Food habits and energy values of prey of striped marlin, *Tetrapturus audax*, off the coast of Mexico

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The waters off the tip of the Baja California peninsula are good fishing grounds for striped marlin, *Tetrapturus audax* (Squire and Suzuki, 1990) because they offer a shallow thermocline and an abundant food supply (Hanamoto, 1974). Although striped marlin are an important game fish, few biological studies have been done on them. Most trophic studies on marlin species have simply identified and determined the relative importance of food consumed in a given geographic region and were based on few samples (Morrow, 1952; Hubbs and Wisner, 1953; Yabuta, 1953; La Monte, 1955; de Sylva, 1962; Williams, 1967; Koga, 1968).

Only two studies have been done off the coast of Mexico in the Pacific Ocean. Evans and Wares (1972) described the stomach contents of striped marlin caught at three locations off southern California and Mexico (San Diego, Mazatlan, and Buenavista) from 1967 to 1969. They found in Buenavista, the site closest to our study area, that the food for marlin consisted mainly of squid and fish, particularly red-eye round herring (*Etrumeus teres*) and chub mackerel (*Scomber japonicus*). In the second study, Eldrige and Wares (1974) described food habits, seasonal abundance, and parasites of striped marlin caught in 1970 near the same locations. The differences found, in comparison with the first study were the absence of *S. japonicus* and a greater importance for three fish species: *E. teres*, black skipjack (*Euthynnus lineatus*), and oceanic puffer (*Lagocephalus lagocephalus*).

This paper provides information on food habits and energy content of the principal prey consumed by striped marlin in waters off the coast of the Baja California peninsula, Mexico.

Materials and methods

Striped marlin were caught by trolling with live chub mackerel, *S. japonicus*, and jacks, *Caranx* spp., as bait or by jigs used by the sport fishing fleet. All fish were collected at approximately 22° 53'N, 109°54'W (Fig. 1) near Cabo San Lucas, Baja California Sur (B.C.S.), Mexico. Stomachs were sampled in port, May 1988 to December 1989, by personnel of the Centro Interdisciplinario de Ciencias Marinas (CICIMAR), La Paz, B.C.S. Each fish was weighed to the nearest kg and its length (eye fork length) measured to the nearest cm. Stomach contents were removed and fixed in 10% formalin. Prey were identified to the lowest possible taxon. Vertebral characteristics (e.g. number, position) were used to identify fish with the help of taxonomic keys (Clothier, 1950; Monod, 1968; Miller and Jorgensen, 1973). The fish collection of CICIMAR was also used for comparison and validation of identifications. For complete, undigested fish, the keys of Jordan and Evermann (1896–1900), Meek and Hildebrand (1923–28), Miller and Lea (1972), and Thomson et al. (1979) were used for identification. Crustacean prey were identified from exoskeleton remains with keys provided by Garth and Stephenson (1966) and Brusca (1980). Cephalopods were identified from mandibles with the keys of Clarke (1962, 1986), Iverson and Pinkas (1971), and Wolff (1982, 1984).

The stomach contents were enumerated (N) and the volume (V) measured to the nearest mL. These two measures and frequency of occurrence (FO) were combined to calculate the index of relative importance (IRI) of Pinkas et al. (1971) as

$$IRI = (\%N + \%V)\ \%FO.$$

IRI is a commonly used measure that provides a more representative summary of dietary composition (Caillet et al., 1986).

A multivariate analysis of variance (MANOVA) was made on IRI values to examine differences in the relative importance of prey by season and between species. The treatment included only five seasons because the data in two seasons (summer and fall 1989) had too few values for statistical analysis (Table 1). The data were standardized following the formula

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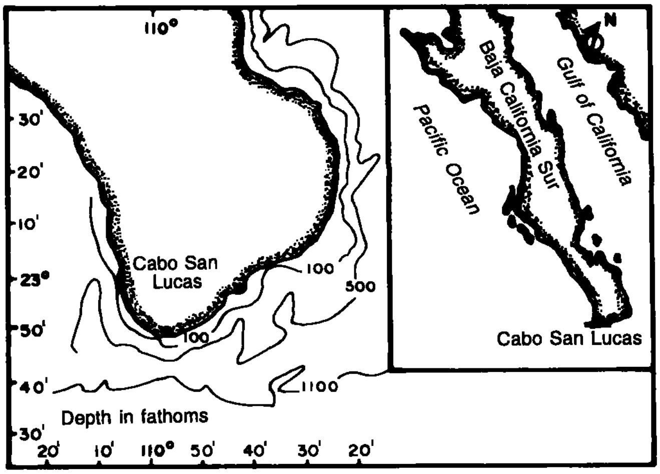

Figure 1

Map showing the location of the study area off the tip of Baja California.

$$x_i - X / SD,$$

where: x_i = the absolute IRI value of each prey species;
X = the mean value of the IRI; and
SD = standard deviation.

