized stock boundaries and different oceanographic regions: northeastern, southern, and western.

rinsing them through a series of sieves with mesh sizes of 12.5 mm, 1.4 mm, and 500 µ. Fish otoliths and other skeletal remains, cephalopod beaks, crustaceans, gastropods, and parasitic nematodes were collected and enumerated.

Left and right fish otoliths for each species were separated and counted. The highest count of either was used as the minimum number of fish present for that species. Fish species were identified to the lowest possible taxon by using voucher collections of otoliths at the Los Angeles County Museum of Natural History (Lavenberg[1]), the Southwest Fisheries Science Center (SWFSC)(Pitman and Carretta[2]), and otolith identification keys published by Fitch and Brownell (1968), Fitch (1969), and Butler (1979). Frigate mackerel (*Auxis thazard*) were identified from vertebral characteristics rather than from otoliths (Clothier, 1950; Uchida, 1981). For cephalopods, upper and lower mandibles were separated and counted for each species; the highest count of either represented the minimum number present in the stomach. Species identifications to the lowest possible taxon were made with the voucher collection of beaks at the Santa Barbara Museum of Natural History[3] and identification keys published by Wolff[4]) and Clarke (1986a). The relative importance of prey was determined by calculating the percent number and percent frequency of occurrence (Hyslop, 1980) for each individual species and family.

Prey size

For analysis of prey size, maximum length of otoliths (tip of the rostrum to the posterior margin) and lower rostral length (LRL) of beaks were measured with an ocular micrometer disc accurate to 0.1 µ, only for those items that showed little sign of erosion. Regression equations and ratios of standard length to otolith length were used to convert measurements to prey lengths and weights (Butler, 1979; Clarke, 1986a; Hecht; 1987; Wolff,[4] Pitman and Carretta[5]). Length measurements of *A. thazard* were obtained by estimating total length from whole fish and skeletons recovered from the stomachs. We used the prey

[1] Lavenberg. R. 1993. Los Angeles County Mus. Natl. History, Ichthyology Dep., 900 Exposition Blvd., Los Angeles, CA 90007.

[2] Pitman, R., and J. Carretta. 1993. Southwest Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038.

[3] Hochberg, E. 1992. Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

[4] Wolff, G. A. 1982. A study of feeding relationships in tuna and porpoise through the application of cephalopod beak analysis. Final Tech. Report for DAR-7924779, 231 p.

[5] Pitman, R., and J. Carretta. 1993. Southwest Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038. Unpubl. data.

size data to test the hypothesis that dolphins of all size classes eat prey of the same size. To do this, we fitted a linear regression to prey size versus the total body length of the dolphins (Norris, 1961). We also tested the null hypothesis of no correlation between size class of prey consumed and number of items consumed by using a Pearson Correlation Matrix (SYSTAT , 1992; unless otherwise noted, all statistical tests are interpreted with $\alpha=0.05$).

Geographic and seasonal variability

To test for variability in diet, we stratified the sample by season and area. For season, we used the two oceanographic seasons characteristic of the ETP: winter (January–June) and summer (July–December; Reilly, 1990). For area, we stratified the sample by the two recognized management stocks: northeastern and western-southern (Perrin et al., 1994). However, we divided the western-southern stock into a western and a southern section at the equator (Fig. 1) because biological differences in pantropical spotted dolphins have been noted between the western and southern sections of the western-southern stock (Perrin et al., 1976, 1979; Barlow, 1985; Hohn and Hammond, 1985; Myrick, et al., 1986; Chivers and Myrick, 1993; Bright and Chivers[6]). With the 10 most numerous species of fish and squid, we used χ^2 to test the null hypothesis that there was no difference in prey consumed by season or area.

Stomach fullness index (SFI)

A relative index of stomach fullness (SFI) was calculated for each stomach with the method of Bernard and Hohn (1989) to estimate when pantropical spotted dolphins were feeding. With this method, the SFI can never equal 100% because the initial weight of the contents includes the weight of the forestomach. To compensate for this method, we adjusted the scale of the SFI to range from 0% to 100% by dividing the index for each stomach by the maximum index value in our sample (Eq. 1):

$$SFI_{adj} = \frac{(w_c / w_i)}{SFI_{max}} \times 100, \qquad (1)$$

where SFI_{adj} = adjusted stomach fullness index;
SFI_{max} = maximum stomach fullness index;
w_i = initial weight of the forestomach with contents (g); and
w_c = weight of the forestomach contents (g).

[6] Bright, A. M., and S. J. Chivers. 1991. Post-natal growth rates: a compariosn of northern and southern stocks of the offshore spotted dolphins. Southwest Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-30, 24 p.

Using a χ^2, we tested the hypothesis of no difference in the SFI during the course of the day (all stomachs were collected between 0600 and 1800 h). The data were stratified by time-of-day collected: 0600–0900, 0901–1200, 1201–1500, and 1501–1800 h and by SFI categories: 0–30%, 31–60%, and 61–100% full.

Reproductive condition

The reproductive condition of female pantropical spotted dolphins was determined by microscopic examination of the ovaries and macroscopic examination of the uteri and mammary glands (Perrin et al., 1976; Akin et al., 1993). Using the mean number of fish and squid consumed by lactating (n=57) and pregnant (n=37) females, we used Student's t-test to test the null hypothesis that there was no difference in consumption of fish and squid between the two groups. We also compared the SFI of lactating and pregnant females by time-of-day as described in the SFI analysis section.

