

Abstract—An ecosystem approach to fisheries management requires an understanding of the impact of predatory fishes on the underlying prey resources. Defining trophic connections and measuring rates of food consumption by apex predators lays the groundwork for gaining insight into the role of predators and commercial fisheries in influencing food web structure and ecosystem dynamics. We analyzed the stomach contents of 545 common dolphinfish (*Coryphaena hippurus*) sampled from 74 sets of tuna purse-seine vessels fishing in the eastern Pacific Ocean (EPO) over a 22-month period. Stomach fullness of these dolphinfish and digestion state of the prey indicated that diel feeding periodicity varied by area and may be related to the digestibility and energy content of the prey. Common dolphinfish in the EPO appear to feed at night, as well as during the daytime. We analyzed prey importance by weight, numbers, and frequency of occurrence for five regions of the EPO. Prey importance varied by area. Flyingfishes, epipelagic cephalopods, tetraodontiform fishes, several mesopelagic fishes, *Auxis* spp., and gempylid fishes predominated in the diet. Ratios of prey length to predator length ranged from 0.014 to 0.720. Consumption-rate estimates averaged 5.6% of body weight per day. Stratified by sex, area, and length class, daily rations ranged up to 9.6% for large males and up to 19.8% for small dolphinfish in the east area (0–15°N, 111°W–coastline). Because common dolphinfish exert substantial predation pressure on several important prey groups, we concluded that their feeding ecology provides important clues to the pelagic food web and ecosystem structure in the EPO.

Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean

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Dolphinfishes (*Coryphaena hippurus* and *C. equiselis*) are abundant, wide-ranging, epipelagic predators in tropical and subtropical oceans (Palko et al., 1982). They support important commercial, artisanal, and recreational fisheries in several regions (Beardsley, 1967; Oxenford and Hunte, 1986; Patterson and Martinez, 1991; Campos et al., 1993; Norton and Crooke, 1994; Lasso and Zapata, 1999). Dolphinfishes are also a large component of the bycatches of the tuna purse-seine and longline fisheries in the Pacific Ocean (Lawson, 1997; IATTC, 1999). They are commonly found near natural and artificial floating objects (Kojima, 1956; Hunter and Mitchell, 1966; Gooding and Magnuson, 1967; Wickham et al., 1973), a trait which facilitates their capture.

Calls have been issued for developing an ecological approach to fisheries management, taking greater note of species interactions and underlying ecosystem dynamics (FAO, 1995; Larkin, 1996; Mangel et al., 1996; Botsford et al., 1997). Removal of predator biomass by commercial fishing represents a “top-down” disturbance of the system. Selective exploitation of apex predators can have profound effects on pelagic ecosystems because of the removal of predation pressure (Essington et al., in press) and because of top-down, trophic-cascade effects (Shiomoto et al., 1997; Estes et al., 1998; Verheye and Richardson, 1998). An understanding of how top-down processes influence the dy-

namics of marine communities derives from a basic understanding of the trophic connections and rates of food consumption of the predators. Although four studies have provided limited data on the food habits of dolphinfishes in coastal areas of the eastern Pacific Ocean (EPO) (Hida, 1973; Campos et al., 1993; Aguilar-Palomino et al., 1998; Lasso and Zapata, 1999), little is known of the predation dynamics of dolphinfishes over the majority of their oceanic habitat.

Common dolphinfish (*C. hippurus*) are renowned for their rapid rates of growth and metabolism. In Hawaiian waters, common dolphinfish have attained average lengths of 120 cm and weights of 12.5 kg at 12 months of age (Uchiyama et al., 1986). Standard metabolic rates of common dolphinfish are comparable to those of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas (Benetti et al., 1995). All three species have large surface areas and thin blood-water interfaces in their gills, morphological features that permit high oxygen diffusion capacity and elevated metabolic rates (Brill, 1996). High energy requirements imply that predators like dolphinfish can account for important amounts of tertiary production removed from an ecosystem (Essington et al., in press), but rates of food consumption by dolphinfish in nature have not been measured.

The objectives of our study were to define the trophic relations of the com-

mon dolphinfish, and their prey in both coastal and oceanic areas of the EPO and to provide preliminary estimates of their daily rates of food consumption.

Materials and methods

The dolphinfish were caught by tuna purse-seine vessels of Colombian, Mexican, Panamanian, and Venezuelan registry from December 1992 through September 1994. The fish were caught as bycatch of the purse-seine fishery for tunas associated with dolphins, with floating objects, and as unassociated schools ("schoolfish"). In dolphin sets, the net is deployed around aggregations of primarily yellowfin tuna and spotted or spinner dolphins (*Stenella attenuata* or *S. longirostris*) (or both dolphin species) after a high-speed chase by speedboats. Floating-object sets are made by encircling flotsam, commonly tree parts and artificial fish-aggregating devices (FADs), and associated fauna with the purse seine, usually in the early morning. Schoolfish are detected by seabird activity and disturbance of the water surface caused by the fish swimming just below. The species composition and size and age distribution of the fauna are distinctly different for the three aggregation types and fishing strategies (Hall, 1998).

Stomach samples

Common dolphinfish stomach samples were taken at sea by observers of the Inter-American Tropical Tuna Commission (IATTC). The purse-seine sets yielding the dolphinfish samples were distributed across the geographical range of the EPO tuna fishery at that time (Fig. 1). We obtained samples from 74 purse-seine sets over a 22-month period: 61 sets (82%) were made on floating objects; 4 sets were made on dolphins; and 9 sets were made on unassociated tuna. On board the vessels, the observers measured the fork length (mm) of each dolphinfish, determined the sex if possible, and excised and immediately froze the stomachs. In the laboratory, we thawed the stomachs and visually estimated the stomach fullness as a percentage of the stomach capacity. Then, we identified the stomach contents to the lowest taxon possible, weighed them to the nearest gram, and enumerated them when individuals were recognizable. The counts of paired structures, such as cephalopod mandibles and fish otoliths, were divided by two to estimate numbers of prey. We categorized the digestion state of the prey: 1 = intact or nearly intact; 2 = soft parts partially digested; 3 = whole or nearly whole skeletons without flesh (or comparable state for nonfish taxa); and 4 = only hard parts remaining (primarily fish otoliths and cephalopod mandibles). We measured the length, or maximum dimension of individual prey to the nearest mm,

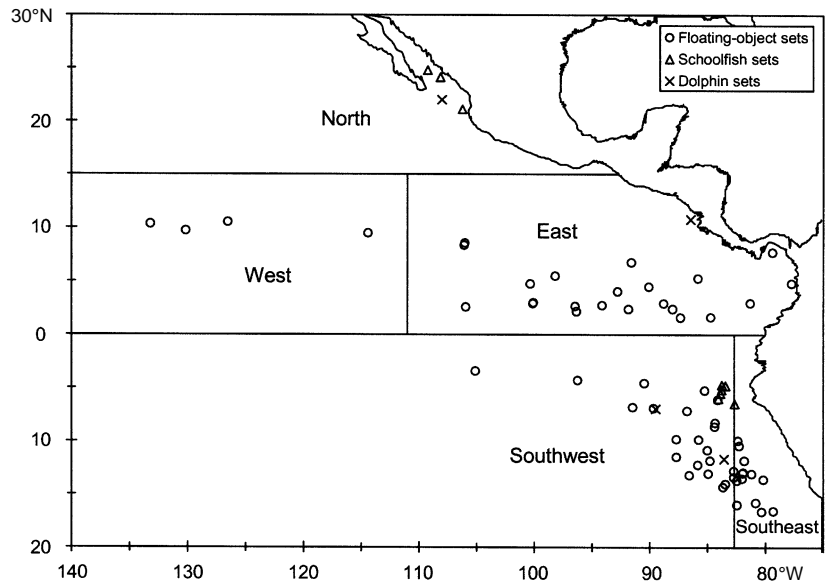


Figure 1

Locations where common dolphinfish samples were caught by three types of purse-seine sets. We stratified the data into the five areas shown.

if sufficiently intact. For cephalopods, we recorded the mantle length excluding tentacles.

Identifying the prey depended on the digestion state of the remains. We used the following keys to identify fish prey in digestion state 1: Jordan and Evermann (1896), Meek and Hildebrand (1923), Parin (1961), Miller and Lea (1972), Thomson et al. (1979), Allen and Robertson (1994), and Fischer et al. (1995b and 1995c). When the fishes were digested to state 2 or 3 we used taxonomic keys of vertebral characteristics (e.g. Clothier, 1950; Monod, 1968; Miller and Jorgenson, 1973) and compared skeletons of whole fishes collected in the EPO. We identified the crustacean prey from exoskeleton remains using the keys of Garth and Stephenson (1966), Brusca (1980), and Fischer et al. (1995a). We identified cephalopod prey from mandible remains (Clarke, 1962; Iverson and Pinkas, 1971; Wolff, 1982; Clarke, 1986). The fish collections at Scripps Institution of Oceanography and the Natural History Museum of Los Angeles County, and the cephalopod collection at the Santa Barbara Museum of Natural History were used to compare and validate prey identifications.

Data analysis

We analyzed the diet data by calculating three diet indices for each prey taxon. We calculated gravimetric importance of the prey (%W) as percentages of the total prey weights, numerical importance (%N) as percentages of total counts, and frequency of occurrence as the number of dolphinfish stomachs that contained a particular prey. We calculated percent occurrence (%O) as a percentage of all the dolphinfish sampled, regardless of whether their stomachs contained food. We present these three indices by prey taxon in detailed tables, summarized at several

levels of taxonomic resolution. To facilitate analysis, we also grouped the prey taxa by order (e.g. Tetraodontiformes), family (e.g. Carangidae), genus (e.g. *Auxis* spp.), or functional group (e.g. flyingfishes).

