THE FEEDING HABITS OF JUVENILE-SMALL ADULT BARRED SAND BASS (*PARALABRAX NEBULIFER*) IN NEARSHORE WATERS OFF NORTHERN SAN DIEGO COUNTY

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ABSTRACT

The feeding habits of juvenile-small adult barred sand bass (*Paralabrax nebulifer*) are described, based on 165 specimens 123-523 mm standard length (SL) collected between San Onofre and Oceanside, California, at depths ranging from 8 to 30 m. Collections were made during an annual cycle from March 1981 to March 1982.

The diet of the barred sand bass indicates that it forages in close proximity to the substrate. Brachyuran crabs, mysids, pelecypods, and epibenthic fishes were the most important prey. These findings are contrary to previous studies, which found northern anchovy (*Engraulis mordax*) to be of major importance in the diet of similar-sized bass. Three functional foraging categories were identified based on body size. The diet of small (< 240 mm SL) barred sand bass was unique because it included crustaceans such as mysids and gammarid amphipods, whereas large (> 320 mm SL) barred sand bass consumed larger prey such as *Porichthys notatus* (80-160 mm SL) and *Octopus*. Bass of intermediate size (240-320 mm SL) contained the species found in both large and small fish.

The temporal and spatial aspects of *Paralabrax nebulifer*'s feeding niche are distinct from those of the other demersal fishes of shallow, soft-bottom habitats in the Southern California Bight. These differences are discussed.

RESUMEN

La descripción de la alimentación de la cabrilla de arena, *Paralabrax nebulifer*, jóvenes y adultos, se basa en 165 ejemplares de 123 a 523 mm de longitud estándar (LE), capturados entre 8 y 30 m de profundidad en la zona que se extiende desde San Onofre hasta Oceanside, California. Las capturas se efectuaron durante un ciclo anual, desde Marzo de 1981 hasta Marzo de 1982.

La dieta de la cabrilla de arena indica que se alimentan en las proximidades del fondo marino. Las presas más importantes son cangrejos, misidáceos, pelecípodos y peces epibentónicos. Estas observaciones no concuerdan con estudios previos, los cuales consideran a la anchoveta del norte, *Engraulis mordax*, como el elemento más importante en la dieta de *P. nebulifer* de tallas similares a las analizadas durante esta estudio. La dieta de *P. nebulifer* pequeños (< 240 mm de longitud estándar) es distinta debido a la presencia de crustáceos (misidáceos y antípodos gamáridos), mientras que los ejemplares grandes (> 320 mm LE) consumieron presas grandes como *Porichthys notatus* (80-160 mm LE) y *Octopus*. *P. nebulifer* de talla mediana (240-320 mm LE) contenían en su estómago presas similares a las consumidas por los ejemplares grandes y pequeños.

El nicho alimenticio ocupado por *P. nebulifer* en cuanto a sus aspectos temporal y espacial resulta distinto al de otros peces demeresales habitantes de zonas someras y fondos blandos de a la Bahía del Sur de California. Estas diferencias son discutidas.

INTRODUCTION

The barred sand bass (*Paralabrax nebulifer*) is among the most poorly known of the popular sportfishes inhabiting the waters off southern California. Prior to 1957, *P. nebulifer* was insignificant in the partyboat catch, and it is believed that warm water conditions are responsible for its recent greater abundance (Frey 1971). Since the sixties, *P. nebulifer* has formed an important component of the sport catch (Feder et al. 1974). Unfortunately, catch statistics for barred sand bass have been combined with those for kelp bass (*Paralabrax clathratus*) within a general "rock bass" category (e.g., Frey 1971). The great abundance of barred sand bass on artificial reefs suggests that it may be the most valuable fish on such reefs (Turner et al. 1969). Most of the biological data gathered on *P. nebulifer* has been taken incidentally during studies of other species. Even management practices are based on life-history parameters determined for *P. clathratus* (Frey 1971).