Results

Our sample of 428 stomachs contained 49,798 prey items, representing 56 fish species and 36 cephalopod species (Table 1). Thirty-eight (38) of the species identified had not been previously reported as prey of pantropical spotted dolphins (Shomura and Hida, 1965; Fitch and Brownell, 1968; Perrin et al., 1973; Bernard and Hohn, 1989; Roberts, 1994). Some species identifications could not be positively confirmed and were designated as species 1, 2, etc. of the lowest identifiable taxon. One crustacean, *Pleuroncodes planipes*, accounted for 2.4% of the crustacean remains (Table 1). The parasitic nematode *Anisakis simplex* was found in 38% of the stomachs.

Cephalopods occurred in 354 (82.7%) of the stomachs and fish occurred in 270, or 63.1%, of the stomachs. However, the percent number of fish (66.6%) was higher than that for cephalopods (32.6%). Of the 56 species of fish identified, 27 belonged to the family Myctophidae (lanternfish). As a family, myctophids had the highest percent by number of all prey (49.7%) and accounted for 74.6% of all fish prey. Myctophids occurred in 40.2% of all stomachs (Table 1).

The cephalopod species identified belonged to two orders: 1) Teuthoidea (squids; 32 species) and 2) Octopoda (octopuses; 4 species). Squids from the family

Table 1

Number and frequency of occurrence for prey recovered from pantropical spotted dolphins, *Stenella attenuata*, (n=428) from the eastern tropical Pacific. "No." represents the total number of a species recovered from all stomachs and "Frequency of occurence" represents the number of stomachs in which that species was found.

	Number		Frequency of occurrence	
Prey	No.	%	No.	%
Class Osteichthyes	33,176	66.6	270	63.1
Order Myctophiformes				
Family Myctophidae	24,747	49.7	172	40.2
Symbolophorus spp.	4,052	8.1	151	35.3
Myctophum aurolaternatum	1,379	2.8	81	18.9
Myctophum nitidulum	182	0.4	11	2.6
Myctophum asperum	160	0.3	16	3.7
Myctophum spinosum	109	0.2	14	3.2
Myctophum spp.	43	<0.1	8	1.9
Lampanyctus parvicauda	6,834	13.7	130	30.4
Lampanyctus omostigma	900	1.8	31	7.2
Lampanyctus festivus	848	1.7	29	6.8
Lampanyctus idostigma	264	0.5	35	8.2
Lampadena luminosa	1,358	2.7	36	8.4
Lampadena sp.	7	<0.1	5	1.2
Diaphus splendidus	1,889	3.8	57	13.3
Daiphus mollis	175	0.4	32	7.5
Diaphus sp. 1 close to *chrysorhynchus*	125	0.3	25	5.8
Diaphus sp. 2 close to *effulgens*	13	<0.1	5	1.2
Diaphus sp. 3	1,533	3.1	62	14.5
Hygophum proximum	331	0.7	46	10.7
Hygophum reinhardtii	2	<0.1	2	0.5
Diogenichthys laternatum	372	0.7	55	12.9
Triphoturus mexicanus	195	0.4	25	5.8
Tarletonbeania crenularis	6	<0.1	3	0.7
Notoscopelus resplendens	23	<0.1	4	0.9
Ceratoscopelus warmingii	254	0.5	13	3.0
Taaningichthys spp.	276	0.6	14	3.2
Parvilux ingens	21	<0.1	8	1.9
Benthosema panamense	16	<0.1	1	0.2
Unidentified myctophids (worn)	3,380	6.8	145	33.8
Order Perciformes				
Family Nomeidae	3,053	6.1	108	25.2
Cubiceps pauciradiatus	2,961	5.9	101	23.6
Cubiceps baxteri	51	0.1	18	4.2
Cubiceps c.f. *paradoxus*	41	<0.1	8	1.9
Family Acropomatidae				
Howella sp.	81	0.2	5	1.2
Family Scombridae				
Auxis thazard	27	<0.1	11	2.5
Family Stromateidae				
Hyperglyphe sp.	6	<0.1	4	0.9
Order Beloniformes				
Family Exocoetidae	858	1.7	82	19.2
Exocoetus volitans	446	0.9	63	14.7
Exocoetus monocirrhus	58	0.1	17	4.0
Cheilopogon sp.	26	<0.1	13	3.0
Family Hemiramphidae				
Oxyporhamphus micropterus	328	0.7	40	9.3

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Table 1 (continued)

Prey	Number No.	Number %	Frequency of occurrence No.	Frequency of occurrence %
Order Gadiformes				
Family Bregmacerotidae				
Bregmaceros bathymaster	1,838	3.7	24	5.6
Order Aulopiformes				
Family Scopelarchidae	30	<0.1	12	2.8
Scopelarchus guentheri	24	<0.1	11	2.5
Benthalbella sp.	6	<0.1	2	0.5
Family Notosudidae				
Scopelosaurus c.f. *harryi*	56	0.1	6	1.4
Family Paralipididae				
Stemonosudis sp.	41	<0.1	14	3.2
Order Beryciformes				
Family Melamphaidae				
Scopelogadus bispinosus	906	1.8	19	4.4
Order Stomiiformes				
Family Phosichthydae	835	1.7	40	9.3
Vinciguerria lucetia	830	1.6	38	8.9
Ichthyococcus sp.	5	<0.1	4	0.9
Family Gonostomatidae				
Gonostomatid spp. close to *Diplophus proximus*	3	<0.1	2	0.5
Order Salmoniformes				
Family Microstomatidae				
Xenopthalmichthys sp.	9	<0.1	2	0.5
Unidentified species				
Unknown no. 1	5	<0.1	3	0.7
Unknown no. 2	20	<0.1	5	1.2
Unknown no. 3	41	<0.1	13	3.0
Unknown no. 4	47	<0.1	6	1.4
Unknown no. 5	9	<0.1	4	0.9
Unknown no. 6	2	<0.1	1	0.2
Unknown no. 7	2	<0.1	2	0.5
Unknown no. 8	1	<0.1	1	0.2
Unknown no. 9	7	<0.1	1	0.2
Unidentified otoliths (worn)	475	0.1	36	8.4
Class Cephalopoda	16,258	32.6	354	82.7
Order Teuthoidea	16,217	32.5	354	82.7
Family Ommastrephidae	4,594	9.2	280	65.2
Ommastrephes bartrami	2,040	4.1	212	49.5
Eucleoteuthis luminosa	713	1.4	174	40.7
Sthenoteuthis oualaniensis	499	1.0	117	27.3
Dosidicus gigas	384	0.7	109	25.5
Hyaloteuthis c.f. *pelagica*	310	0.6	35	8.2
Nototodarus c.f. *hawaiiensis*	7	<0.1	5	1.2
Ommastrephid sp. no. 1	7	<0.1	4	0.9
Ommastrephid sp. no. 2	512	1.0	71	16.6
Ommastrephid sp. no. 3	2	<0.1	2	0.5
Ommastrephid sp. no. 4	120	0.2	28	6.5
Family Onychoteuthidae	1,151	2.3	177	41.4
Onychoteuthis banksi	1,029	2.1	168	39.3
Onychoteuthis sp. no. 1	116	0.2	26	6.1
Onychoteuthis sp. no. 2	6	<0.1	3	0.7