The caloric content of each prey, based on three samples obtained from stomach contents, was measured with a Parr 1241 adiabatic calorimeter and expressed as calories per gram of dry weight, wet weight, and ash-free dry weight following Phillipson (1964). One-way analysis of variance was used to evaluate differences between ash-free dry weight caloric values of particular prey. Also a post-hoc test *T*-method (Sokal and Rohlf, 1981) was used to compare the means of dry-weight caloric values.

The calories provided by each prey species were calculated by multiplying the values (calories/g wet weight) of each prey by the sum of their total contribution (weight) in the diet. To convert prey volumes to calories we assumed a density of 1.0 g/mL.

Results

Food habits

Striped marlin (403) were sampled. The mean postorbital length was 177 ± 15 cm (standard deviation) and the mean weight was 58.4 ± 12.8 kg. Of those specimens sampled, 27 (6.7%) had empty stomachs and 26 (6.5%) had regurgitated their stomach contents. A total of 33 prey taxa were identified that comprised fish, cephalopods, and crustaceans. Only 17 prey types could be identified to species (Table 2).

The most important prey by volume were fish (86.2%), including *S. japonicus* (25.7%), California pilchard, *Sardinops caeruleus,* (18.8%), and *E. teres* (10.2%). Cephalopods made up 12.8% of the total volume, and jumbo flying squid, *Dosidicus gigas*, was particularly important (11.3%). Crustaceans, mainly red crab, *Pleuroncodes planipes,* represented only 1% of the total volume.

A total of 2,679 organisms were enumerated, 68.6% of which were fish, 21.3% cephalopods, and 10.2% crustaceans. The dominant fish prey by number were *S. caeruleus* (18.9%), *S. japonicus* (14.3%), and Pacific hake, *Merluccius productus,* (9.6%). The cephalopod *D. gigas* represented 14.9%, and *Argonauta* spp. 3.0% of the total stomach contents by number. *Pleuroncodes planipes* was the most abundant crustacean, representing 7.2% of the total number of food items.

In frequency of occurrence, fish were the most important food in the diet of striped marlin (93.4%), particularly *S. japonicus* (45.4%), *S. caeruleus* (27.7%), and *E. teres* (12.6%). Cephalopods occurred in 32.9 % of the samples; and *D. gigas* was the most common species (28.3%). Crustaceans, mainly *P. planipes*, occurred in 6.3% of samples.

According to the IRI, fish were the most important prey (80.7%) of striped marlin, followed by cephalopods (18.5%), and crustaceans (0.8%). *Scomber japonicus*, *S. caeruleus*, and *D. gigas* were the most important fish prey (Fig. 2).

Relative importance of several prey varied seasonally (Table 1). During 1988, fish were the most important prey in spring and fall, cephalopods the most important prey in summer. In spring 1988, *S. caeruleus* was the most important fish in the diet, followed by *S. japonicus* and *E. teres*. In summer 1988, the most important species was *D. gigas*, followed by the fish *Selar crumenophtalmus*, *S. japonicus,* and *E. teres.* In fall 1988, the highest IRI values were for *S. japonicus, D. gigas, E. teres*, and *M. productus.*

During 1989, fish were the most important prey in all seasons, followed by cephalopods and crustaceans. In winter, the dominant species were *S. japonicus*, *M. productus*, and *S. caeruleus*. In spring, *S. japonicus*, *D. gigas*, *S. caeruleus*, and *E. teres* were the most important species. In summer, *Caranx caballus* was the most important prey. In fall, the highest IRI values were for *S. caeruleus, S. japonicus,* and *Decapterus hypodus.* The MANOVA showed no significant differences among seasons in the IRI values of food groups consumed (F=1.96; df=4; P=0.11). However, when we considered taxa consumed (33 recorded), we found significant differences (F=17.6; df= 32; P<0.005), probably caused by the greater

Table 1

Summary of food categories in stomach contents of striped marlin from Cabo San Lucas, B.C.S., Mexico, expressed as percentages based on frequency of occurrence (FO), number (*n*), volume (Vol.), and index of relative importance (IRI).