Because the three diet indices provide different insights into predation habits, we applied a graphical representation of these measures, proposed by Cortés (1997), to help interpret the data. We made three-dimensional scatter plots of %O, %W, and %N for all samples and for the data pooled by sampling area to help evaluate the degree of dominance of particular prey and the feeding strategy (generalized vs. specialized) of the dolphinfish. Although we measured the three components of the index of relative importance (IRI) (Pinkas et al., 1971), we did not calculate IRI values because the index is dependent upon the taxonomic resolution of the prey (Hansson, 1998). Also, for a predator that consumes a large size range of prey (see heading "Prey size," below), the IRI is overly influenced by numerous small prey.

We examined diel feeding characteristics by stratifying the data according to stomach fullness of the predator and digestion state of the prey. The scheme for grouping the data, patterned after Calliet (1976), is diagrammed in Figure 2. Prey in digestion states 1 and 2 were categorized as from "recent" feeding events, whereas prey in states 3 and 4 were categorized as from "previous" feedings. These two strata were further subdivided according to stomach fullness. Prey from stomachs $\leq 50\%$ full were categorized as "low" fullness or empty, whereas those from stomachs $>50\%$ full were categorized as "high" fullness (Fig. 2). We plotted the percent occurrence of the prey items in these four digestion and fullness strata by area and the time of day the sets were made: "early morning" (05:12–09:00), "late morning" (09:01–12:00), "early afternoon" (12:01–15:00), and "late afternoon" (15:01–18:16 hours).

We fitted regression trees (Breiman et al., 1984) to the gravimetric data for each prey group to detect statistically important differences by area and dolphinfish size. Regression trees are well suited for detecting and extracting important relations and complex interactions in multivariate ecological (De'ath and Fabricius, 2000) and fisheries data (Watters and Deriso, 2000). We used a two-step process. For both steps, the %W of each prey group in the stomach contents was the response variable. For the first step, defining area strata (see next paragraph), we used latitude and longitude as the predictor variables. For the second step, modeling the importance of area and dolphinfish size in explaining variation in the %W for each prey group, we used area designations (north, west, east, southwest, and southeast) and fork length as the predictor variables. We used the tree functions in S-Plus (MathSoft Inc., 1999) and cross-validation to prune fully grown trees so that only important splits remained. Prediction errors were used as pruning criteria (Breiman et al., 1984; De'ath and Fabricius, 2000).

We stratified the data by area (Fig. 1) according to two criteria. Latitude divisions at 15°N and 0° were based on the spatial and seasonal heterogeneity of the purse-seine sets that provided the samples. All the sets sampled from

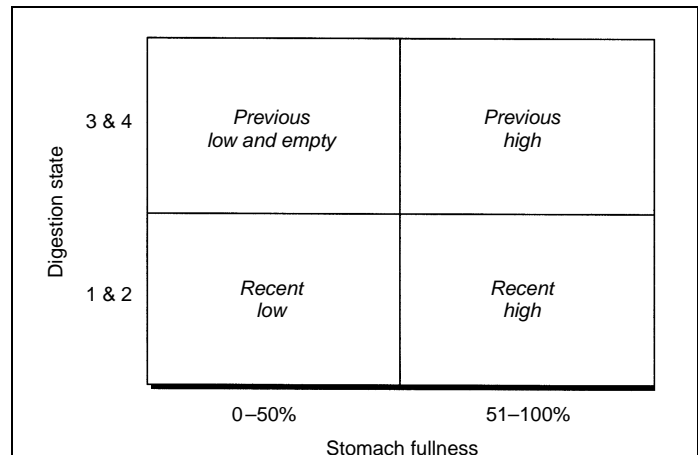


Figure 2

Schematic diagram showing prey digestion-state and predator stomach-fullness criteria used to analyze diel feeding characteristics of common dolphinfish in the eastern Pacific Ocean.

May through November each year were made north of the equator, and most sets sampled during December through April were made south of the equator. Also, the regression trees indicated that latitude and longitude were important in explaining the variability in the gravimetric data for several prey taxa. Epipelagic-cephalopod taxa were most important in the diet of the common dolphinfish caught east of $82^{\circ}41'\text{W}$ and south of $1^{\circ}46'\text{S}$, and flyingfishes were most important in the diet of those caught west of 81°W . Therefore, we stratified the data from south of the equator into "southwest" and "southeast" areas separated at $82^{\circ}41'\text{W}$ (Fig. 1). Similarly, we stratified the data from samples collected between 0° and 15°N into "west" and "east" areas divided at 111°W because a regression tree fitted to the gravimetric data for the Tetraodontiformes indicated that this meridian was important in explaining variation in %W for this taxon. Tetraodontiformes were more important in the diet of the fish caught west of 111°W .

Consumption rates

We employed a method described by Olson and Mullen (1986) to calculate preliminary estimates of daily rates of food consumption by common dolphinfish. The model predicts feeding rate (\hat{r} , grams per hour) by dividing the mean weight of the stomach contents per predator (\bar{W} , grams) by the integral (A , proportion \times hours = hours) of the function that best fits experimental gastric evacuation data. For a predator that consumes a variety of prey that are evacuated at different rates,

$$\hat{r} = \sum_{i=0}^I \frac{\bar{W}_i}{A_i}, \quad (1)$$

where subscripts i refer to each of I prey types.

Table 1

Numbers of common dolphinfish sampled by size, sex, and area with undigested food in their stomachs (first number) and with empty stomachs or trace amounts of hard parts (in parentheses).

Fork length (mm)	Sex			Area					Total no. of dolphinfish
	Males	Females	Undetermined sex	North	West	East	Southwest	Southeast	
417–650	2 (14)	14 (39)	4 (5)	0 (1)	0 (3)	4 (24)	16 (21)	0 (9)	20 (58)
651–800	12 (21)	48 (47)	8 (3)	1 (0)	2 (9)	14 (11)	37 (47)	14 (4)	68 (71)
801–950	24 (29)	51 (70)	11 (7)		11 (11)	13 (13)	43 (60)	19 (22)	86 (106)
951–1100	26 (25)	15 (21)	3 (1)		0 (2)	10 (10)	19 (19)	15 (16)	44 (47)
1101–1250	9 (6)	10 (6)	2 (1)	2 (0)		10 (5)	5 (1)	4 (7)	21 (13)
1251–1770	6 (1)	1 (1)	0 (1)			1 (1)	2 (1)	4 (1)	7 (3)
Total	79 (96)	139 (184)	29 (18 ¹)	3 (1)	13 (25)	52 (64)	122 (150 ¹)	56 (59)	246 (299 ¹)

¹ Including one dolphinfish with no length or sex data.

Daily meal is \hat{r} multiplied by 24 h for fish that feed both day and night. Daily ration is daily meal expressed as a percent of body weight. We estimated the body weight of each dolphinfish from the length, according to the relationships of Lasso and Zapata (1999):

$$M = aL^b, \quad (2)$$

where M = body weight (g); and
 L = fork length (cm).

They estimated that $a = 0.0406, 0.0420,$ and $0.0224,$ and $b = 2.6588, 2.6328,$ and 2.78 for males, females, and common dolphinfish of undetermined sex, respectively. We estimated daily consumption rates for dolphinfish of six size strata by sex and area.

The time-course of gastric evacuation has not been adequately described for dolphinfishes. This fact prevents a rigorous analysis of consumption rates using stomach-contents data. However, we provide preliminary, first-order estimates of daily rations of common dolphinfish because this information is important for analyses of ecosystem effects of fishing (see "Discussion" section). A preliminary experiment indicated that the gastric evacuation rate for squid tissue by juvenile dolphinfish is comparable to that for squid by yellowfin tuna. Five juvenile common dolphinfish passed pellets of moist squid tissue through the digestive tract in 6–8 h at 27°C (Suzuki, 1992). The fastest gastric evacuation times for squid (*Loligo opalescens*) voluntarily ingested by yellowfin tuna (mean $L=36.2$ cm) in the laboratory were about 8 h at 23.5–25.5°C (Olson and Boggs, 1986). We assume, therefore, that gastric evacuation rates measured for yellowfin tuna are adequate for estimating daily rations of dolphinfish. We assigned values of A (Eq. 1) for squid (4.48), mackerel (*Scomber japonicus*) (5.29), smelt (*Hypomesus pretiosus*) (4.12), and nehu (*Stolephorus purpureus*) (2.24), and the mean for four experimental food species (3.77) determined by Olson and Boggs (1986) to the various prey taxa of common dolphinfish, as they

did for yellowfin tuna. We omitted the data for the trace hard parts (cephalopod mandibles and fish otoliths), which apparently accumulate in the stomachs, when calculating consumption rates because of the possibility that these remained from predation on previous days.

Results

Stomach samples were obtained from 545 dolphinfish: 175 males, 323 females, and 47 of undetermined sex. Two hundred and forty-six specimens had fresh or partially digested food remains in their stomachs, 274 had empty stomachs, and 25 had only trace amounts of digestion-resistant hard parts (cephalopod mandibles and fish otoliths). We present the sample sizes by sex and area in Table 1 and the detailed prey-composition data by area in Tables 2–4. We analyzed the prey composition data by sex but did not discover important differences or trends.