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Enoploteuthidae (enope squids) accounted for most of the cephalopod prey by number (31.8%) and represented 10.5% of all prey (fish and squid) by number. The next most numerous squids belonged to the family Ommastrephidae (flying squids), which accounted for 28.2% of all cephalopod species by num-

Table 1 (continued)

Prey	Number No.	Number %	Frequency of occurrence No.	Frequency of occurrence %
Family Enoploteuthidae	5,175	10.4	235	54.9
Abraliopsis affinis	4,880	9.8	199	46.5
Ancistrocheirus lesueuri	183	0.4	78	18.2
Pterygioteuthis giardi	112	0.2	40	9.4
Family Mastigoteuthidae				
Mastigoteuthis dentata	1,163	2.3	188	43.9
Family Cranchiidae	2,057	4.1	214	50.0
Leachia dislocata	1,075	2.3	133	31.1
Megalocranchia sp.	628	1.3	87	20.3
Liocranchia reinhardti	354	0.7	81	18.9
Family Pholidoteuthidae				
Pholidoteuthis boschmai	225	0.5	57	13.3
Family Thysanoteuthidae				
Thysanoteuhtis rhombus	129	0.3	66	15.4
Family Octopoteuthidae	103	0.2	56	13.1
Octopoteuthis deletron	102	0.2	56	13.1
Octopoteuthis sp.	1	<0.1	1	0.2
Family Ctenopterygidae				
Ctenopteryx sicula	64	0.1	31	7.2
Family Grimalditeuthidae				
Grimalditeuthis bomplandi	8	<0.1	7	1.6
Family Architeuthidae				
Architeuthis sp.	3	<0.1	1	0.2
Family Histioteuthidae	3	<0.1	3	0.7
Histioteuthis dofleini	1	<0.1	1	0.2
Histioteuthis meleagroteuthis	2	<0.1	2	0.5
Unidentified squid species				
Unknown no. 1	1	<0.1	1	0.2
Unknown no. 2	7	<0.1	5	1.2
Unknown no. 3	1	<0.1	1	0.2
Unidentified upper beaks	1,533	3.1	183	42.8
Order Octopoda	37	<0.1	19	4.4
Family Argonautidae				
Argonauta sp. (Type A)	16	<0.1	14	3.3
Family Tremoctopodidae				
Tremoctopus violaceus	10	<0.1	5	1.2
Family Bolitaenidae				
Japatella heathi	8	<0.1	5	1.2
Family Alloposidae				
Alloposus mollis	3	<0.1	3	0.7
Unidentified octopus beaks	4	<0.1	4	0.9
Class Gastropoda	31	<0.1	10	2.3
Class Crustacea				
Order Decapoda	333	0.7	60	14.0
Family Galatheidae				
Pleuroncodes planipes	8	<0.1	7	1.6
Unidentified shrimp	26	<0.1	12	2.8
Order Isopoda	299	0.60	52	12.1
Total	49,798			

ber and represented 9.2% of all prey consumed. However, the family Ommastrephidae had the highest percent frequency of occurrence at 65.2%, followed by the family Enoploteuthidae at 54.9%. Octopus accounted for only 0.23% of cephalopod prey and occurred in 4.4% of the stomachs examined (Table 1).

Prey size

The beaks of 18 out of 32 squid species could be converted to mantle length and weight (Table 2). The average mantle length of squid was 75.8 mm (SE=0.54) and ranged in size from 2.4 to 321 mm. The largest species of squid, on average, was *Dosidicus gigas* at 181 mm (SE=2.9), and the smallest species of squid was *Pterygioteuthis giardi* (mean=22 mm, SE=0.41). The otoliths of only eight fish species could be converted to total length (TL) (Table 3). The average size fish consumed was 92.9 mm TL (SE=1.41) with a range of 34–260 mm TL. The largest species of fish, on average, was *A. thazard* (mean=211.5 mm TL, SE=8.08) and the smallest was *Ceratoscopelus warmingii* (mean=49.3 mm TL, SE=0.45).

We found that the size of fish and squid consumed increased significantly with dolphin length (Fig. 2; fish: r^2=0.648, P<0.001; squid: r^2=0.791, P<0.0001). We also found that the number of prey consumed was negatively correlated with the size of prey (squid: r^2= –0.555, P<0.001; fish: r^2=–0.624, P<0.003). If a prey species was small, more were consumed by the dolphins.

