Abstract.– The diets of pelagic juveniles of widow rockfish *Sebastes entomelas*, yellowtail rockfish *S. flavidus*, chilipepper *S. goodei*, shortbelly rockfish *S. jordani*, and bocaccio *S. paucispinis* were compared using samples collected during 1984–87. All five species co-occur as pelagic juveniles off central California. Frequency of occurrence, percent by number, and a ranking index of prey items were determined from 1088 stomachs. Major prey of pelagic juvenile rockfish were the various life stages of calanoid copepods and sub-adult euphausiids (including eggs).

For each year, dietary overlap was quantified between interspecific pairs using the Colwell and Futuyma (1971) index. Amount of overlap varied from year to year. Long-term intraspecific dietary overlap, based on the 4 years of data, was generally less than interspecific overlap within years. Year-to-year variation in the diets of these species was generally greater than within-year variation among them, suggesting that, as a group, pelagic juvenile rockfishes are opportunistic feeders. Also, if interannual variation in the distribution and abundance of foods has a major impact on recruitment, the high dietary overlaps of these co-occurring species would suggest parallel survival and year-class success.

Multivariate analysis of variance was used to examine the effects of latitude, depth, and fish size on food consumption. Alterations in diet were related to latitude, depth, and a latitude-depth interaction for three species in 1987 and, also, for shortbelly rockfish in 1984–86. Diet was apparently unrelated to fish size.

Interannual variation and overlap in the diets of pelagic juvenile rockfish (Genus: *Sebastes*) off central California

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Rockfishes of the genus *Sebastes* are a major component of the west coast groundfish fishery (Gunderson and Sample 1980), yet little is known of their early life history. Kendall and Lenarz (1987) noted a particular lack of information on the biology of the pelagic juvenile life-stage. To date most work on pelagic juveniles has addressed problems in identification (e.g., Moser et al. 1977, Laroche and Richardson 1980 and 1981, Matarese et al. 1989), growth (Boehlert 1981a, Boehlert and Yoklavich 1983, Penney and Evans 1985, Laidig et al. 1991, Woodbury and Ralston 1991), and vertical distribution (Boehlert 1977 and 1981b, Moser and Alhstrom 1978, Moser and Boehlert 1991, Lenarz et al. 1991).

Female rockfishes undergo internal fertilization and the eggs develop within the ovary for a 40–50 day period (Kendall and Lenarz 1987). Larvae hatch internally, are extruded approximately 1 week later, and begin feeding. Larvae grow and transform into juveniles, a developmental stage characterized by the attainment of full meristic characters. Many rockfishes have a pelagic juvenile stage. Pelagic juveniles ranging in size from 15–100 mm SL are abundant off central California from April to June, although distributional patterns vary markedly among species and years (Wyllie Echeverria et al. 1990). The pelagic juvenile stage ends with settlement into demersal or nearshore habitats.
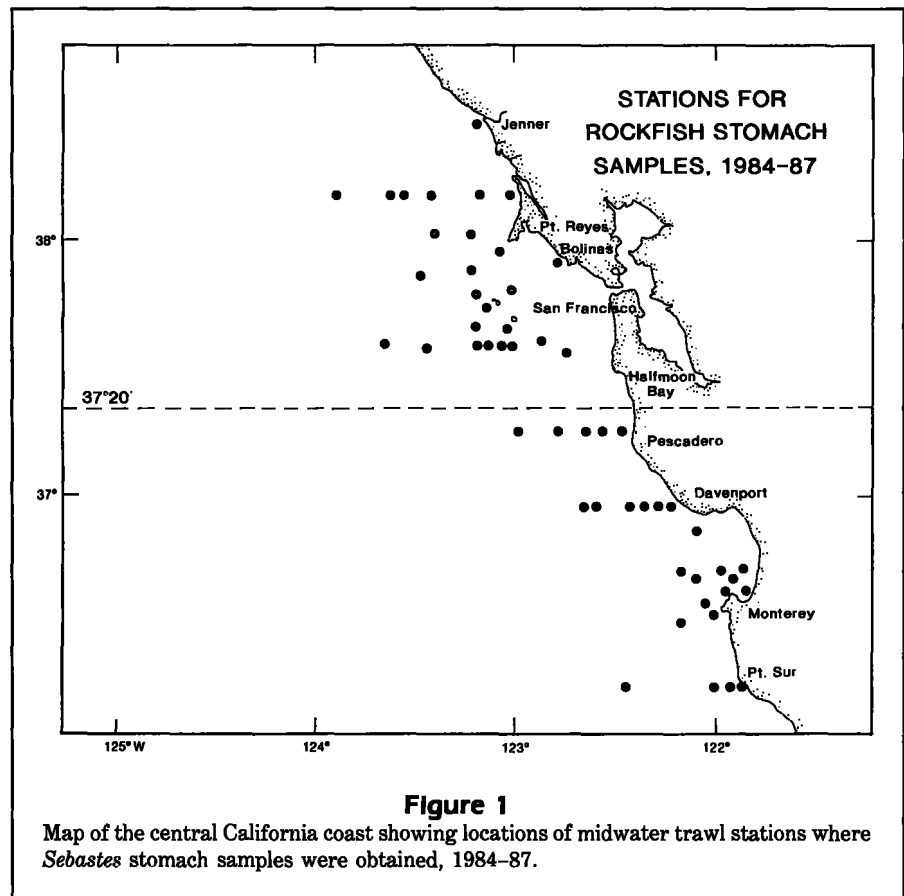
Evidence strongly indicates that the recruitment of marine fishes is heavily influenced by events that occur early in the life history (Blaxter 1974). A frequently proposed explanation is that the availability and abundance of foods appropriate for first-feeding larval and later juvenile stages are critical to adequate survival and growth. A reduction in the fine-scale density of suitable prey items, whether due to an absolute decrease in prey abundance (Hjort 1914) or to a randomized dispersion of what formerly was a patchy prey resource (Lasker 1975), can have a negative impact on survival. Reduced prey densities can affect survivorship directly through starvation, or indirectly by reducing growth rates and thereby prolonging exposure to other size-specific mortality factors