Previous studies of the food habits of *Paralabrax nebulifer* have relied heavily on specimens collected on partyboats (Quast 1968b; Smith 1970). The authors of these studies have acknowledged that such collections attribute undue importance to northern anchovy (*Engraulis mordax*) as a prey item, since anchovies

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are used extensively as bait and chum on partyboats. In this report we characterize the feeding habits of *P. nebulifer*, from fish collected with a variety of methods in different habitats. Our findings should yield a more comprehensive understanding of the ecological interrelationships of the barred sand bass, its prey, and the fishes with which it co-occurs.

MATERIALS AND METHODS

Fish Collections

Paralabrax nebulifer were collected from 16 different locations ranging from 3-14 km northwest of Oceanside, California, from March 1981 to March 1982. Depths of capture were 8-30 m. (See Plummer et al. 1983 for a chart of the sampling region.) Fish were collected by spearfishing (40% of total specimens), otter trawls (36%), angling (23%), and lampara seines (1.2%). Angling was done during dawn and morning hours in the vicinity of giant kelp (*Macrocystis pyrifera*) beds and other rock and cobble reefs; spearfishing was done during midday (0900-1500 hrs). For angling, "scampi" lures were used in lieu of live bait. No collections were made in the vicinity of partyboats using live anchovies as chum. Cracked sea urchins were sometimes used as chum by spearfishers; however, urchin parts were easily identified in stomachs and were disregarded in the analysis. All trawling and seining were done over sandy substrates at various times of day and night.

Since, in most instances, fish were collected from particular locations with a consistent technique, at the same depth, and during the same diel period, these parameters were interrelated. Non-independence thus prevents us from comparing diets among microhabitats, longshore locations, diel periods, or depths. Different biases are inherent in each technique, and for each microhabitat and location. All data were therefore pooled to provide the best average characterization of feeding habits.

Analysis of Stomach Samples

Viscera were removed from *P. nebulifer* within one hour of capture and fixed in 10% Formalin. Eviscerated fish were returned to the laboratory to be sexed, weighed (0.1 g), and measured (standard length, SL in mm). After a minimum of four days fixation, viscera were soaked in tap water for 48-72 hrs and then stored in 70% ethanol.

Stomach contents were identified to the lowest taxonomic level permitted by condition of the material. In many cases, partially digested items could be identified only to the class level. Intestine contents were excluded from the analysis because these prey were often unidentifiable. The number and wet weights (0.01 g) of prey items were recorded. Mysid weights were reconstructed wet weights based on standardized values determined for each species by Marine Ecological Consultants of Southern California (L. Gleye, pers. comm.). The extent of prey digestion and stomach fullness were estimated on a scale from zero (totally undigested or empty) to 10 (digested or completely full).

Statistical Analysis of Diet

Prey were grouped into major taxonomic categories, usually at the class level, for comparing diet among *Paralabrax nebulifer* of different body sizes (Table 1). All analyses were based on these categories unless otherwise stated. This grouping resulted in the loss of species-level information; however, the number of *P. nebulifer* collected was not sufficient to adequately describe its diet at the species level, based on an analysis of the cumulative numbers of prey species in bass of three different body sizes (Figure 1). Taxon accumulation curves based on prey categories showed that the number of stomachs examined was sufficient to characterize the diet of *P. nebulifer* at this level of resolution. Since all prey items could not be identified

TABLE 1
All Prey Categories for *Paralabrax nebulifer*, Ordered by Percent Index of Relative Importance Values for the Small Size Class

	Size class		
Prey category	Small[a]	Intermediate[b]	Large[c]
Brachyurans	39.34	27.39	23.32
Pelecypods	18.39	24.10	—
Mysids	18.00	6.56	—
Fish	4.39	6.98	12.26
Carideans	4.23	9.46	0.75
Crustacean parts	4.04	0.88	0.36
Amphipods	3.15	—	—
Pelecypod siphons	2.89	0.43	0.37
Unidentifiable	1.58	9.30	8.58
Porichthys notatus	1.46	7.70	39.58
Ophiuroids	0.53	2.66	—
Urechis caupo	0.47	—	0.62
Gastropods	0.41	0.92	1.46
Polychaetes	0.40	0.60	2.94
Isopods	0.25	—	—
Bryozoans	0.12	—	—
Copepods	0.09	—	—
Octopus	0.08	—	7.60
Hydroids	0.07	—	—
Decapods—unident.	0.05	—	—
Anomurans	0.02	0.76	—
Ascidians	0.01	—	1.66
Macrurans	0.01	—	—
Algae	0.01	0.05	0.51
Holothuroids	—	0.77	—
Stomatopods	—	1.45	—