Prey	FO	% FO	*n*	% *n*	Vol.	% Vol.	IRI	% IRI
Mollusca								
Cephalopoda								
Teuthoidea								
Enoploteuthidae								
Abraliopsis affinis	12	3.43	46	1.72	1,254	0.65	8.13	0.19
Ommastrephidae								
Dosidicus gigas	99	28.3	399	14.9	21,866	11.3	740.37	17.8
Stenoteuthis oualaniensis	15	4.28	34	1.27	688	0.35	6.93	0.17
Octopoda								
Octopodidae								
Octopus spp.	4	1.14	11	0.41	131	0.07	0.55	0.01
Argonautidae								
Argonauta spp.	13	3.71	80	2.99	819	0.42	12.65	0.3
Total			570	21.29	24,758	12.79	768.63	18.47
Arthropoda								
Crustacea								
Amphipoda	2	0.57	22	0.82	13.5	0.01	0.47	0.01
Isopoda	3	0.86	8	0.3	3	0	0.26	0
Stomatopoda								
Squillidae								
Squilla spp.	1	0.28	1	0.04	15.1	0	0.01	0
Euphausiacea	3	0.86	48	1.79	11	0.05	1.55	0.04
Decapoda								
Galatheidae								
Pleuroncodes planipes	14	4	193	7.2	1,929	0.99	32.76	0.79
Total			272	10.15	1,971.6	1.05	35.05	0.84
Chordata								
Osteichthyes								
Clupeiformes								
Clupeidae	30	8.57	12	0.44	3,206	1.65	17.99	0.43
Etrumeus teres	44	12.57	199	7.42	19,681	10.16	220.98	5.31
Ophistonema libertate	10	2.86	27	1.01	4,985	2.57	10.24	0.25
Sardinops caeruleus	97	27.7	507	18.92	36,492	18.83	1,046.05	25.15
Gadiformes								
Merluccidae								
Merluccius productus	19	5.43	257	9.59	16,619	8.58	98.66	2.37
Cyprinodontiformes								
Belonidae								
Strongylura spp.	1	0.28	1	0.04	340	0.17	0.06	0
Syngnathiformes								
Fistulariidae								
Fistularia spp.	16	4.57	38	1.42	5,065	2.61	18.42	0.44
Scorpaeniformes								
Triglidae								
Prionotus spp.	1	0.28	1	0.04	10	0.01	0.01	0
Perciformes								
Serranidae	1	0.28	2	0.07	245	0.13	0.06	0
Carangidae	10	2.86	15	0.56	2,111	1.09	4.72	0.11
Caranx caballus	11	3.14	15	0.56	1,988.5	1.02	4.96	0.12
Caranx hippos	9	2.57	10	0.37	796	0.41	2	0.05
Decapterus hypodus	18	5.14	87	3.25	8,365	4.32	38.91	0.93
Selar crumenophthalmus	16	4.57	31	1.16	3,337	1.72	13.16	0.32
Coryphaenidae								

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Table 1 (continued)

Prey	FO	% FO	*n*	% n	Vol.	% Vol	IRI	% IRI
Coryphaena hippurus	1	0.28	1	0.04	180	0.09	0.04	0
Mugilidae								
Mugil spp.	1	0.28	1	0.04	290	0.15	0.05	0
Sphyraenidae								
Sphyraena ensis	1	0.28	2	0.07	680	0.35	0.12	0
Scombridae								
Auxis spp.	10	2.85	83	3.09	7,870.5	4.06	20.38	0.49
Scomber japonicus	159	45.43	382	14.26	49,778.5	25.69	1,814.93	43.63
Tetraodontiformes								
Balistidae								
Balistes polylepis	18	5.14	164	6.12	4,844.5	2.5	44.31	1.06
Xanthichthys mento	1	0.28	1	0.04	110	0.06	0.03	0
Diodontidae								
Diodon spp.	1	0.28	1	0.04	27	0.01	0.01	0
Total			1,837	68.55	167,021	86.18	3,356.09	80.66
Unidentified organic matter	1	0.28			145	0.07	0.02	0