Geographic and seasonal variability

To test the hypotheses of variability in prey composition between areas and seasons, 10 species that accounted for 55% of the sample by number were selected for the analyses (Table 1). These included five species of fish: *Symbolophorus* spp., *Myctophum aurolaternatum*, *Lampanyctus parvicauda*, *Diaphus splendidus*, *Cubiceps pauciradiatus*, and five species of squid: *Ommastrephes bartrami*, *Onychoteuthis banksii*, *Abraliopsis affinis*, *Mastigoteuthis dentata*, and *Leachia dislocata*. A significant difference was found in the prey composition by area and season (χ^2=13,373, df=45, P<0.0001).

Fish were the dominant prey species of *S. attenuata* in the winter: *L. parvicauda* was found in the highest numbers in the northeast, *M. aurolaternatum* in the south, and *Symbolophorus* spp. in the west. Squid were the dominant prey species in the summer; *A. affinis* was found in highest numbers in both the northeast and west, and *O. bartrami* in the south (Fig. 3).

Table 2

Mean, standard deviation, and range of mantle length and weight of cephalopod species consumed by spotted dolphin, calculated with regression equations (Clarke, 1986a; Wolff[4]). 'Number' represents the total number of cephalopod beaks that were measurable, without being broken or worn.

		Estimated prey length		Estimated prey weight (g)			
Species of prey	Number	Mean ±SD	Range	Mean ±SD	Range	Total	% weight
Cephalopods							
Ommastrephes bartrami	1,158	129.2 ±35.3	69.7–273.5	63.9 ±69.6	2.3–463.0	74,048	31.90
Eucleoteuthis luminosa	475	112.7 ±33.9	51.6–219.4	40.4 ±38.5	2.5–226.9	19,186	8.30
Sthenoteuthis oualaniensis	287	144.2 ±42.1	73.4–320.9	136.5 ±147.1	11.8–1,248.2	39,165	16.90
Dosidicus gigas	207	180.8 ±43.1	99.2–319.4	177.9 ±134.3	15.7–853.2	36,822	15.90
Hyaloteuthis pelagica	141	75.3 ±12.7	50.6–117.9	11.9 ±5.3	3.7–34.0	1,688	0.70
Nototodarus hawaiiensis	5	70.8 ±9.9	65.0–87.9	16.3 ±9.9	10.9–33.6	82	0.03
Onychoteuthis banksii	646	74.3 ±20.0	8.6–139.9	14.9 ±11.3	0.2–77.3	9,676	4.20
Abraliopsis affinis	3,671	30.0 ±4.9	18.7–45.4	2.3 ±1.2	0.4–7.0	8,424	3.60
Ancistrocheirus lesueuri	139	46.9 ±29.6	8.8–203.1	21.9 ±50.7	0.3–484.7	3,043	1.30
Pterygioteuthis giardi	65	21.8 ±3.4	16.4–31.7	0.7 ±0.4	0.2–2.5	50	0.02
Mastigoteuthis dentata	870	69.1 ±14.2	20.6–132.4	17.4 ±10.7	0.6–98.3	15,166	6.50
Leachia dislocata	628	127.9 ±33.4	49.6–248.1	12.4 ±7.6	0.8–52.3	7,782	3.40
Liocranchia reinhardti	238	125.4 ±34.4	42.2–199.6	18.3 ±10.6	1.2–48.0	4,363	1.90
Megalocranchia sp.	479	109.1 ±54.2	2.4–253.9	15.4 ±12.2	0.4–63.8	7,296	3.10
Pholidoteuthis boschmai	150	97.3 ±25.5	42.9–181.9	26.5 ±23.0	1.3–149.2	3,978	1.70
Octopoteuthis deletron	63	45.6 ±23.5	10.3–130.2	15.8 ±20.2	0.4–125.4	996	0.40
Ctenopteryx sicula	39	34.7 ±6.3	21.7–51.6	3.9 ±2.5	0.5–12.5	153	0.06
Architeuthis sp.	2	62.9 ±25.8	44.7–81.2	4.8 ±4.2	1.9–7.7	10	<0.01

Table 3

Mean, standard deviation, and range of fish length (total length) and weight of fish species consumed by spotted dolphin, calculated with regression equations (see Footnote 2 in the main text) and ratios of otolith length to fish length (Butler, 1979; Hecht, 1987). 'Number' represents the total number of otoliths that were measurable, without being broken or worn. For *A. thazard*, '8' represents the number of fish measured.

		Estimated prey length		Estimated weight (g)		
Prey species	No.	Mean ±SD	Range	Mean ±SD	Range	Total
Fish						
Symbolophorus spp.	273	66.6 ±7.0	40.9–82.4	4.1 ±1.3	0.8–7.9	1,105
Myctophum nitidulum	14	56.4 ±5.2	46.7–63.1			
Ceratoscopelus warmingii	114	49.3 ±4.8	33.8–61.5			
Exocoetus volitans	68	158.7 ±22.2	90.9–187.4			
Exocoetus monocirrhus	19	164.7 ±16.8	136.9–193.7	50.9 ±8.3	37.2–65.2	967
Oxyporhamphus micropterus	40	143.4 ±15.1	122.2–180.1			
Cubiceps pauciradiatus	233	109.1 ±9.8	74.6–129.8			
Cubiceps baxteri	3	140.9 ±4.9	136.1–145.8			
Auxis thazard	8	211.5 ±22.9	190.0–260.0			

Stomach fullness index (SFI)

The SFI ranged from 0.4% to 86.4% (average: 29.4%) after all measures were scaled to the maximum SFI. A statistically significant difference was found in the SFI between quarters of the day (χ^2=112.99, df=6, P<0.0001). A SFI >60% was calculated for 42.0% of the animals collected between 0600 and 0900 h, whereas only 1.0% of the sample collected between 1501 and 1800 h had a SFI >60% (Fig. 4).