[a]<240 mm
[b]240-320 mm
[c]>320 mm

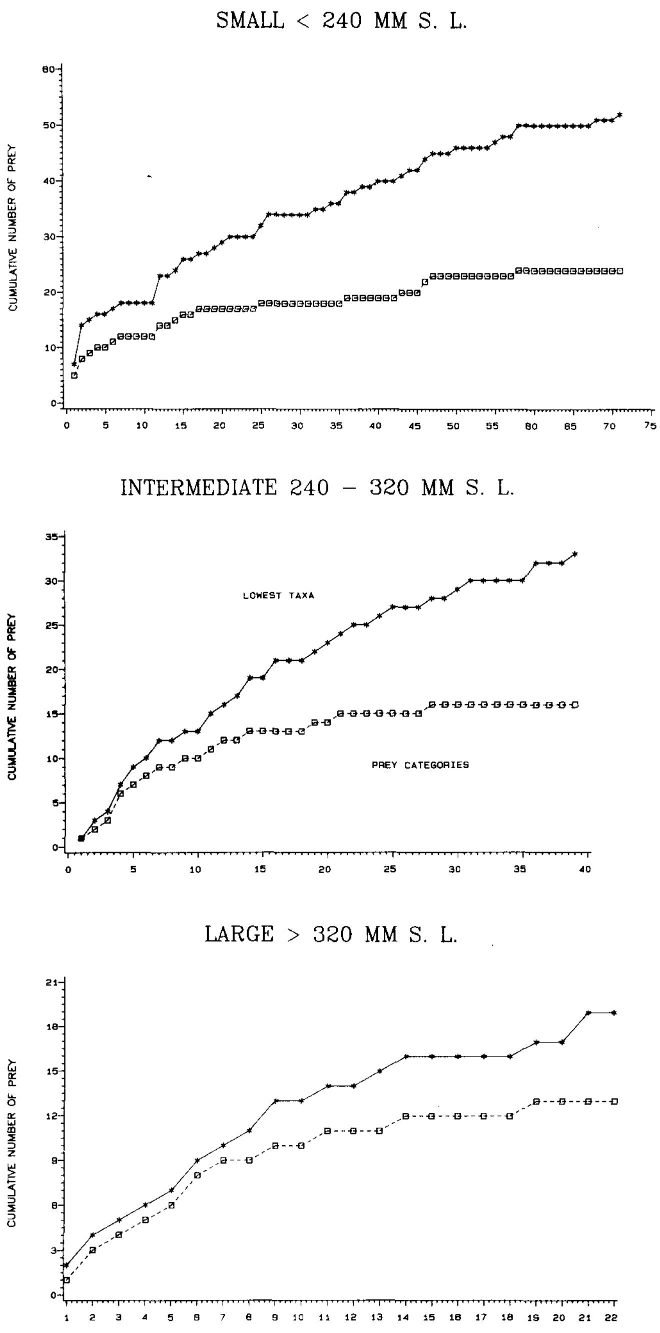

Figure 1. Cumulative frequency of prey categories and lowest prey taxa present in *Paralabrax nebulifer* of three different size classes. Analysis is based on prey present in individual fish selected randomly from the total fish in each size class.

to the species level, grouping prey into categories allowed comparisons to be made at a more uniform taxonomic level. When comparisons are made between prey categories at nonuniform taxonomic levels, the importance of more general categories such as "crustacean parts" obviously becomes exaggerated. Lowest-level identifications of all taxa with percent IRI values (see below) greater than one are presented in Table 2.