Few samples were obtained in the north and west areas. Therefore, we briefly summarize those data here and in Tables 2–4 and do not include them in the detailed treatments of diel feeding periodicity, diet measures by area, and size-specific predation. Only four common dolphinfish were sampled in the north area, three from sets on schoolfish and one from a set on dolphins. Three of the stomach samples contained food and one was empty. A large dolphinfish (1149 mm) had recently eaten a large squid (*Stenoteuthis oualaniensis*) in the early morning. Another large fish (1239 mm) had a full stomach containing 7 fresh *Coryphaena equiselis* in the late afternoon. Both fish had been collected from schoolfish sets. A smaller dolphinfish (768 mm) from a dolphin set in the late afternoon had remains of various taxa, principally *C. equiselis*, flyingfishes, and galatheid red crabs (*Pleuoncodes planipes*) in advanced states of digestion. In addition, a 564-mm dolphinfish from a schoolfish set was found to have an empty stomach.

Thirty-eight common dolphinfish were sampled in the west area from 4 sets on floating objects between 05:40 and

Table 2

Taxonomic composition in %W of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. Weights do not include hard parts (cephalopod mandibles and fish otoliths). Prey category codes are as follows: EC = epipelagic cephalopods, MC = mesopelagic cephalopods, Cr = Crustacea, MiF = miscellaneous fishes, MsF = mesopelagic fishes, F = flyingfishes, Co = Coryphaenidae, Ca = Carangidae, G = Gempylidae, A = *Auxis* spp., YT = yellowfin tuna, N = Nomeidae, T = Tetraodontiformes. A_i is the integral of the function fitted to experimental gastric evacuation data and is used to calculate consumption rates (Eq. 1). Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

Taxon	Category	Assumed A_i	Area					
			N	W	E	SW	SE	All
Phylum Mollusca		4.48	16.35	2.54	9.48	21.69	82.73	32.20
Class Cephalopoda		4.48	16.35	2.54	9.48	21.69	82.73	32.19
Order Teuthoidea		4.48	16.35	2.54	9.48	21.66	81.84	31.91
Family Enoploteuthidae	EC	4.48		*		*	*	*
<i>Abraliopsis falco</i>	EC	4.48		*		*	*	*
Family Mastigoteuthidae	MC	4.48			0.15	0.01		0.04
<i>Mastigoteuthis</i> spp.	MC	4.48			0.15	0.01		0.04
Family Ommastrephidae	EC	4.48	16.35	2.54	5.47	21.40	81.84	30.72
<i>Dosidicus gigas</i>	EC	4.48		2.54	0.78	5.08	70.73	19.27
<i>Sthenoteuthis oualaniensis</i>	EC	4.48	16.35		4.69	16.32	11.11	11.45
Family Onychoteuthidae	EC	4.48			3.26	0.09		0.91
<i>Onychoteuthis banksii</i>	EC	4.48			3.26	0.09		0.91
<i>Onychoteuthis</i> spp.	EC	4.48				*		*
Family Pholidoteuthidae	EC	4.48				*		*
<i>Pholidoteuthis boschmani</i>	EC	4.48				*		*
Family Thysanoteuthidae	EC	4.48			*	0.17		0.07
<i>Thysanoteuthis rhombus</i>	EC	4.48			*	0.17		0.07
Order Octopoda	EC	4.48		*	*	0.02	1.16	0.29
Family Tremoctopodidae	EC	4.48					1.16	0.28
<i>Tremoctopus violaceus</i>	EC	4.48					1.16	0.28
Family Argonautidae	EC	4.48		*	*	0.02	*	0.01
<i>Argonauta</i> spp.	EC	4.48		*	*	0.02	*	0.01
Family Bolitaenidae	MC	4.48		*		*		*
<i>Japetella diaphana</i>	MC	4.48		*		*		*
Phylum Arthropoda		3.37	1.39		3.26	0.01		0.94
Class Crustacea	Cr	3.37	1.39		3.26	0.01		0.94
Order Decapoda	Cr	3.37	1.39		3.26	0.01		0.94
Family Galatheidae	Cr	3.37	1.39					0.06
<i>Pleuroncodes planipes</i>	Cr	3.37	1.39					0.06
Family Penaeidae	Cr	3.37			0.61			0.16
Family Portunidae	Cr	3.37			2.65			0.71
<i>Portunus xantusii</i>	Cr	3.37			2.65			0.71
Phylum Chordata		4.12	82.26	97.46	87.24	78.30	17.00	66.84
Class Osteichthyes		4.12	82.26	97.46	87.24	78.30	17.00	66.84
Order Clupeiformes	MiF	4.12			0.08			0.02
Family Engraulidae	MiF	4.12			0.08			0.02
Order Stomiiformes	MsF	2.24			0.48	4.53		2.01
Family Phosichthyidae	MsF	2.24			0.48	4.53		2.01
<i>Vinciguerrria lucetia</i>	MsF	2.24			0.48	4.53		2.01
Order Myctophiformes	MsF	2.24	0.07	4.26	3.11	*		0.97
Family Myctophidae	MsF	2.24	0.07	4.26	3.11	*		0.97
<i>Benthoosema panamense</i>	MsF	2.24		*				*

continued

Table 2 (continued)

Taxon	Category	Assumed A_i	Area					
			N	W	E	SW	SE	All
<i>Myctophum aurolaternatum</i>	MsF	2.24			0.97			0.26
<i>Myctophum nitidulum</i>	MsF	2.24			*			*
<i>Symbolophorus</i> spp.	MsF	2.24		4.26	2.14	*		0.71
Order Lampridiformes	MsF	5.29				3.04		1.27
Family Trachipteridae	MsF	5.29				3.04		1.27
<i>Desmodesma polystictum</i>	MsF	5.29				3.04		1.27
Order Beloniformes			1.59	26.50	49.58	31.64	9.29	29.58
Family Belonidae	MiF	5.29			0.26		1.34	0.39
<i>Strongylura</i> spp.	MiF	5.29			0.26		1.34	0.39
Family Exocoetidae	F	4.12		16.14	30.77	28.43	7.95	22.48
<i>Cheilopogon furcatus</i>	F	4.12				0.66		0.27
<i>Cheilopogon spilonopterus</i>	F	4.12				0.12		0.05
<i>Cheilopogon</i> spp.	F	4.12		10.96	0.53	3.59	2.94	2.68
<i>Exocoetus monocirrhus</i>	F	4.12			19.19	0.69	1.09	5.69
<i>Exocoetus volitans</i>	F	4.12		5.18	5.34	17.64	1.58	9.31
<i>Exocoetus</i> spp.	F	4.12			0.92	5.04	1.81	2.77
<i>Hirundichthys speculiger</i>	F	4.12			3.17		0.53	0.98
<i>Prognichthys</i> spp.	F	4.12			1.22	0.47		0.52
Family Hemiramphidae	F	4.12	1.59	10.36	18.55	3.21		6.71
<i>Oxyporhamphus micropterus</i>	F	4.12	1.59	10.36	18.55	3.21		6.71
Order Perciformes			80.11		32.60	36.32	5.76	28.90
Family Echeneidae	MiF	3.77				2.48		1.03
<i>Rhombochirus osteochir</i>	MiF	3.77				2.48		1.03
Family Coryphaenidae	Co	5.29	80.11		1.43	2.36	0.20	5.08
<i>Coryphaena equiselis</i>	Co	5.29	80.11			0.01		3.67
<i>Coryphaena hippurus</i>	Co	5.29				1.23		0.51
Family Carangidae	Ca	5.29			0.34	5.48		2.37
<i>Naucrates ductor</i>	Ca	5.29			0.34	3.88		1.71
Family Gempylidae	G	5.29			16.53	3.93	0.01	6.07
<i>Gempylus serpens</i>	G	5.29			16.53	3.93	0.01	6.07
Family Scombridae	MiF	5.29			13.18	15.97	5.54	11.50
<i>Acanthocybium solandri</i>	MiF	5.29			0.04			0.01
<i>Auxis</i> spp.	A	5.29			10.15	15.78		9.29
<i>Euthynnus lineatus</i>	MiF	5.29			1.50			0.40
<i>Thunnus</i> spp.	YT	5.29			1.49	0.19	5.54	1.80
Family Nomeidae	N	2.24			1.12	6.11		2.84
<i>Cubiceps pauciradiatus</i>	N	2.24			1.12	6.11		2.84
Order Tetraodontiformes	T	3.77	0.49	66.70	1.38	2.77		3.63
Family Balistidae	T	3.77	0.21	38.78				1.22
<i>Xantichthys mento</i>	T	3.77		38.78				1.21
Family Ostraciidae	T	3.77		25.99				0.81
<i>Lactoria diaphanum</i>	T	3.77		25.99				0.81
Family Tetraodontidae	T	3.77	0.28	1.93	1.38	2.77		1.60
<i>Lagocephalus lagocephalus</i>	T	3.77	0.28	1.93	1.38	2.77		1.60
Unidentified fishes	MiF	3.77					1.95	0.47
Total prey weight (g)			1443	985	8459	13,118	7523	31,527

* Only trace quantities of hard parts were present.