Reproductive condition

The mean number of squid differed significantly between pregnant and lactating females (Student's t-test=–2.65, P=0.010); however, no significant difference was found in the mean number of fish consumed (Student's t-test=0.25, P=0.803). When stratified by time-of-day, the mean SFI was significantly higher for lactating dolphins during all time periods (χ^2=46.98, df=6, P<0.0001; Table 4).

Table 4

The average stomach fullness (%) for lactating and pregnant spotted dolphins throughout the day. The day is divided into three hour increments from 0600 h to 1800 h. 'No.' is equal to the number of stomachs in each time category.

	Average stomach fullness			
	Lactating		Pregnant	
Time (h)	%	No.	%	No.
0600–0900	52.7	15	38.6	6
0901–1200	37.3	18	23.1	10
1201–1500	27.2	15	15.2	7
1501–1800	26.1	9	10.9	14
Overall average	44.3	57	19.5	37

Discussion

Mesopelagic prey were found to dominate the diet of pantropical spotted dolphins; myctophid fish, and enoploteuthid and ommastrephid squid accounted for 69% of all prey consumed (Table 1). These mesopelagic species are associated with the deep scattering layer and most undergo diel vertical migration, moving into the upper 200 m at dusk to feed and retreating to depth at dawn to avoid predation (Gibbs and Roper, 1971; Clarke, 1973, 1978; Wisner, 1974; Roper and Young, 1975; Roper et al., 1984; Smith and Heemstra, 1986). The SFI, which we found to be highest in the morning hours (i.e. 0600–0900 h, Fig. 4), suggests that pantropical spotted dolphins feed during the night when these prey are nearest to the surface. In fact, Shomura and Hida (1965) hypothesized that the spotted dolphin caught off Hawaii fed just before dawn, prior to descent of the deep scattering layer, because fresh mesopelagic prey were found in its stomach (enoploteuthid squid and myctophid fishes). Evidence of nighttime feeding by pantropical spotted dolphins has also been presented by Scott (1991), who reported that the highest proportion of undigested prey was recovered from spotted dolphin stomachs collected between 0700 and 0930 h and that

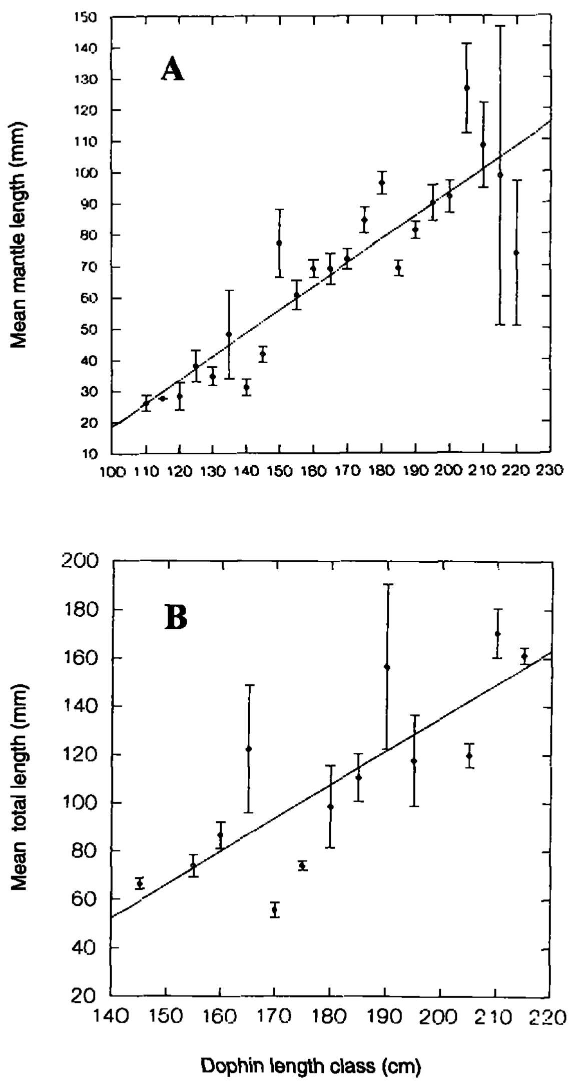

Figure 2

Mean estimated length of squid (**A**) and fish (**B**) with 2 SE shown for each 5 cm dolphin length class. Significant differences were found in the size of prey consumed with increasing dolphin length for both squid (r^2=0.791, P<0.0001) and fish (r^2=0.648, P<0.001).

no fresh prey was recovered from stomachs collected after 1200 h. More recently, the collection of data on dive patterns has provided additional evidence of nighttime feeding by spotted dolphins. The dive patterns show marked diurnal changes and both deeper and longer dives at night. In particular, the dawn–dusk diving patterns suggest that dolphins were following the ascent and descent of the deep scattering layer (Scott et al.[7]).

The capture of prey by dolphins in the deep scattering layer may be facilitated by abundance of prey, schooling size of prey, and bioluminescence of prey (Clarke, 1973; Crawford, 1981; Clarke, 1986b). The top three prey families in our study (Myctophidae, Enoploteuthidae, Ommastrephidae) are all abundant in the ETP and have bioluminescent organs (Clarke, 1973, 1978; Wisner, 1974; Okutani, 1974; Clarke, 1977; Crawford, 1981; Roper et al., 1984; Harman and Young, 1985; Clarke, 1986b). Myctophids, which accounted for 49.7% of all prey recovered in our sample, are the most abundant deep scattering layer species, representing 25% of the biomass of all mesopelagic fishes (Karnella, 1987). Myctophids are small in size, school in large numbers, and have bioluminescent organs, all characteristics that might facilitate detection by dolphins (Crawford, 1981).