The contribution of each prey category to the diet of *Paralabrax nebulifer* was evaluated based on three commonly used measures of importance: percent number (% N), percent weight (% W), and the frequency with which each prey category occurred among all of the *P. nebulifer* sampled (% FO). An index of relative importance, IRI = (% N + % W) % FO (Pinkas et al. 1971) was derived. The IRI is particularly useful in that it combines % N, % W, and % FO into a single measure that also allows its three components to be evaluated separately.

In order to determine how *P. nebulifer*'s size affected its food preference, feeding data were analyzed separately for barred sand bass of three length (size) classes: small < 240 mm; intermediate, 240-320 mm; and large, > 320 mm SL. These three "feeding stanzas" were determined based on the method of Tyler (1978), which uses an iterative contingency Chi-square process applied to the presence-absence of major prey in the diet. Prey categories chosen for this analysis were mysids and fish.

Percent IRI values for dietary arrays of the three size classes were compared pair-wise using the Percent Similarity Index (PSI) (Whittaker 1952):

$$\mathrm{PSI} = 100 \sum_{i=1}^{S} \min\,(a_i, b_i),$$

where a_i and b_i were the percent IRI for the i^{th} prey category in the diets of fish of sizes A and B, respectively, and S is the total number of categories in the diets of fish of both sizes. This index was chosen because it has been shown to be an appropriate measure for comparing the diets of predators that feed on unequal numbers and proportions of prey items (Cailliet and Barry 1978). The PSI has also been shown to be independent of sample size differences between the groups being compared (Kohn and Riggs 1982). The prey category "unidentifiable" was not included in the calculations because it would bias comparisons toward artificially greater similarities.

RESULTS

From March 1981 to March 1982, 170 *Paralabrax nebulifer* were collected. They ranged in size from 123 to 523 mm SL, including 81 "small," 50 "intermediate," and 34 "large" individuals. The stomachs of five of these specimens were ruptured or everted upon capture and were disregarded. Small *P. nebulifer* had a lower proportion (x^2 = 8.1, 2 d.f., $0.02 > P > 0.01$) of empty stomachs (12.3%) than either intermediate (22.0%) or large (35.3%) individuals