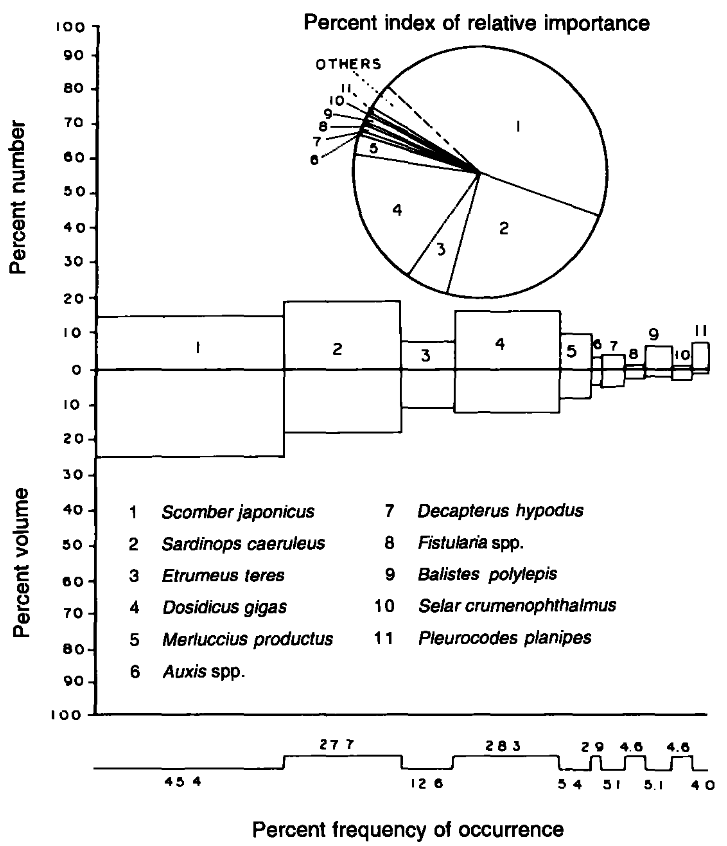

Figure 2

The major prey species found in the stomachs of striped marlin presented as percentages of number of individuals, volume, frequency of occurrence, and IRI.

number of five prey species: *D. gigas*, *S. japonicus*, *S. caeruleus*, *E. teres*, and *M. productus*.

Calorimetric analysis

The energy content of the most important prey of striped marlin as wet, dry, and ash-free dry weights, is given in Table 3. Values ranged from 3.42 kcal/g dry weight for red crab, *P. planipes*, to 6.14 kcal/g dry weight for the cornet fish, *Fistularia* spp. The ANOVA showed that the caloric values of the 11 most important prey were significantly different (F=904.3; df=10; P=2.3E-26). When the means of the caloric values were compared by T-method, a significant difference was obtained (α=0.05) (Fig. 3).

Caloric percentages of the 11 major prey types (Fig. 4), indicate two species, *S. japonicus* (32.4%) and *S. caeruleus* (21.2%), contributed 53.7% of the total calories to the diet of striped marlin.

Discussion

Food habits

Previous studies have shown that striped marlin mainly consume prey that school near the surface. Such prey are generally fish of the families Engraulidae (Hubbs and Wisner, 1953; de Sylva, 1962; Evans and Wares, 1972; Holts and Bedford, 1990), Clupeidae (Hubbs and Wisner, 1953; Koga, 1968), Scombridae (Backer, 1966; Evans and Wares, 1972), Scomberesocidae (Morrow, 1952; Hubbs and Wisner, 1953), and Carangidae (de Sylva, 1962; Backer, 1966; Evans and Wares, 1972), and some cephalopods (Morrow, 1952; Yabuta, 1953; La Monte, 1955; de Sylva, 1962; Williams, 1967; Eldrige and Wares, 1974).

We also found that striped marlin feed on demersal species, such as *M. productus* and searobins, *Prionotus* spp, as well as on benthic species, such as mantis shrimp, *Squilla* spp. Other authors have found occasional prey from benthic or reef habitats in striped marlin (Morrow, 1952; Backer, 1966; Williams, 1967; Evans and Wares, 1972; Eldrige and Wares, 1974); thus, it appears that striped marlin move to the bottom to prey on benthic organisms.