Prey size

There does appear to be some selectivity of prey by size because larger dolphins tend to eat larger prey (Fig. 2). Our results support the supposition that because most dolphins have been observed to consume their prey whole, the size of prey ingested is limited by the size that can be swallowed (Fiscus and Kajimura, 1981; Fiscus and Jones, 1990; Wolff[4]). The size of prey in our study indicated that prey consumed by juveniles through adults ranged from 2.4 to 320.9 mm (Okutani, 1974, Butler, 1979; Uchida, 1981; Roper et al., 1984; Clarke, 1986a; Smith and Heemstra, 1986; Karnella, 1987; Murata and Hayase, 1993; Welch and Morris, 1993). Most of our size ranges corresponded with those reported by Wolff,[4] who examined the squid prey of spotted dolphins from the Perrin et al. (1973) study, except for *A. affinis*, which had a narrower size range in our study, and *O. banksii*, which encompassed a broader size range. Wolff[4] also showed an increase in the size of squid consumed by spotted dolphins; there was a 30-mm mantle length increase for squid found in dolphins from 140 to 205 cm in length. He also found that a broader size range of squid was consumed for larger dolphins, which was also the case in our study.

Geographic and seasonal variability

The composition of prey species consumed by pantropical spotted dolphins changed both temporally and spatially (Fig. 3), suggesting that they are opportunistic feeders, as is the case with many other

[7] Scott, M. D., S. J. Chivers, H. Rhinehart, M. Garcia, R. Lindsey, R. L. Olson, W. Armstrong, and D. A. Bratten. 1997. Movements and diving behavior of pelagic spotted dolphins. Inter-Am. Tropical Tuna Comm., c/o Scripps Institution of Oceanography, Univ. Calif., San Diego, CA 92037.

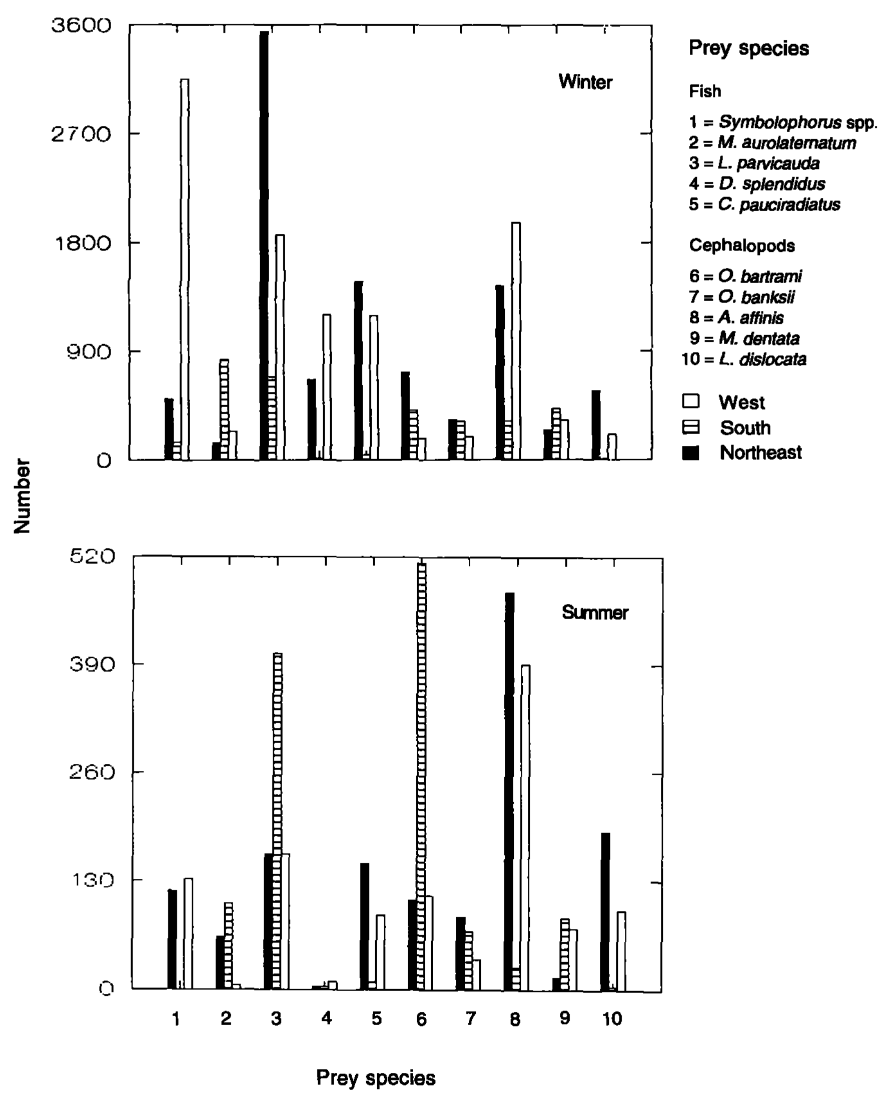

Figure 3

The percent number of the 10 most numerous prey species by season: winter and summer, and geographic area: northeast (n=159), south (n=72), and west (n=198). See text for full name of the species listed.

dolphin species (Brown and Norris, 1956; Ross, 1979; Jones, 1981; Fiscus, 1982; Gaskin, 1982; Leatherwood et al., 1983; Evans, 1987; Young and Cockcroft, 1995). Geographic and seasonal changes in prey composition could be a result of migration of prey into or out of an area, prey spawning seasons, or simply distributional boundaries of prey. It has been suggested that the movements of dolphin may correspond to the movement or availability of prey (Jones, 1981; Reilly, 1990; Young and Cockcroft, 1994). There is evidence that the distribution of pantropical spotted dolphin shifts westward along the 10°N latitude as the summer season progresses, and it has been hypothesized that this change in distribution is due to changes in prey distribution resulting from the equatorial currents (Au and Perryman, 1985; Reilly, 1990). Unfortunately, information on precise distributions and seasonal movements of identified prey species in the ETP is limited; therefore this hypothesis cannot be addressed properly (Clarke, 1973; Okutani, 1974; Wisner, 1974; Clarke, 1977; Roper et al., 1984; Clarke, 1986, a and b).