TABLE 2
Contribution of Prey Taxa[a] to Diet of *Paralabrax nebulifer*

Lowest taxonomic classification	Prey category	Pct. number	Pct. wt.	Pct. freq.	IRI	Pct. IRI
Small *P. nebulifer* (< 240 mm SL)						
Neomysis kadiakensis	Mysids	30.4	1.7	8.5	271.7	16.2
Misc. crustacean parts	Crustacean parts	4.4	1.2	29.6	166.5	9.9
Pelecypoda	Pelecypods	2.4	9.2	14.1	162.6	9.7
Caridea	Carideans	6.1	2.0	19.7	158.9	9.5
Solenidae-siphons	Pelecypod siphons	5.2	1.8	16.9	119.1	7.1
Majidae	Brachyurans	3.0	3.1	18.3	113.0	6.7
Solen sicarius	Pelecypods	1.2	13.6	5.6	83.5	5.0
Cancer—unident.	Brachyurans	2.2	2.6	14.1	67.6	4.0
Unident. material	Unidentifiable	2.4	0.9	19.7	65.2	3.9
Porichthys notatus	*Porichthys*	0.3	21.0	2.8	60.0	3.6
Caprellid amphipod	Amphipods	5.1	0.1	9.9	50.8	3.0
Brachyura	Brachyurans	1.9	1.6	14.1	48.9	2.9
Cancer—3 ident. spp[b]	Brachyurans	1.5	1.4	12.7	36.8	2.2
Engraulis mordax	Fish	1.2	10.4	2.8	32.6	1.9
Teleostei	Fish	1.5	1.2	11.3	30.7	1.8
Metamysidopsis elongata	Mysids	5.2	0.0	5.6	29.7	1.8
Ophiuroid	Ophiuroids	1.4	0.9	9.9	21.8	1.3
Pinnixa sp	Brachyurans	1.5	0.5	9.9	20.1	1.2
Urechis caupo	*Urechis*	0.2	13.6	1.4	19.4	1.2
Gammarid amphipod	Amphipods	1.7	0.1	9.9	17.3	1.0
Intermediate *P. nebulifer* (240-320 mm SL)						
Unident. material	Unidentifiable	6.4	1.7	33.3	271.4	18.1
Porichthys notatus	*Porichthys*	2.0	41.8	5.1	224.6	15.0
Pelecypoda	Pelecypods	4.5	5.4	15.4	151.8	10.1
Caridea	Carideans	5.9	0.9	17.9	123.6	8.2
Teleostei	Fish	2.0	8.3	10.3	105.6	7.0
Neomysis kadiakensis	Mysids	35.6	1.2	2.6	94.4	6.3
Ophiuroid	Ophiuroids	3.5	0.9	17.9	77.8	5.2
Brachyura	Brachyurans	2.5	2.0	12.8	56.9	3.8
Solen sicarius	Pelecypods	1.5	5.6	7.7	54.6	3.6
Alpheus sp	Carideans	2.0	3.1	10.3	52.1	3.5
Squilla sp	Stomatopod	1.0	7.3	5.1	42.3	2.8
Pyromaia tuberculata	Brachyurans	3.0	0.8	10.3	38.7	2.6
Cancer—unident.	Brachyurans	2.0	0.7	10.3	27.3	1.8
Misc. crustacean parts	Crustacean parts	2.0	0.5	10.3	25.6	1.7
Holothuroidea	Holothuroids	0.5	8.2	2.6	22.4	1.5
Anomura	Anomurans	1.0	3.3	5.1	22.2	1.5
Polychaeta	Polychaetes	1.5	0.8	7.7	17.4	1.2
Pectinidae	Pelecypods	5.9	0.2	2.6	15.8	1.1
Engraulis mordax	Fish	2.5	0.5	5.1	15.1	1.0
Large *P. nebulifer* (> 320 mm SL)						
Porichthys notatus	*Porichthys*	20.0	35.7	22.7	1266.5	49.0
Cancer antennarius	Brachyurans	12.5	12.2	13.6	337.4	13.1
Unident. material	Unidentifiable	10.0	5.1	18.2	274.5	10.6
Octopus sp	*Octopus*	5.0	21.7	9.1	243.1	9.4
Teleostei	Fish	7.5	0.6	13.6	110.6	4.3
Polychaeta	Polychaetes	7.5	2.8	9.1	94.0	3.6
Salpidae	Ascidians	2.5	9.2	4.5	53.0	2.1
Embiotocidae	Fish	2.5	8.0	4.5	47.7	1.8

[a]Only taxa with IRI values greater than or equal to 1.0% have been listed.
[b]Juv. rock crabs: includes *Cancer antennarius, C. anthonyi,* and *C. jordani.*

(Table 3). For bass whose stomachs contained food, there was no correlation between either fullness or the extent of prey digestion and the time of capture (fullness: Spearman's rho = -0.14, $P = 0.12$; digestion: rho = -0.12, $P = 0.18$; both $n = 132$). *P. nebulifer* fed almost exclusively on epibenthic prey. Sixty-nine total prey taxa were grouped into 26 categories based on taxonomic and, in a few cases, morphological criteria (e.g., pelecypod siphons) (Tables 1 and 2).

The extent to which many prey categories were exploited was a function of predator size (Figures 2 and 3). Small *P. nebulifer* consumed a large number of small prey like the mysid shrimp *Neomysis kadiakensis* and *Metamysidopsis elongata* (Table 2; Figure 3).