Our results show the importance of seasonal prey availability off Cabo San Lucas. During spring 1988, *S. caeruleus* was the main prey of striped marlin, whereas in fall and winter, *S. japonicus* was more important. The latter is probably more abundant in

Table 2

Seasonal absolute values of the index of relative importance (IRI) of the stomach contents of striped marlin from Cabo San Lucas, B.C.S., Mexico (WI = Winter, SP = Spring, SU = Summer, FA = Fall).

Species	1988 SP $n = 55$	1988 SU $n = 34$	1988 FA $n = 92$	1989 WI $n = 56$	1989 SP $n = 67$	1989 SU $n = 11$	1989 FA $n = 35$
Cephalopoda							
Abraliopsis affinis	0	0	6.13	160.62	0.82	0	0
Dosidicus gigas	21.08	2,637.22	480.66	59.48	1,031.04	0	672.83
Stenoteuthis oualaniensis	12.21	8.58	24.28	0.97	1.79	0	0
Octopus spp.	1	1.99	0.31	0	2.49	0	0
Argonauta spp.	4.14	42.34	38.08	2.04	0	0	0
Crustacea							
Amphipoda	0	0	0	0	0	0	33.57
Isopoda	0	0	1.05	0	0	0	0
Squilla spp.	0	0	0	0	0.45	0	0
Euphausiacea	10.32	21.49	0	0	3.04	0	0
Pleuroncodes planipes	22.56	3.09	104.10	16.99	13.50	628.17	0
Osteichthyes							
Clupeidae	49.08	27.96	9.59	18.31	33.27	0	0
Etrumeus teres	368.43	346.57	357.95	67.47	369.22	0	51.76
Sardinops caeruleus	8,049.39	30.58	102.05	473.74	739.77	644.94	2,072.04
Opisthonema libertate	0	0	0	0	295.76	0	0
Merluccius productus	0	0	203.19	855.85	49.07	0	0
Strongylura spp.	0	0	0	2.27	0	0	0
Fistularia spp.	0	0	83.03	40.63	0	0	51.76
Prionotus spp.	0	0	0	0.50	0	0	0
Serranidae	0	0	0.81	0	0	0	0
Carangidae	0	74.97	1.97	27.56	1.55	0	0
Caranx caballus	25.30	27.81	4.17	0	0	780.10	0
Caranx hippos	4.48	0	0.59	2.86	0	0	19.88
Decapterus hypodus	54.50	58.56	1.62	0	0	0	1,036.23
Selar crumenophthalmus	1.60	446.19	28.31	2.17	0	0	0
Coryphaena hippurus	0	0	0	1.41	0	0	0
Mugil spp.	1.87	0	0	0	0	0	0
Sphyraena ensis	0	0	0	0	0	586.04	0
Auxis spp.	2.69	8.76	131.51	22.63	0	0	0
Scomber japonicus	1,299.15	351.06	1,957.42	4,324.37	2,117.20	0	1,073.73
Balistes polylepis	0	0	115.06	0	0	0	864.20
Xanthichthys mento	0	0	0.37	0	0	0	0
Diodon spp.	0	2.09	0	0	0	0	0
Unidentified organic matter	0	0	0.07	0	0.03	0	0

the area, as happens in waters off southern California where fall and winter catches present large numbers of chub mackerel (Roedel, 1952). Both *S. japonicus* and *S. caeruleus* were found in some stomachs, but this finding is not surprising because *S. japonicus* is abundant off Baja California and in the Gulf of California (MacCall, 1973), where mixed populations of *S. japonicus* and *S. caeruleus* are often found (Kramer, 1969). During summer, the greater numbers of the jumbo squid *D. gigas* in striped marlin stomachs are not surprising because this squid is very common in waters from 200 to 2,000 m in depth off Cabo San Lucas (Sato, 1976). This species, from subtropical and tropical waters, undergoes long, large seasonal migrations. The presence of *D. gigas* can be associated with tropical water masses at the entrance of the Gulf of California (25° to 29°C) and with the occurrence of prey species (pilchards and mackerels) in this area (Erhardt et al., 1986).