Reproductive condition

Changes in diet composition between lactating and pregnant dolphins have been documented in a number of species (Perez and Mooney, 1986; Bernard and Hohn, 1989; Recchia and Read, 1989; Cockcroft and Ross, 1990; Young and Cockcroft, 1994, 1995). The physiological energy required to maintain lactation is quite high for mammals and may require a change in diet composition to include food with a higher caloric content (Clutton-Brock et al., 1982; Perez and Mooney, 1986; Recchia and Read, 1989; Iverson, 1993). In fact, Bernard and Hohn (1989) presented evidence for a shift in diet between pregnant and lactating pantropical spotted dolphins and suggested that it was due to the physiological demands of lactation. They found a higher proportion of flying fish (family Exocoetidae) in the diet of lactating females and a higher proportion of ommastrephid squid in the diet of pregnant females. We tested the same hypothesis for our sample, but our results were different. Although the proportion of fish (family Myctophidae) in the diet was higher than the proportion of squid (family Ommastrephidae) for both pregnant and lactating females, the proportion of squid was significantly higher in the diet of lactating females. Fish may provide most of the caloric intake for both lactating and pregnant females because both lanternfish and flying fish have a high caloric and lipid content in comparison with squid (Childress and Nygaard, 1973; Sidwell et al.,

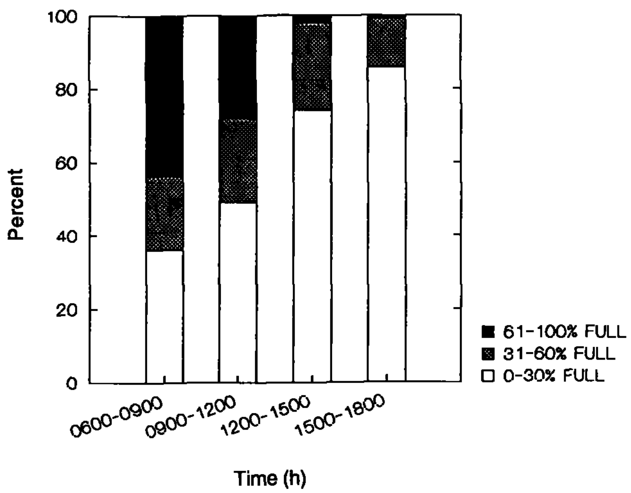

Figure 4
Percent of the sample in each of the stomach fullness categories: 0–30%, 31–60%, and 61–100% for spotted dolphins collected between 0600–1800 h: 0600–0900 h (n=106), 0901–1200 h (n=87), 1201–1500 h (n=134), and 1501–1800 h (n=101). The SFI was scaled to 100% by using the stomach of maximum fullness in the sample (see text for details).

1974; Sidwell, 1981; Croxall and Prince, 1982). A possible explanation for increased consumption of squid by lactating spotted dolphins is that milk production increases the demand for metabolic water (Croxall and Prince, 1982; Young and Cockcroft, 1994) and most squid have a higher water content than fish (Sidwell, 1981; Croxall and Prince, 1982). Cetacean milk has been estimated to be 40–60% water (Eichelberger et al., 1940; Gregory et al., 1955; Slijper, 1966; Best, 1982; Lockyer, 1984).

Rather than by a change in diet composition, the high metabolic demands of lactation could be met by increasing the amount of food consumed (Baldwin, 1978; Millar, 1979; Clutton-Brock et al., 1982; Yasui and Gaskin, 1986; Perez and Mooney, 1986; Kastelein et al., 1993). Estimates of food intake for lactating versus nonlactating females have been estimated to increase by 75–86% for lactating minke whales (*Balaenoptera acutorostrata*) and fin whales (*Balaenoptera physalus*) (Lockyer, 1978, 1981), by 500 g for lactating harbor porpoise (*Phocoena phocoena*) (Recchia and Read, 1989), and by 30% for captive Commerson's dolphins (*Cephalorhynchus commersoni*) (Kastelein et al., 1993). For spotted dolphins, Bernard and Hohn (1989) reported a SFI that was 24% higher for lactating females (Mann-Whitney, $0.05<P<0.10$). Similarly, we found that the SFI of lactating females was 16% higher than that for pregnant females and that a higher SFI was maintained by lactating females throughout the day (Table 4). This finding parallels those of Cockcroft and Ross (1990) in which they estimated that lactating bottlenose dolphins (*Tursiops truncatus*) would need to consume 3 or 4 stomachfuls of food per day to keep up with energetic demands, whereas males and resting females (not pregnant or lactating) had to consume only 2 stomachfuls to maintain their energetic requirements. Our results also suggest that lactating spotted dolphins may consume more food throughout the day to meet the higher energetic and nutritional demands of lactation.

Biases associated with analyses

As in every food-habit study, there are inherent biases associated with the analyses. Differential prey digestibility and secondary prey can bias all measures. The importance of small prey species can be overestimated by methods that determine both the percent number and the percent frequency of occurrence. Furthermore, infrequently consumed species may be overemphasized by the percent frequency-of-occurrence method (Hyslop, 1980; Bigg and Fawcett, 1985; Bigg and Perez, 1985).