Table 3

Taxonomic composition in %N of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. Numbers include hard parts (cephalopod mandibles and fish otoliths) divided by two. Numbers are not complete for some taxa because sometimes prey could not be enumerated due to being in an advanced digestion state. Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

Taxon	Area					All
	N	W	E	SW	SE	
Phylum Mollusca	2.17	12.36	24.46	19.97	87.35	37.43
Class Cephalopoda	2.17	12.36	24.46	19.97	87.35	37.37
Order Teuthoidea	2.17	7.87	24.21	16.93	85.25	35.27
Family Enoploteuthidae		1.12		3.62	0.23	1.62
<i>Abraliopsis falco</i>		1.12		3.62	0.23	1.62
Family Mastigoteuthidae			0.24	0.29		0.18
<i>Mastigoteuthis</i> spp.			0.24	0.29		0.18
Family Ommastrephidae	2.17	6.74	4.60	11.87	85.01	28.20
<i>Dosidicus gigas</i>		6.74	2.91	9.99	82.20	26.23
<i>Sthenoteuthis oualaniensis</i>	2.17		1.69	1.74	2.81	1.92
Family Onychoteuthidae			18.16	0.72		4.79
<i>Onychoteuthis banksii</i>			18.16	0.58		4.73
<i>Onychoteuthis</i> spp.				0.14		0.06
Family Pholidoteuthidae				0.29		0.12
<i>Pholidoteuthis boschmani</i>				0.29		0.12
Family Thysanoteuthidae			0.24	0.14		0.12
<i>Thysanoteuthis rhombus</i>			0.24	0.14		0.12
Order Octopoda		4.49	0.24	3.04	2.11	2.10
Family Tremoctopodidae					0.94	0.24
<i>Tremoctopus violaceus</i>					0.94	0.24
Family Argonautidae		2.25	0.24	2.75	1.17	1.62
<i>Argonauta</i> spp.		2.25	0.24	2.75	1.17	1.62
Family Bolitaenidae		2.25		0.29		0.24
<i>Japetella diaphana</i>		2.25		0.29		0.24
Phylum Arthropoda	69.57		12.38	0.14		5.05
Class Crustacea	69.57		12.38	0.14		5.05
Order Decapoda	69.57		12.38	0.14		5.03
Family Galatheidae	69.57					1.92
<i>Pleuroncodes planipes</i>	69.57					1.92
Family Penaeidae			1.69			0.42
Family Portunidae			10.65			2.63
<i>Portunus xantusii</i>			10.65			2.63
Phylum Chordata	2.17	87.64	62.95	79.88	12.65	57.31
Class Osteichthyes	2.17	87.64	62.95	79.88	12.65	57.31
Order Clupeiformes			0.48			0.12
Family Engraulidae			0.48			0.12
Order Stomiiformes			*	41.97		17.37
Family Phosichthyidae			*	41.97		17.37
<i>Vinciguerria lucetia</i>			*	41.97		17.37
Order Myctophiformes	2.17	57.30	14.77	0.14		6.83
Family Myctophidae	2.17	57.30	14.77	0.14		6.83
<i>Benthoosema panamense</i>		16.85				0.90

continued

Table 3 (continued)

Taxon	Area					
	N	W	E	SW	SE	All
<i>Myctophum aurolaternatum</i>			3.39			0.84
<i>Myctophum nitidulum</i>			3.15			0.78
<i>Symbolophorus</i> spp.		40.45	8.23	0.14		4.25
Order Lampridiformes				0.58		0.24
Family Trachipteridae				0.58		0.24
<i>Desmodesma polystictum</i>				0.58		0.24
Order Beloniformes	4.35	11.24	36.08	29.52	10.77	24.61
Family Belonidae			0.24		0.23	0.12
<i>Strongylura</i> spp.			0.24		0.23	0.12
Family Exocoetidae		6.74	19.13	26.34	10.54	18.68
<i>Cheilopogon furcatus</i>				0.29		0.12
<i>Cheilopogon spilonopterus</i>				0.29		0.12
<i>Cheilopogon</i> spp.		2.25	0.48	1.74	2.34	1.56
<i>Exocoetus monocirrhus</i>			8.96	0.87	0.47	2.69
<i>Exocoetus volitans</i>		4.49	5.33	13.31	3.51	7.96
<i>Exocoetus</i> spp.			1.94	9.55	3.98	5.45
<i>Hirundichthys speculiger</i>			1.45		0.23	0.42
<i>Prognichthys</i> spp.			0.97	0.29		0.36
Family Hemiramphidae	4.35	4.49	16.71	3.18		5.81
<i>Oxyporhamphus micropterus</i>	4.35	4.49	16.71	3.18		5.81
Order Perciformes	17.39		10.41	6.80	1.64	6.29
Family Echeineidae				0.29		0.12
<i>Rhombochirus osteochir</i>				0.29		0.12
Family Coryphaenidae	17.39		0.24	0.72	0.47	0.96
<i>Coryphaena equiselis</i>	17.39			0.14		0.54
<i>Coryphaena hippurus</i>				0.29		0.12
Family Carangidae			0.97	1.88		1.02
<i>Naucrates ductor</i>			0.97	1.45		0.84
Family Gempylidae			3.63	1.01	0.47	1.44
<i>Gempylus serpens</i>			3.63	1.01	0.47	1.44
Family Scombridae			1.69	1.88	0.70	1.38
<i>Acanthocybium solandri</i>			0.24			0.06
<i>Auxis</i> spp.			0.97	1.74		0.96
<i>Euthynnus lineatus</i>			0.24			0.06
<i>Thunnus</i> spp.			0.24	0.14	0.70	0.30
Family Nomeidae			3.87	1.01		1.38
<i>Cubiceps pauciradiatus</i>			3.87	1.01		1.38
Order Tetraodontiformes	4.35	19.10	1.21	0.72		1.74
Family Balistidae	2.17	2.25				0.18
<i>Xantichthys mento</i>		2.25				0.12
Family Ostraciidae		15.73				0.84
<i>Lactoria diaphanum</i>		15.73				0.84
Family Tetraodontidae	2.17	1.12	1.21	0.72		0.72
<i>Lagocephalus lagocephalus</i>	2.17	1.12	1.21	0.72		0.72
Unidentified fishes				0.14	0.23	0.12
Total number of prey	46	89	412	691	427	1665

* Individual prey could not be enumerated.

Table 4

Taxonomic composition in %O of the prey of common dolphinfish from five areas of the eastern Pacific Ocean (Fig. 1) and from all areas combined. The occurrence of hard parts (cephalopod mandibles and fish otoliths) was included. Area codes are N = north, W = west, E = east, SW = southwest, SE = southeast.

Taxon	Area					All
	N	W	E	SW	SE	
Phylum Mollusca	25.0	15.79	15.52	14.34	45.22	21.28
Class Cephalopoda	25.0	15.79	15.52	13.97	45.22	21.10
Order Teuthoidea	25.0	10.53	15.52	12.13	43.48	19.45
Family Enoploteuthidae		2.63		0.37	0.87	0.55
<i>Abrialopsis falco</i>		2.63		0.37	0.87	0.55
Family Mastigoteuthidae			0.86	0.74		0.55
<i>Mastigoteuthis</i> spp.			0.86	0.74		0.55
Family Ommastrephidae	25.0	7.89	8.62	10.29	43.48	16.88
<i>Dosidicus gigas</i>		7.89	6.03	7.35	37.39	13.39
<i>Sthenoteuthis oualaniensis</i>	25.0		4.31	2.57	8.70	4.22
Family Onychoteuthidae			9.48	1.84		2.94
<i>Onychoteuthis banksii</i>			9.48	1.47		2.75
<i>Onychoteuthis</i> spp.				0.37		0.18
Family Pholidoteuthidae				0.74		0.37
<i>Pholidoteuthis boschmani</i>				0.74		0.37
Family Thysanoteuthidae			0.86	0.37		0.37
<i>Thysanoteuthis rhombus</i>			0.86	0.37		0.37
Order Octopoda		7.89	0.86	3.68	5.22	3.67
Family Tremoctopodidae					3.48	0.73
<i>Tremoctopus violaceus</i>					3.48	0.73
Family Argonautidae		5.26	0.86	3.68	1.74	2.75
<i>Argonauta</i> spp.		5.26	0.86	3.68	1.74	2.75
Family Bolitaenidae		2.63		0.74		0.55
<i>Japetella diaphana</i>		2.63		0.74		0.55
Phylum Arthropoda	25.0		8.62	1.10		2.75
Class Crustacea	25.0		8.62	1.10		2.75
Order Decapoda	25.0		7.76	0.37		2.02
Family Galatheidae	25.0					0.18
<i>Pleuroncodes planipes</i>	25.0					0.18
Family Penaeidae			4.31			0.92
Family Portunidae			3.45			0.73
<i>Portunus xantusii</i>			3.45			0.73
Phylum Chordata	50.0	36.84	43.10	42.28	25.22	38.53
Class Osteichthyes	50.0	36.84	43.10	42.28	25.22	38.53
Order Clupeiformes			0.86			0.18
Family Engraulidae			0.86			0.18
Order Stomiiformes			0.86	2.21		1.28
Family Phosichthyidae			0.86	2.21		1.28
<i>Vinciguerria lucetia</i>			0.86	2.21		1.28
Order Myctophiformes	25.0	10.53	6.90	0.37		2.57
Family Myctophidae	25.0	10.53	6.90	0.37		2.57
<i>Benthoosema panamense</i>		2.63				0.18

continued

Table 4 (continued)