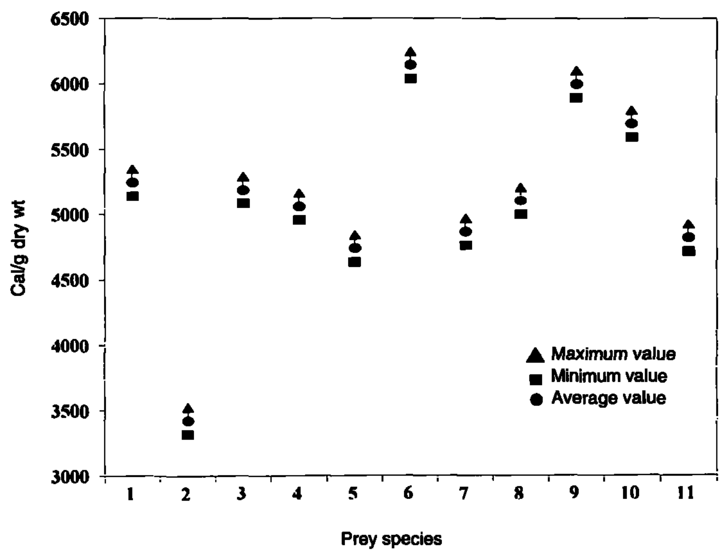

Figure 3

Comparison of group caloric values (cal/g dry wt) of dominant prey: 1 = *D. gigas*, 2 = *P. planipes*, 3 = *E. teres*, 4 = *S. caeruleus*, 5 = *M. productus*, 6 = *Fistularia* sp., 7 = *D. hypodus*, 8 = *S. crumenophtalmus*, 9 = *Auxis* spp., 10 = *S. japonicus*, and 11 = *B. polylepis*.

Our results, compared with those of studies in other areas, showed similar types of prey consumed by striped marlin. Previous studies found that striped marlin commonly feed on clupeids, scombrids, jacks, and cephalopods. Striped marlin in New Zealand ate saury and squid (Morrow, 1952). Baker (1966), in the same area, found that jacks and cephalopods were the main prey. In Peru and Chile, La Monte (1955) and de Sylva (1962) found cephalopods, engraulids, and jacks in the stomach contents of striped marlin. In East Africa, Williams (1967) found cornet fish (*Fistularia* sp.), bullet mackerel (*Auxis thazard*), and unidentified squid. Fish of the families Alepisauridae and Clupeidae are common in the Tasman Sea (Koga, 1968). Around the Bonin Islands, striped marlin ate *Gempylus* sp., *Pseudoscopelus* sp., *Alepisaurus* sp., *Ostracion* sp., cephalopods, and crustaceans (Yabuta, 1953). In the eastern Pacific Ocean, Hubbs and Wisner (1953) found that striped marlin consumed saury, anchovy, and sardine. Evans and Wares (1972) and Eldrige and Wares (1974) found that the most important prey of striped marlin off Buenavista, Mexico, included the fish *E. teres, Euthynnus lineatus, Lagocephalus lagocephalus*, and *S. japonicus*, as well as the squid *D. gigas*. These findings are similar to those of our study, even though the relative importance of the main species differed; e.g. in our study *S. japonicus* and *S. caeruleus* were more important than *E. teres*, and squid were less important. These results indicate that the prey composition of striped marlin probably has not changed drastically off the coast of

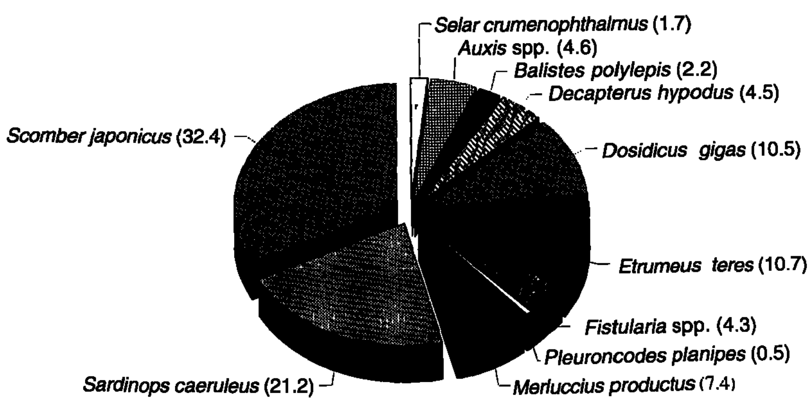

Figure 4

Caloric contribution (expressed as a percent) of the eleven dominant prey types of striped marlin.

Table 3

Mean and standard deviation (SD) caloric values, water content, and ash content of prey in the diet of striped marlin.