TABLE 3
General Characterization of the Feeding Habits of *Paralabrax nebulifer*

	Size class (mm)			All sizes
	<240	240-320	>320	
No. stomachs	81	50	34	165
% empty stomachs	12.3	22.0	35.3	20.0
Total no. prey items	592	202	40	834
Total wt. prey items (g)	152.0	213.2	365.4	730.6
Mean no. prey items per stomach with food	8.3	5.2	1.8	6.3
Mean wt. prey items (g)	2.1	5.5	16.6	5.5
Mean no. prey categories per stomach	2.7	2.1	1.4	2.3
Mean no. lowest level prey taxa per stomach	3.2	2.3	1.4	2.6

The most important prey was brachyuran crabs, whose IRI value was over one-third of the total value (Table 1; Figure 3). Brachyurans were also important for *P. nebulifer* of intermediate size. Brachyurans ranked first in IRI and occurred in 41% of the stomachs that contained food (Table 1; Figure 3). Although mysids remained the most numerous prey, they were not as significant for intermediate-sized *P. nebulifer* as for small bass, owing to the increased importance of carideans and fish. Fish were even more important prey of large *P. nebulifer*. Like bass of intermediate size, large fish relied heavily on *Porichthys notatus*. This species of toadfish ranked first by IRI, whereas all other fish prey ranked third (Table 1; Figure 3). *Cancer antennarius* was the most important brachyuran found in large *P. nebulifer*.

Although many components of the diet of *P. nebulifer* change ontogenetically, certain prey were consistently found in bass of more than one size class. Brachyurans (particularly majid crabs) occurred with approximately equal frequencies over nearly the entire size range of fish (Figures 2 and 3). Pelecypods were important to both small and intermediate *P. nebulifer*, although conspicuously absent from the diet of large fish (Figures 2 and 3).

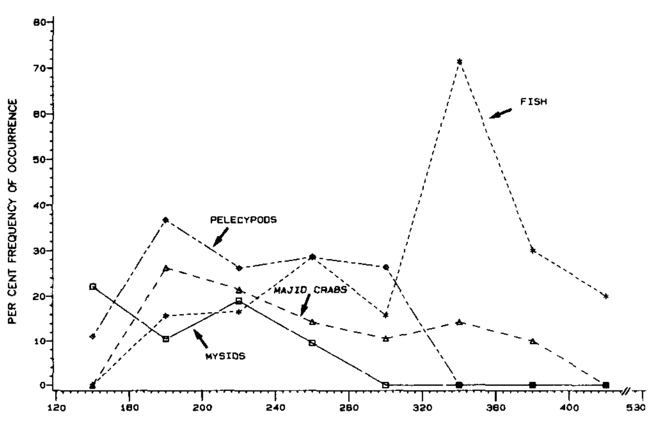

Figure 2. Four representative patterns of change in the frequency of prey occurrence for different sizes of *Paralabrax nebulifer*. Analysis is based on prey present in 40-mm size classes, with the exception of fish > 400 mm (N = 5 fish, with the largest 523 mm SL), for which the class interval was 130 mm. Data are plotted at midpoints of the class intervals.