Taxon	Area					
	N	W	E	SW	SE	All
<i>Myctophum aurolaterdatum</i>			6.03			1.28
<i>Myctophum nitidulum</i>			0.86			0.18
<i>Symbolophorus</i> spp.		7.89	3.45	0.37		1.47
Order Lampridiformes				0.74		0.37
Family Trachipteridae				0.74		0.37
<i>Desmodesma polystictum</i>				0.74		0.37
Order Beloniformes	25.0	13.16	36.21	32.35	20.00	29.17
Family Belonidae			0.86		0.87	0.37
<i>Strongylura</i> spp.			0.86		0.87	0.37
Family Exocoetidae		13.16	25.86	28.68	19.13	24.77
<i>Cheilopogon furcatus</i>				0.74		0.37
<i>Cheilopogon spilonotopterus</i>				0.37		0.18
<i>Cheilopogon</i> spp.		5.26	1.72	4.04	4.35	3.67
<i>Exocoetus monocirrhus</i>			12.07	0.74	0.87	3.12
<i>Exocoetus volitans</i>		7.89	6.90	18.01	6.09	12.29
<i>Exocoetus</i> spp.			2.59	6.99	9.57	6.06
<i>Hirundichthys speculiger</i>			1.72		0.87	0.55
<i>Prognichthys</i> spp.			1.72	0.74		0.73
Family Hemiramphidae	25.0	2.63	24.14	6.99		8.99
<i>Oxyporhamphus micropterus</i>	25.0	2.63	24.14	6.99		8.99
Order Perciformes	50.0		17.24	11.40	5.22	10.83
Family Echeineidae				0.37		0.18
<i>Rhombochirus osteochir</i>				0.37		0.18
Family Coryphaenidae	50.0		0.86	1.84	1.74	1.83
<i>Coryphaena equiselis</i>	50.0			0.37		0.55
<i>Coryphaena hippurus</i>				0.74		0.37
Family Carangidae			1.72	1.84		1.28
<i>Naucrates ductor</i>			1.72	1.47		1.10
Family Gempylidae			7.76	1.47	0.87	2.57
<i>Gempylus serpens</i>			7.76	1.47	0.87	2.57
Family Scombridae			5.17	4.41	2.61	3.85
<i>Acanthocybium solandri</i>			0.86			0.18
<i>Auxis</i> spp.			2.59	4.04		2.57
<i>Euthynnus lineatus</i>			0.86			0.18
<i>Thunnus</i> spp.			0.86	0.37	2.61	0.92
Family Nomeidae			6.90	1.84		2.39
<i>Cubiceps pauciradiatus</i>			6.90	1.84		2.39
Order Tetraodontiformes	25.0	18.42	3.45	1.47		2.94
Family Balistidae	25.0	5.26				0.55
<i>Xantichthys mento</i>		5.26				0.37
Family Ostraciidae		10.53				0.73
<i>Lactoria diaphanum</i>		10.53				0.73
Family Tetraodontidae	25.0	2.63	3.45	1.47		1.83
<i>Lagocephalus lagocephalus</i>	25.0	2.63	3.45	1.47		1.83
Unidentified fishes				0.74	0.87	1.10
Total number of samples	4	38	116	272	115	545

08:34 hours; 13 fish had stomachs with undigested food remains, 23 had stomachs that were empty, and 2 had stomachs that contained only trace amounts of hard parts. One of the two dolphinfish in the 651–800 mm size group contained remains of flyingfishes and the other contained tetraodontid puffers. In the larger group (801–950 mm), 11 dolphinfish ate mostly triggerfishes (*Balistidae*), boxfish (*Ostraciidae*), and flyingfishes. In addition, 3 fish \leq 650 mm and 2 fish in the 951–1100 mm class had empty stomachs or contained only trace amounts of hard parts.

Diel feeding periodicity

Although common dolphinfish are thought to be visual predators that feed primarily in the daytime (Massuti et al., 1998), our data suggest that they also feed at night. In the areas where sufficient sample sizes were obtained (east, southwest, and southeast), an average of about 15% of the dolphinfish caught in the early morning contained food classified in the “previous-high” category (Fig. 3). Many of these prey were flyingfishes, cephalopods, dolphinfishes, wahoo, and snake mackerel in digestion states 3 or 4 and were found in stomachs that were over 50% full. Prey of these or similar taxa were found to be completely evacuated from the stomachs of yellowfin tuna in about 6–18 h (Olson and Boggs, 1986). If dolphinfish gastric evacuation rates are on the order of those of yellowfin tuna (see “Discussion,” and “Consumption rates” sections), these prey would have been ingested during the night.

We examined the time of day that the dolphinfish fed, by area. In the east area, the data indicated peak feeding activity in the early morning and early afternoon, although few samples were obtained in the late morning and late afternoon (Fig. 3, “recent high”). The most important prey taxa by percent biomass in the early morning were flyingfishes (54%), snake mackerel (*Gempylidae*, 18%), and epipelagic cephalopods (10%). The most important prey taxa in the early afternoon were frigate or bullet tunas (*Auxis* spp., 37%) (or a combination of both), pelagic portunid crabs (27%), and *Thunnus* spp. (yellowfin and bigeye tunas, 15%).

In the southwest area, feeding appears to have occurred throughout the day (Fig. 3). The frequency of observations in the two “recent” categories combined was highest in the early afternoon (41%) and lowest in the late afternoon (22%). The highest proportion of empty stomachs and those containing only residual hard parts occurred in the late afternoon, followed by the early and late morning. The flying-

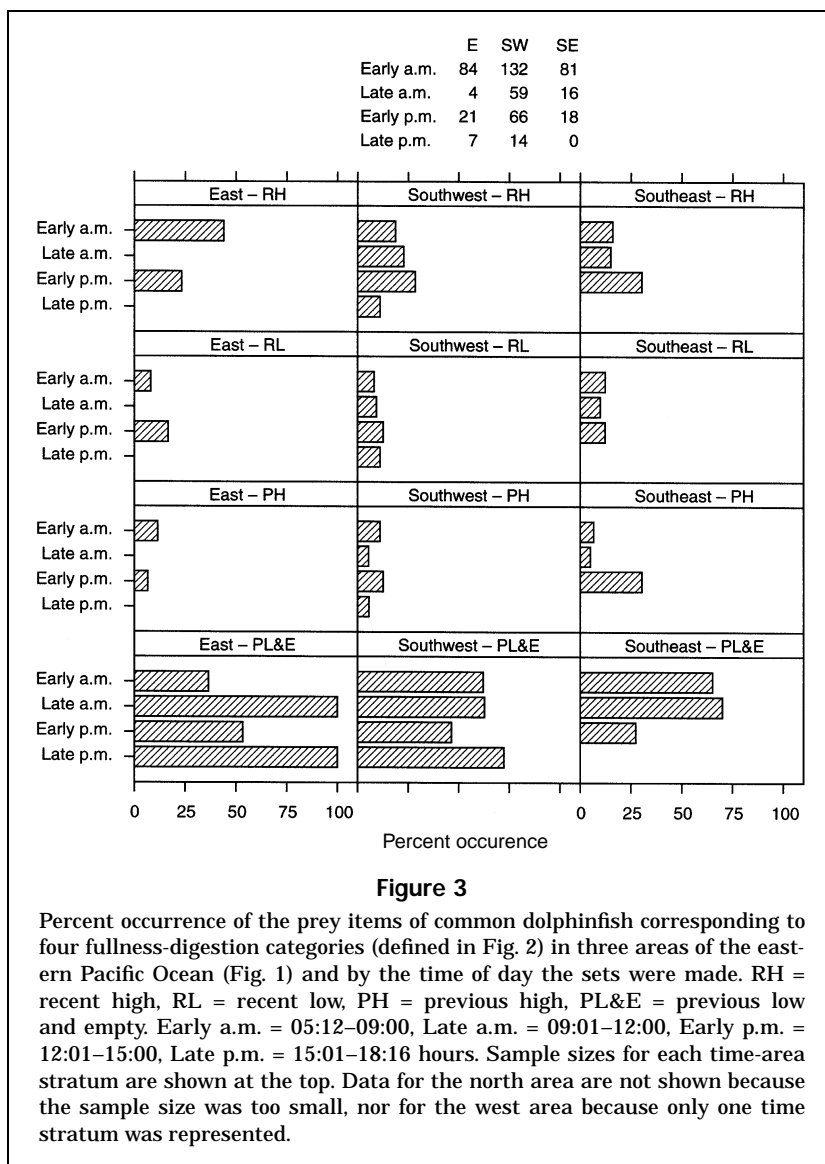
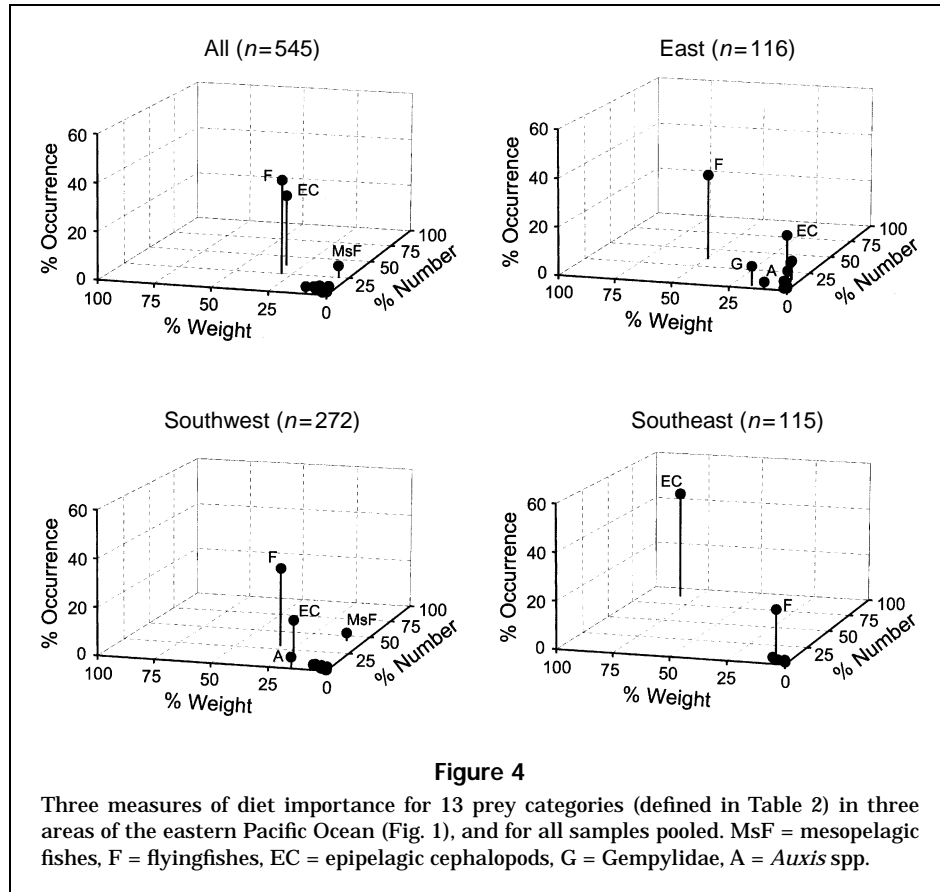


Figure 3
Percent occurrence of the prey items of common dolphinfish corresponding to four fullness-digestion categories (defined in Fig. 2) in three areas of the eastern Pacific Ocean (Fig. 1) and by the time of day the sets were made. RH = recent high, RL = recent low, PH = previous high, PL&E = previous low and empty. Early a.m. = 05:12–09:00, Late a.m. = 09:01–12:00, Early p.m. = 12:01–15:00, Late p.m. = 15:01–18:16 hours. Sample sizes for each time-area stratum are shown at the top. Data for the north area are not shown because the sample size was too small, nor for the west area because only one time stratum was represented.

fishes dominated in the diet between 09:00 and 15:00 hours (64% and 57% by weight), and 71% of the diet of dolphinfish caught in the late afternoon was epipelagic cephalopods. The important prey in the early morning were more varied and comprised frigate and bullet tunas (*Auxis* spp., 28%), flyingfishes (18%), epipelagic cephalopods (17%), and mesopelagic fishes (primarily *Vinciguerrria lucetia*, 15%).