Analysis of only hard parts can be biased through differential passage, retention, and degradation rates of beaks and otoliths (Hyslop, 1980; Bigg and Fawcett, 1985; Bigg and Perez, 1985; Pierce and Boyle, 1991). The importance of squid can be exaggerated by using only hard parts because beaks tend to get stuck in the stomach rugae and accumulate (Ross, 1979; Shroud et al., 1981; Clarke, 1986a). There are few data available on the passage and retention rates of various prey in cetaceans, although work on captive bottlenose dolphins (*Tursiops aduncus*) has indicated that fish otoliths were retained for up to 48 h and squid beaks for up to 72 h (Ross, 1979). Similarly, Clarke (1980) reported that sperm whales (*Physeter macrocephalus*) retained squid beaks for 36–60 h. The only way to avoid biases introduced by using hard parts is to use only fresh or whole prey recovered from stomachs. Although this method can tremendously limit the sample size and underestimate the importance of squid because squid flesh digests more quickly than fish flesh (Bigg and Fawcett, 1985).

Another source of bias may have affected the interpretation of our results. Ninety-six percent (96%) or 411 of the stomachs were recovered from net sets from which more than one stomach was collected. We tested whether multiple samples per set would bias our interpretation of important prey species by calculating the percent number for prey families,

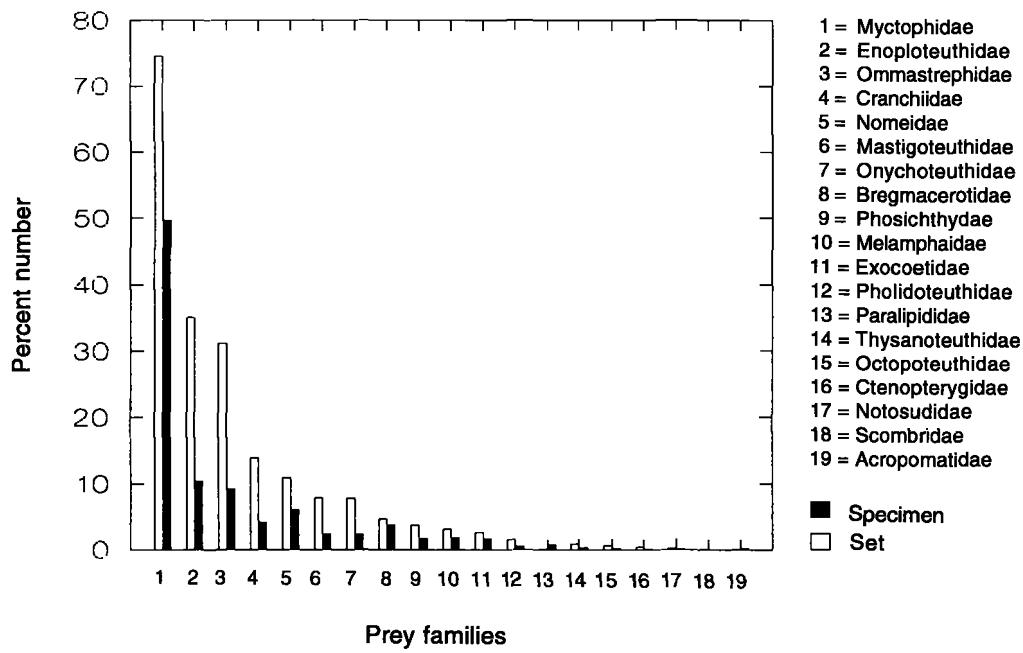

Figure 5

Percent number for each prey family calculated by using set as the sampling unit and each specimen as the sampling unit. Only those prey families with a percent number >0.100 are shown.

using each set as a sampling unit. The percent numbers, for set as the sampling unit and specimen as the sampling unit, were then compared by using a Mann-Whitney rank test, and no significant difference was found in the rank order of prey families between the set and specimen methods (Zar, 1984, p. 141–143; P=0.05, Fig. 5). Therefore, we conclude that for our data set, there was no bias introduced by using multiple specimens collected from the same set.

Summary

Based on the analysis and identification of fish otoliths and cephalopod beaks, our results provide evidence that pantropical spotted dolphins feed primarily at night on mesopelagic fish and squid. The dominant prey species belong to the families Myctophidae, Enoploteuthidae, and Ommastrephidae. Composition of the diet differed by season and area; thus pantropical spotted dolphins are likely opportunistic feeders. Prey included a wide range of sizes of both fish and squid, with the largest prey consumed by the largest dolphins, and the smallest prey consumed in the largest numbers. Furthermore, the diet of female dolphins differed by reproductive condition. Lactating females consumed more food and a higher proportion of squid than did pregnant females.

Acknowledgments

We would like to thank the biological technicians (NMFS, Southwest Region) who collected the stomachs for this study, F. G. Hochberg for assistance in identifying the cephalopod beaks (Santa Barbara Museum of Natural History), R. Lavenberg for the use of the otolith reference collection at the Los Angeles County Museum of Natural History, and R. Lindsey (Inter-American Tropical Tuna Commission [IATTC]) and R. Rassmussen (Southwest Fisheries Science Center [SWFSC]) for time-of-day data. We would also like to thank J. Carretta and R. Pitman (SWFSC) for their assistance with identifying myctophid and flying fish otoliths. We are grateful to M. Henshaw (SWFSC), W. F. Perrin (SWFSC), R. Olson (IATTC), M. Scott (IATTC), and two anonymous reviewers for their helpful comments and meticulous reviews of the manuscript.

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