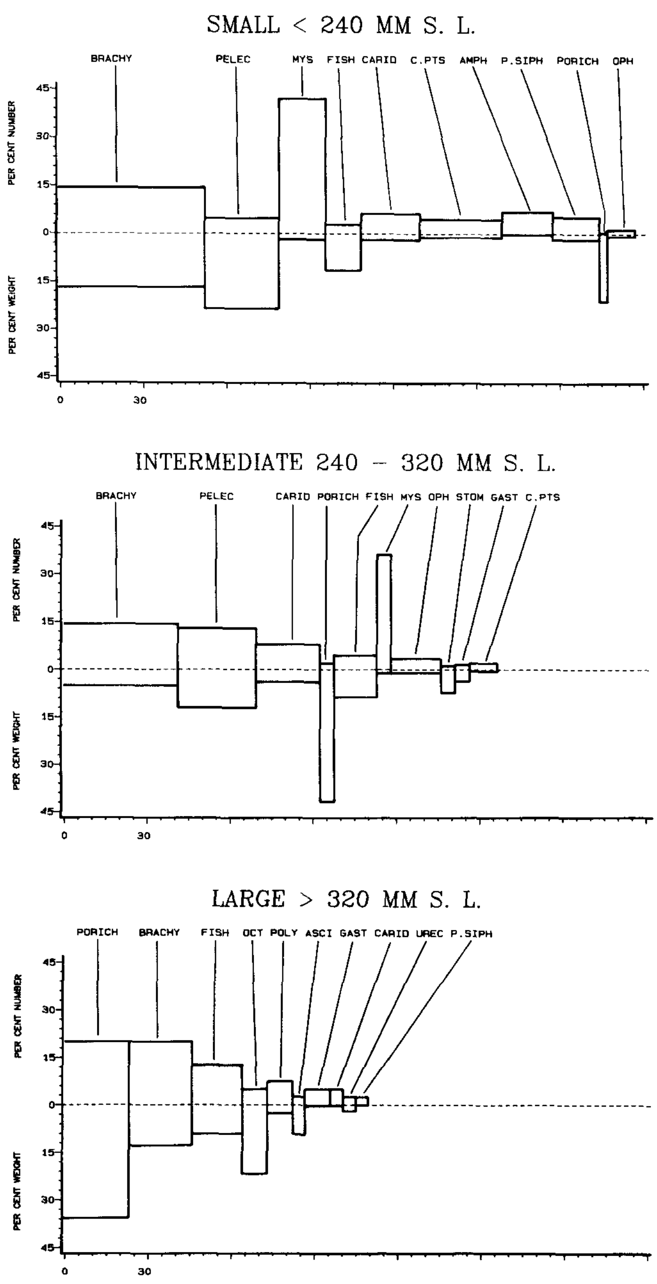

Figure 3. Relative importance of the top 10 (by IRI, ordered from left to right) categories of prey consumed by *Paralabrax nebulifer* of three different size classes, as expressed by % number, % weight, % frequency of occurrence and IRI.
Key to abbreviations: Amph = amphipods; Asci = ascidians; Brachy = brachyurans; C. pts = crustacean parts; Carid = carideans; Gast = gastropods; Mys = mysids; Oct = octopods; Oph = ophiuroids; P. siph = pelecypod siphons; Pelec = pelecypods; Poly = polychaetes; Porich = *Porichthys notatus*; Stom = stomatopods; Urec = *Urechis caupo*.

The greatest overall dietary similarity was between small and intermediate barred sand bass (PSI = 65.1); greatest dissimilarity was between the small and large size classes (PSI = 32.0). The diets of *P. nebulifer* of large and intermediate sizes overlapped to a moderate extent (PSI = 41.0).

DISCUSSION

The very generalized (Hobson 1974) serranid morphology of *Paralabrax nebulifer* allows it to occupy a uniquely cosmopolitan feeding niche in shallow sandy, rocky, and kelp bed habitats of the Southern California Bight. Diet, habitat preference, and feeding behavior also distinguish *P. nebulifer* from the species with which it co-occurs.

Habitat preference isolates *P. nebulifer* from two co-occurring congeners, the spotted sand bass (*Paralabrax maculatofasciatus*) and the kelp bass (*Paralabrax clathratus*). Although *P. nebulifer* can be found near kelp beds, rocky reefs, and within bays, it prefers shallow (generally < 30 m deep) sand-bottom habitats (Limbaugh 1955; Feder et al. 1974; Ebeling et al. 1980). Large numbers of these fish have been observed on sand plains in the vicinity of artificial reefs (Turner et al. 1969; Davis et al. 1982). *P. maculatofasciatus* prefers warmer water (Stephens and Zerba 1981) and is generally found near eelgrass beds and around harbors and rock jetties (Limbaugh 1955; Feder et al. 1974). *P. clathratus* prefers kelp beds and rocky reefs to sandy habitats (Limbaugh 1955; Quast 1968a; Feder et al. 1974); in kelp beds it frequently occurs throughout the water column (Ebeling et al. 1980). Although both *P. clathratus* and *P. nebulifer* could be classified as food generalists, the two species feed on fundamentally different prey because of microhabitat differences. *P. clathratus* feeds mainly on plankton and free-swimming nekton (Quast 1968a; Love and Ebeling 1978; Hobson et al. 1981), whereas *P. nebulifer* primarily consumes demersal prey (Limbaugh 1955; Quast 1968b; Turner et al. 1969; Smith 1970; Feder et al. 1974; Davis et al. 1982; this study, Tables 1 and 2; Figure 3).