In the southeast area, although no samples were obtained in the late afternoon, the data suggested peak feeding activity in the early afternoon (Fig. 3). The frequency of observations in both “recent” categories in the early afternoon summed to 42% of the total, compared with only 25% in the late morning. Most of the empty stomachs were from fish captured in sets made before noon. The epipelagic cephalopod *Dosidicus gigas* dominated in the diet during all time periods. Fifteen percent of the stomach contents of the common dolphinfish caught before 09:00 hours were small yellowfin tuna.



Diet measures by area

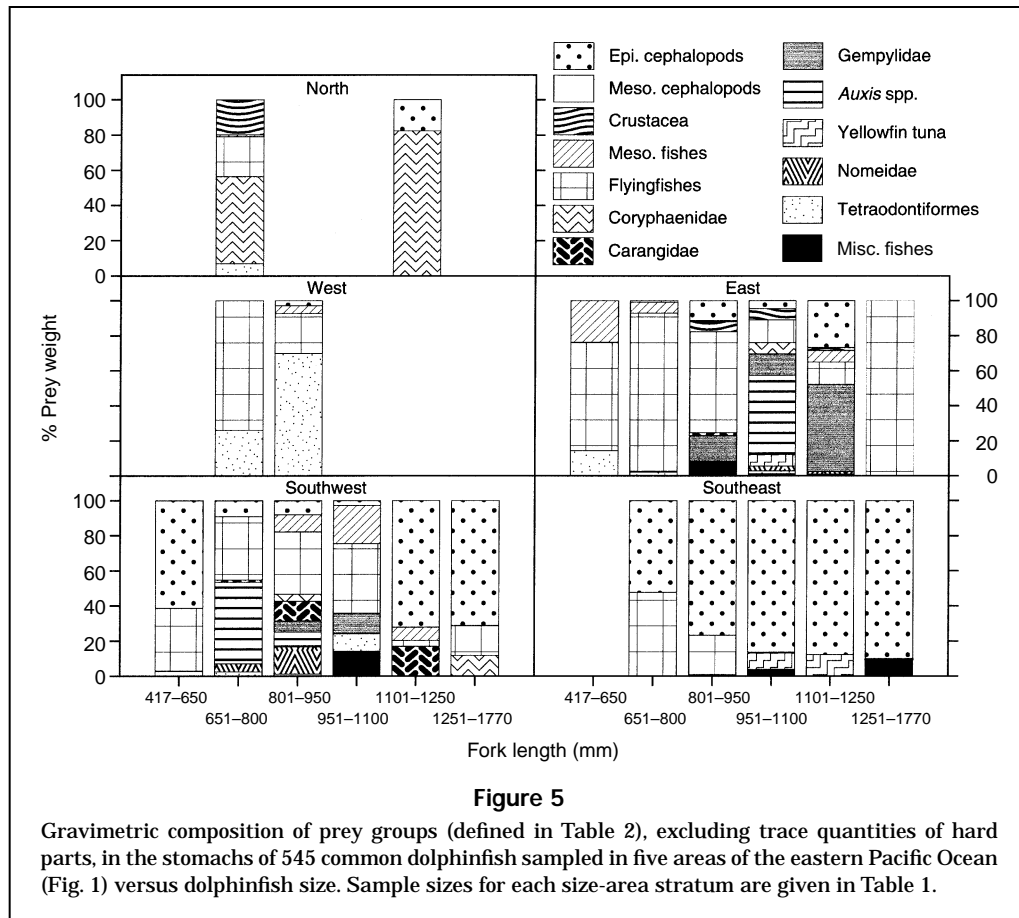
We present three measures of diet importance, %W, %N, and %O, in Figure 4 for all samples pooled, and by area. We included the data for trace quantities of hard parts (cephalopod mandibles and fish otoliths) in the analysis of %N and %O, but not of %W.

The graphical representation indicates that, when all data are pooled, most components of the diet appear to be quite rare (close to the origin of the graph, Fig. 4, all). However, when the data are examined by area, the diet proves to be more varied. Flyingfishes and epipelagic cephalopods were clearly the dominant prey. Overall, flyingfishes were eaten by more of the dolphins (29% occurrence) than any other category, followed by epipelagic cephalopods (21% occurrence). Because 274 stomach samples were totally empty, these are equivalent to 58% and 42% occurrence, respectively, in the stomachs that contained food or hard parts. Prey counts contributed more than prey biomass to the apparent importance of mesopelagic fishes and epipelagic cephalopods in the diet. This is partly due to the accumulation of digestion-resistant hard parts of these two taxa in the stomachs.

Area was an important source of variation in the %W of three prey groups. The regression tree for epipelagic cephalopods indicated that 25% of the apparent variation in the %W of that prey was explained by area (southeast vs. oth-

ers). Area was also an important predictor of flyingfish predation; 15% of the apparent variation in the %W was explained by area (north, west, and southeast vs. other areas). The regression tree for Tetraodontiformes indicated that 41% of the apparent variation in predation on that taxon was explained by area (west vs. others). The gravimetric importance of the 10 other prey taxa could not be modeled by regression trees (i.e. the trees pruned back to the overall mean %W for those prey) owing to their infrequency in the diet or low sample size (or to both). Nevertheless, we present our results by area to illustrate the substantial spatial variability of the diet of common dolphins in the EPO.

In the east area, the stomachs of 116 common dolphins were sampled from 1 dolphin set and 22 floating-object sets. Sixty-two of these stomachs were empty and 2 contained only trace hard parts (58.0% of the females, 52.5% of the males). The flyingfishes were the dominant prey in the east area in terms of all three indices (Fig. 4, east). Flyingfishes were eaten by 35% of the dolphins sampled and comprised 49% of the total weight of the stomach contents. Epipelagic cephalopods were also eaten by substantial numbers of dolphins (16% occurrence), and accounted for 24% of the prey counts. The epipelagic cephalopods were numerically important, but less so by weight, because their mandibles resist digestion and may accumulate in the stomachs over time. The other prey taxa were fairly rare in the east area.



In the southwest area, the stomachs of 272 common dolphinfish were sampled from 2 dolphin sets, 5 schoolfish sets, and 22 floating-object sets. One hundred and thirty-six of the samples were empty and 14 contained only trace hard parts (60.1% of the females, 47.6% of the males). Flyingfishes and epipelagic cephalopods were found in 32% and 14% of the dolphinfish sampled, and also ranked first and second in biomass, respectively (Fig. 4, southwest). The dietary importance of both, as well as *Auxis* spp., was determined more by weight than by numbers of individuals, whereas the contrary was true for mesopelagic fishes. All the other prey categories were relatively rare in the diet according to all three measures.