Prey	% Water	SD	% Ash	SD	Kcal/g wet wt	SD	Kcal/g dry wt	SD	Kcal/g ash-free dry wt	SD
Cephalopoda										
Dosidicus gigas	70.02	0.97	2.95	0.04	1.57	0.08	5.24	1.20	5.40	0.13
Crustacea										
Pleuroncodes planipes	72.66	0.05	4.67	0.03	0.94	0.01	3.42	0.11	3.59	0.01
Osteichthyes										
Etrumeus teres	64.34	1.10	3.78	0.04	1.80	0.05	5.06	0.03	5.26	0.01
Sardinops caeruleus	65.92	0.38	2.71	0.01	1.77	0.02	5.19	0.09	5.33	0.01
Merluccius productus	68.92	1.01	5.60	0.01	1.47	0.06	4.74	0.57	5.02	0.06
Fistularia spp.	64.44	0.72	13.05	0.07	2.18	0.04	6.14	0.11	7.06	0.01
Decapterus hypodus	64.95	0.34	6.09	0.03	1.79	0.01	5.11	0.12	5.44	0.01
Selar crumenophthalmus	68.64	0.60	7.00	0.01	1.53	0.03	4.87	0.02	5.24	0.00
Auxis spp.	66.31	0.83	1.53	0.03	1.92	0.05	5.69	0.28	5.78	0.03
Scomber japonicus	63.90	0.10	3.16	0.03	2.16	0.01	5.99	0.01	6.19	0.00
Balistes polylepis	69.38	0.54	2.83	0.15	1.48	0.02	4.83	0.14	4.97	0.01

Mexico in the last two decades. Cabo San Lucas appears to be an area with stable prey populations, probably the result of prevailing oceanographic conditions (Roden and Groves, 1959; Alvarez, 1983).

In waters off Baja California, the thermocline is generally shallow and there is a correspondingly high standing crop of zooplankton (Brandhorst, 1958). Laevastu and Rosa (1963) suggested that the shallow thermocline promotes a high standing crop of zooplankton and thus increases the production of small foraging organisms, which in turn may result in the aggregation of top predators. It is likely that the seasonal shifts in good fishing areas for striped marlin coincide with shallow thermocline areas. Feeding ecology, however, may play a major role in determining the distribution and abundance of striped marlin in some areas.

Calorimetric analysis

Of the eleven most important prey analyzed, *P. planipes* had a significantly low caloric content, common in crustaceans (Golley, 1961; Slobodkin and Richman, 1961; Thayer et al., 1973). Paine (1964) concluded that the presence of calcium carbonate and calcium phosphate in cuticle and valves was the cause of their low caloric value.

We found our results agree well with values from other studies. Thayer et al. (1973) found a caloric value of 5.74 kcal/g dry weight and 1.05 kcal/g wet weight for the squid *Loligo brevis*. For crustaceans, caloric values ranged between 2.12 and 6.03 kcal/g dry weight (average value: 5.74 kcal/g dry weight, range: 0.80–1.48 kcal/g wet weight). They also found fish contained 4.39 to 6.0 kcal/g dry weight and 0.67 to 1.57 kcal/g wet weight. Cortes and Gruber (1990) estimated the energy content of prey of lemon shark, *Negaprion brevirostris*, and found caloric values of 4.81 kcal/g dry weight and 0.68 kcal/g wet weight for cephalopods, *Octopus* spp. Crustaceans of the genus *Callinectes* yielded 3.2 kcal/g dry weight and 1.04 kcal/g wet weight. For fish, Cortes and Gruber found values that ranged from 3.38 to 4.73 kcal/g dry weight and 0.96 to 1.86 kcal/g wet weight.

Our results show that pelagic fishes and cephalopods yielded more than 80% of the caloric content in the diet of striped marlin. However, if we take into account that more than 70% of the stomachs were less than full and that the predatory capacity of striped marlin allows them to consume large quantities of prey in a short time, as is the case with yellowfin tuna, *Thunnus albacares* (Olson and Boggs, 1986), a pelagic species with feeding habits similar to those of marlin in the eastern Pacific Ocean, we believe the estimated caloric values underestimated actual energy intake.

In summary, we consider that striped marlin is a generalist as a predator and has a high predatory capacity, foraging mainly on schools of epipelagic organisms in neritic and oceanic zones.

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