There is some dietary overlap between *P. nebulifer* and other demersal fishes that occupy shallow, soft-bottom habitats off southern California. Major prey and foraging behavior, however, usually differ among the various species. The bothids *Citharichthys sordidus, C. stigmaeus, Hippoglossina stomata*, and small *Paralichthys californicus* feed on small epibenthic and meroplanktonic crustaceans such as copepods, amphipods, and mysids (Allen 1982; Plummer et al. 1983). Although small *P. nebulifer* feed on these prey (particularly mysids), demersal macroinvertebrates (brachyurans, pelecypods) are more important in the diet (Table 1; Figure 3).

The scorpaenid *Scorpaena guttata* and the bothid *Xystreurys liolepis* are the two demersal, soft-bottom species whose general food and habitat are most similar to that of *Paralabrax nebulifer.* Both *S. guttata* and *X. liolepis* also feed heavily on crabs (IRI values of 60% and 45%, respectively; Allen 1982). Each species forages at least partly by ambushing prey (Allen 1982; authors' obs.).

Paralabrax nebulifer, Scorpaena guttata, and *Xystreurys liolepis* are ecologically distinct, however, in their preferred depths, foraging microhabitats, and feeding behaviors. *Scorpaena guttata* appears to segregate bathymetrically from both *X. liolepis* and *P. nebulifer*. Shallow-water scuba surveys have characterized both *S. guttata* and *P. nebulifer* as species that prefer depths less than 26 m (Limbaugh 1955; Turner et al. 1969; Feder et al. 1974). Although this is likely true for *P. nebulifer*, trawl surveys reported in Allan (1982) showed that *S. guttata* was most common in deeper (50-m) water. *Xystreurys liolepis* occurred most frequently in trawls made at 10-m depth (Allen 1982).

Flatfishes like *Xystreurys liolepis* are adapted to forage in ways unlike those of roundfishes (Allen 1982). *Paralabrax nebulifer*, like *S. guttata,* feeds on prey that are active upon the substrate surface; but the frequent occurrence of entire pelecypods (in addition to clam siphons) in its diet suggests that the sand bass also is able to disinter prey buried close to the sediment surface. Burrowing forms such as callianassids and hoplocarid (mantis) shrimp and the echiuroid *Urechis caupo* probably are seized when they appear at the entrances to their burrows. Pinnotherid crabs, known to inhabit such burrows, and clam siphons (Prince 1975) were also found in some stomachs.

Paralabrax nebulifer and *Scorpaena guttata* are known to differ in diel foraging patterns. *S. guttata* is nocturnal (Turner et al. 1969; Fager 1971; Allen 1982). *P. nebulifer* is most active during the day (Fager 1971); the presence of certain nocturnal prey (*Porichthys notatus:* Arora 1948; Ibara 1970; *Octopus* and brachyurans: Ebeling and Bray 1976; Hines 1982) also support Fager's (1971) observations of some crepuscular activity.

Like the rockfishes (genus *Sebastes*) of California waters, *Paralabrax* spp possess a swim bladder. *Scorpaena guttata* does not. Most abundant shallow-water rockfishes of the bight are either limited to rough, rocky bottoms (e.g., *Sebastes chrysomelas, S. carnatus:* Larson 1980), are largely restricted to kelp forests (*S. atrovirens*: Coyer 1979), or have midwater habits (*S. mystinus, S. serranoides*: Love and Ebeling 1978).

The rockfishes that occupy soft-bottom habitats are most abundant in much deeper water (Allen 1982). *Paralabrax nebulifer* seems morphologically adapted to forage like a demersal rockfish, and has successfully adopted that feeding mode in sand-rock ecotone and sandy bottom habitats. A swim bladder affords enhanced mobility (Allen 1982) and has allowed *P. nebulifer* to forage in a manner unlike any other large-mouthed, demersal fish of local, shallow, soft bottoms.

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