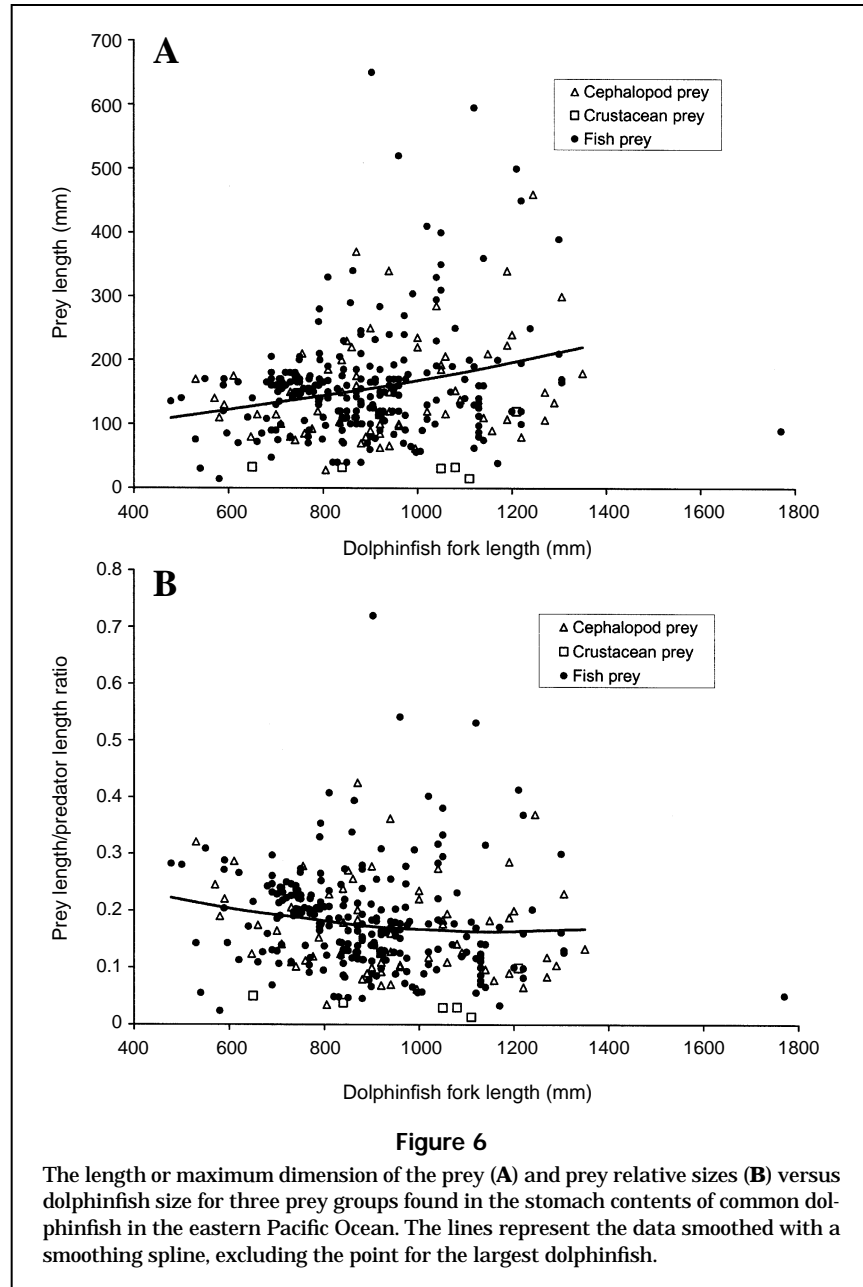
In the southeast area, the stomachs of 115 dolphinfish were sampled from 1 schoolfish set and 13 floating-object sets. Fifty-two of the stomachs were empty and 7 contained only trace hard parts (44.6% of the females, 61.5% of the males). The epipelagic cephalopods were, by far, the dominant component in the diet in this area (Fig. 4, southeast). They were present in 45% of the stomachs sampled. Biomass and counts contributed about equally to the overall importance of epipelagic cephalopods in the diet. Flyingfishes also occurred in many of the samples (19%), but their contribution to the diet by weight and numbers was overshadowed by the epipelagic cephalopods. Four other diet categories were rare.

Size-specific predation

We present the prey composition in %W, excluding trace quantities of hard parts (cephalopod mandibles and fish otoliths), by six dolphinfish size strata for five areas (Fig. 5). Sample sizes for each stratum are given in Table 1.

Considerable variability in the diet was apparent for common dolphinfish of different sizes. However, the statistical importance of size could be detected by the regression trees for only two prey groups because of the rarity of the other prey in the diet or because of small sample sizes. The regression tree for flyingfishes indicated that 7% of the apparent variation in the %W of these prey was explained by dolphinfish size. Size was also an important predictor of predation on Tetraodontiformes, explaining 9% of the apparent variation in the %W of these prey. Although dolphinfish size was not an important predictor of predation on the other prey categories, we present the feeding data by size strata within each area because we believe this variability is biologically important.

In the east area, the flyingfishes were the most important prey group overall for dolphinfish of the three smallest size classes and of the largest size class. For the two size classes between 951 and 1250 mm, frigate and bullet tuna (*Auxis* spp.), snake mackerels (Gempylidae), and epipelagic cephalopods were dominant (Fig. 5, east).

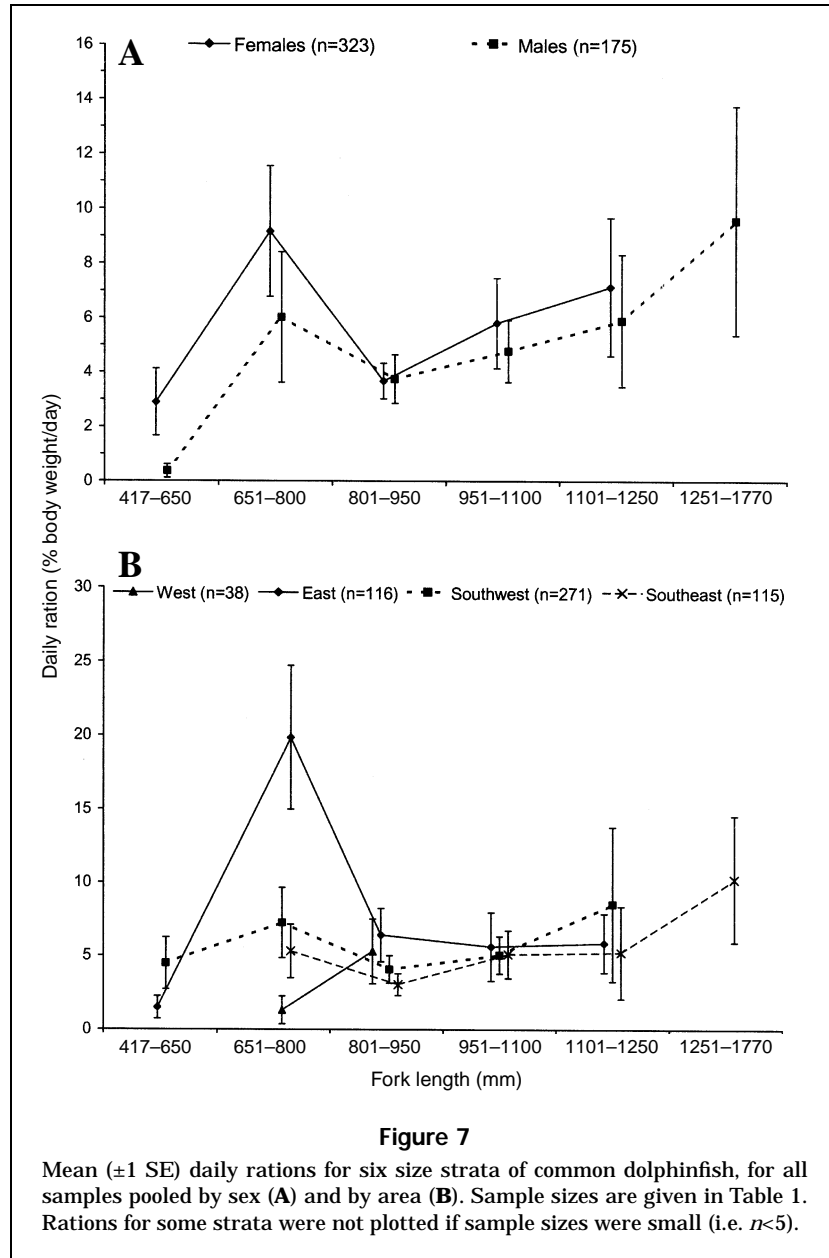


In the southwest area, few large common dolphinfish were sampled (Table 1). The flyingfishes were important prey for the four smallest size groups (up to 1100 mm). Epipelagic cephalopods were important for the smallest and two largest size groups. *Auxis* spp. represented over 46% of the diet of dolphinfish between 651 and 800 mm fork length (Fig. 5, southwest).

In the southeast area, the epipelagic cephalopods dominated the diet (52–90%) of dolphinfish of all five size strata (Fig. 5, southeast). The flyingfishes comprised most of the remaining prey composition in the 651–800 and 801–950 mm categories, and *Thunnus* spp. (assumed to be mostly yellowfin tuna) comprised most of the remaining in the 951–1100 and 1101–1250 mm categories.

Prey size

We present the sizes of cephalopod, crustacean, and fish prey found in the dolphinfish stomach contents in Figure 6A. Intact prey ranged from 14 to 650 mm in length, and averaged 160 mm overall. The data smoothed with a smoothing spline showed an increasing trend of prey size with dolphinfish size. The maximum prey sizes increased gradually for dolphinfish up to about 760 mm, then abruptly to a maximum of about 600 mm for dolphinfish of approximately 1000 mm. This pattern was largely consistent for fish and cephalopod prey. Crustacean prey were small, but were consumed by a wide size range of dolphinfish.



The ratios of prey length to predator length ranged from 0.014 to 0.720, and averaged 0.177 (Fig. 6B). The length ratios, smoothed with a smoothing spline, showed a slight decreasing trend with dolphinfish size.

Consumption rates

The values of A_i (Eq. 1) chosen for the various prey taxa are listed in Table 2. We estimated a daily ration of $5.6 \pm 0.56\%$ (mean ± 1 SE) of body weight per day for all common dolphinfish samples pooled. Mean ration estimates stratified by sex ranged from 0.4% of body weight per day for males of the smallest size group to 9.6% for males of the largest size group (Fig. 7A). Except for the 801–950 mm stratum, mean rations increased with dolphinfish size. Ration esti-

mates were comparable for females and males, except for those in the smallest size stratum. The estimate for females in the 1251–1700 mm class was excluded from Figure 7A owing to a low sample size ($n=2$).

We present mean (± 1 SE) daily ration estimates stratified by area in Figure 7B, if sample sizes were five fish or more. The calculations revealed that the 25 fish of the 651–800 mm group from the east area had ingested large amounts of food. These dolphinfish accounted for the high rations overall for both males and females of that size class (Fig. 7A). Except for that group and perhaps the 651–800 mm group in the west area, the ration estimates were comparable for all size classes in all areas (Fig. 7B). The number of empty stomachs did not unduly influence the consumption estimates by area. The percent of empty

stomachs (or containing only hard parts) ranged from 51% to 66% for the southeast, southwest, east, and west areas, respectively.

Discussion

Four previous studies of the food habits of common dolphinfish have been conducted in the EPO. Our results are difficult to compare meaningfully with those because they used different analytical techniques and had lower sample sizes. Larger sample sizes typically demonstrate greater trophic diversity (Manooch et al., 1983). Hida (1973) examined the stomachs of seven dolphinfish (two *C. hippurus* and five *C. equiselis*) caught at about 4°N–119°W. The largest component of the diet was flyingfishes (33%), followed by cephalopods (22%). Campos et al. (1993) sampled an unspecified number of *C. hippurus* caught off the Pacific coast of Costa Rica by experimental longline. Our results were similar to theirs in that flyingfishes was the most important component of the diet, and in both studies snake mackerel (Gempylidae) were found in the stomachs. Our samples from the east area, which encompasses the coastal waters of Costa Rica, contained more prey diversity, including mesopelagic fishes, portunid crabs, and penaeid shrimps. Campos et al. (1993) identified tuna of unknown species in the diet, and we found small amounts of predation on *Thunnus* spp. (yellowfin or bigeye tuna) in the east and southeast areas. Aguilar-Palomino et al. (1998) reported on the food habits of 500 *C. hippurus* caught by sport hook-and-line fishing in a small area at the tip of the Baja California peninsula, Mexico. They determined that the cephalopod *Dosidicus gigas* was the most important component of the diet, followed by the red crab *Pleuroncodes planipes*, a triggerfish, a flyingfish, and *Auxis* spp. Their results, however, could not be quantitatively compared with ours because they presented only the index of relative importance (IRI) (Pinkas et al., 1971), but not its three components (%W, %N, and %O). For example, it is impossible to determine if the apparent importance of *Dosidicus gigas* in their study was due to the presence of fresh biomass (i.e. high %W), the accumulation of numerous, small mandibles from previous meals (i.e. high %N and/or %O), or both. Likewise, the IRI indicated that small red crabs were important in the diet, but this index can be overly influenced by numerous small prey. We sampled only four dolphinfish in the north area near the south end of the Baja California peninsula and found some of the same prey taxa reported by Aguilar-Palomino et al. (1998). Lasso and Zapata (1999) analyzed the stomach contents of 228 *C. hippurus* using nonstandard methods. Their results were presented only by large categories, fishes, mollusks, and crustaceans.

Feeding periodicity

Our analysis of diel feeding periodicity suggests that, although common dolphinfish may be primarily visual predators (Massuti et al., 1998), they also feed at nighttime. Fish prey, such as flyingfishes, dolphinfishes, wahoo, and

snake mackerel, would need to be ingested during nighttime hours to reach digestion states 3 or 4 before 09:00 hours the next morning, as we observed in our study, unless gastric evacuation rates are much faster than expected. Shcherbachev (1973) concluded from the presence of partially digested flyingfishes, myctophid fishes, and squids in the stomachs of *C. hippurus*, and crustacea in *C. equiselis* that dolphinfishes feed around the clock in the Indian Ocean. Rothschild (1964) described active feeding on flyingfishes and myctophids at night by *C. hippurus* in the central Pacific. Massuti et al. (1998) found that almost half of the stomachs of *C. hippurus* sampled at sunrise contained mesopelagic prey. Massuti et al. (1998) and Oxenford and Hunte (1999) also concluded that common dolphinfish feed at night, as well as during the day.

Our data analysis by area revealed an apparent relationship between the principal prey taxa in the diet and feeding periodicity. In the southwest and southeast areas, recently eaten cephalopods were in the stomachs throughout the daytime sampling period, although no samples were taken in the southeast in the late afternoon (Fig. 3). In contrast, in the east area the dolphinfish preyed mostly on fishes (flyingfishes, *Auxis* spp., and gempylids) that require more time than cephalopods for gastric evacuation (Olson and Boggs, 1986). In the east area, recently eaten prey were present only in the early morning and early afternoon, and the food remains in the late morning and late afternoon were in advanced stages of digestion. These results suggest that foraging activity may have been influenced by the digestibility and energy content of the available prey. Cephalopods are typically low in energy content, whereas fishes store lipids in the musculature and viscera and have higher energy densities (Cummins and Wuycheck, 1971). Grove et al. (1978), Flowerdew and Grove (1979), and Jobling (1981) demonstrated that low-energy foods are emptied from the stomach more rapidly than foods of higher caloric content. Elevated lipid content in natural organisms is thought to have a retarding effect on gastric evacuation (Fänge and Grove, 1979). In yellowfin tuna, gastric evacuation rates were inversely correlated with total lipid content of four food organisms (Olson and Boggs, 1986). Apparently, the dolphinfish in the southwest and southeast areas spent more time foraging to fulfill their energy requirements than the dolphinfish in the east area.

Diet considerations

Our study indicated that only two prey groups, flyingfishes and epipelagic cephalopods, were dominant in the diet of common dolphinfish in the EPO (Fig. 4).

Diet differences we attributed to spatial stratification also had a seasonal component. Of the stomach samples obtained north of the equator in the north, west, and east areas, most (85%) of those that contained fresh food, were caught from May through November. The trends described for common dolphinfish in the southwest and southeast areas may also have been attributable to seasonality of the prey from December through April because all the dolphinfish in these areas were caught during these months.

The marked differences in food habits with predator size are noteworthy. For all areas combined, the general trend was for increased predation on cephalopods and decreased predation on flyingfishes as the dolphinfish grew larger. The exception was the smallest size group (417–650 mm). These dolphinfish ate 50% cephalopods and 40% flyingfishes by weight. Zavala-Camin (1986) also found greater predation on cephalopods by large dolphinfish (>850 mm) than by smaller specimens off Brazil.

Piscivores are known to feed selectively according to prey body size (Tonn et al., 1992). Maximum prey size is determined by the mouth gape of the predator (Magnuson and Heitz, 1971; Hambright, 1991), and minimum prey size was correlated with the gap width between the gill rakers for a variety of tunas, mackerels, and dolphinfishes (Magnuson and Heitz, 1971). Preference for the largest prey a predator can ingest is supported on theoretical grounds (Ivlev, 1961; Harper and Blake, 1988), but a survey of studies examining prey-size selectivities of piscivorous fishes showed a consistent pattern of selection for small prey (Juanes, 1994). In our study, the common dolphinfish of all sizes ingested small prey (Fig. 6A). Ratios of prey size to predator size for piscivores tend to average 0.2–0.3 (Juanes, 1994). In our study, the dolphinfish ingested prey that averaged slightly smaller, 17% of their length. A few dolphinfish ate prey that were greater than the maximum reported for piscivores, 50% of their length (Juanes, 1994).

Consumption rates

The method we employed for estimating daily rates of food consumption was judged by Cortés (1997) to be among the two most appropriate methods for top predators. However, applying gastric evacuation rates derived for yellowfin tuna to estimate daily rations of common dolphinfish requires justification. Suzuki's (1992) observations of gut-evacuation times of small dolphinfish do not unequivocally justify our assumption that gastric evacuation rates are comparable to those of yellowfin tuna, which were based on food passage through the stomach alone. However, energetics requirements suggest that gastric evacuation times for dolphinfish, at the same temperature, would be on the order of those for yellowfin. Our hypothesis is supported by the similar standard metabolic rates of common dolphinfish and yellowfin (Benetti et al., 1995; Brill, 1996). Brill (1996) argued that high rates of digestion are consistent for high-performance fishes like tunas, billfishes, and dolphinfishes and demonstrated that dolphinfishes share several characteristics of high-performance physiology with tunas and billfishes. Other, similar-size teleost fishes require about five times as long as yellowfin and skipjack to evacuate a meal (Magnuson, 1969; Olson and Boggs, 1986). Until gastric evacuation rates of dolphinfish are measured, we are confident that our first-order estimates are adequate approximations of daily rations of common dolphinfish in nature.

Our ration estimates for common dolphinfish are greater than those for yellowfin tuna of comparable size, estimated by the same method (Olson and Boggs, 1986; Olson and Mullen, 1986). Our estimates are consistent with the

observation that, although standard metabolic rates and locomotion costs are comparable for these species, common dolphinfish have greater growth rates than yellowfin (Uchiyama et al., 1986; Wild, 1986) and may require more energy for growth.

In summary, dolphinfish are an important component of the pelagic food web in the EPO, and as such, their feeding ecology provides clues to the underlying ecosystem structure. Clearly, *C. hippurus* imparts predation pressure on cephalopods, flyingfishes, and other prey that are shared by a suite of predators (Juhl, 1955; King and Ikehara, 1956; Blunt, 1960; Perrin et al., 1973; Nakamura, 1985; Olson and Boggs, 1986; Robertson and Chivers, 1997; Markaida and Sosa-Nishizaki, 1998). This predation pressure lends support to the hypothesis that cephalopods and flyingfishes are abundant or have high ratios of production to biomass (P/B) (or both) in the EPO. This hypothesis is based on 1) high consumption rates on these prey, indicated by the stomach contents in our present study, 2) high P/B of dolphinfish (Oxenford, 1999), 3) high consumption rates of cephalopods and flyingfishes by other predators (cited above), and 4) high P/B of those predators (Boggs, 1989; IATTC, 1999). This analysis illustrates the importance of diet studies for providing ecological insights.

Our study provides key data for implementing ecosystem analyses based on food-web models (Christensen and Pauly, 1992; Walters et al., 1997). For example, *Ecopath with Ecosim* (www.ecopath.org) requires data on both the diet compositions and consumption rates of predators. Accordingly, we summarized the prey data by several levels of taxonomic resolution and functional groups for dolphinfish sampled at multiple spatial scales and size classes. These data help lay the groundwork for a community- and ecosystem-level approach to fisheries management in the EPO.

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