(e.g., predation, advection, etc.). Regardless of the mechanism, variation in the availability of food can have a major effect on year-class strength (Lasker 1981). The study of food utilization patterns and diet overlap is, therefore, useful in understanding survival mechanisms during the pelagic juvenile life stage. Moreover, annual variation in the extent of interspecific dietary overlap may indicate changes in the distribution and abundance of prey (e.g., Zaret and Rand 1971). Since this may well be critical in determining the success of a year-class, similarity in food habits among pelagic juvenile rockfish may result in similar recruitment dynamics.

Previous published dietary studies of juvenile rockfish have been limited to (1) experimental work on food ration and growth in black rockfish (*S. melanops*, Boehlert and Yoklavich 1983); (2) a description of the diet of newly settled Pacific ocean perch (*S. alutus*, Carlson and Haight 1976); (3) a comparison of the food habits of seven *Sebastes* spp. in a nearshore kelp-forest habitat (Singer 1985); and (4) predation on barnacle larvae by a mixed assemblage of settled kelp resident juvenile rockfishes (Gaines and Roughgarden 1987). The purpose of this study was to examine the feeding ecology of several co-occurring young-of-the-year pelagic juvenile rockfishes, including widow rockfish *S. entomelas*, yellowtail rockfish *S. flavidus*, chili-pepper *S. goodei*, shortbelly rockfish *S. jordani*, and bocaccio *S. paucispinis*. Specific goals of this study were to (1) identify the food habits of these five species during the pelagic juvenile stage, (2) determine the extent of dietary overlap among the five species, and (3) determine the degree of interannual variation in patterns of prey utilization.

Materials and methods

Juvenile rockfish used in this study were obtained from midwater trawl samples made during a series of annual pelagic juvenile rockfish surveys conducted off central California during 1984–87. Details of these surveys are described in Wyllie Echeverria et al. (1990).

Figure 1
Map of the central California coast showing locations of midwater trawl stations where *Sebastes* stomach samples were obtained, 1984–87.

The primary purpose of the surveys was to estimate the distribution and abundance of the pelagic-stage juveniles of age-0 rockfishes. Survey areas and dates differed somewhat from year to year (Fig. 1, Table 1). The surveys were conducted during June, except in 1987 when the survey extended from late-May to June. In 1984 and 1985, the survey area extended from Point Sur (lat. 36°18′N) to Point Cabrillo (lat. 39°20′N). Bottom depths at each trawl station ranged from <50 m at nearshore localities to >3700 m beyond the continental shelf. The sampling plan was revised in 1986; seven transects composed of 36 stations were selected based on previous records of rockfish abundance and the availability of ship time. These stations were sampled repetitively during three consecutive sweeps of the area. After 1985, the survey area extended from Cypress Point (lat. 36°35′N) to Point Reyes (lat. 38° 00′N), with station depths ranging from <50 to 1000 m.

Collections were made from the RV *David Starr Jordan* with a modified Cobb midwater trawl net having a 24.4 m head rope and 0.76 cm mesh liner in the codend. The standard depth sampled was 30 m. However, at shallow stations (bottom depth <100 m) the net was set at 5–10 m. At some deep stations samples were

Table 1

Number of juvenile *Sebastes* stomachs examined from juvenile rockfish surveys, 1984–87.

Year	Survey dates	Species	No. of stomachs	Range (mm SL)
1984	8–24 June	Widow rockfish	15	40–63
		Yellowtail rockfish	40	36–56
		Chilipepper	20	38–55
		Shortbelly rockfish	120	30–65
		Bocaccio	50	21–77
1985	5–30 June	Widow rockfish	75	43–63
		Yellowtail rockfish	30	39–48
		Shortbelly rockfish	85	49–75
1986	3–25 June	Yellowtail rockfish	10	35–47
		Shortbelly rockfish	168	15–47
		Bocaccio	25	18–40
1987	23 May–21 June	Widow rockfish	105	48–80
		Yellowtail rockfish	17	39–52
		Chilipepper	125	41–76
		Shortbelly rockfish	150	17–78
		Bocaccio	53	22–86
Total stomachs examined			1088	

also collected at 100 m. Nets were fished for 15 min at depth during the night, ~30 min after sunset, or before sunrise.

Five specimens of each species were randomly subsampled from each haul for dietary analysis. Generally, no samples were taken if fewer than five individuals were taken in a haul. Specimens were tentatively identified to species and preserved whole in 10% buffered formalin, usually within 1 hour of collection. Identifications were later verified ashore with meristics keys (Matarese et al. 1989, Moreland and Reilly 1991); samples were transferred to 70% isopropyl alcohol within 1 month of collection. Standard length (SL) was later measured to the nearest 0.1 mm. Stomachs were removed and stored in 70% isopropyl alcohol until examined.

Stomach contents were examined with a dissecting microscope. Empty stomachs were noted and the digestive state of each prey item was coded on a scale of 1–3, with 3 representing digestion too advanced for identification. All prey types were identified to the lowest possible taxonomic level and counted. When possible, a subsample of all prey types was measured along the longest axis with an ocular micrometer. Heads or eyes were used to obtain total counts when food items were fragmented. For each rockfish species, the proportion of prey types in the diet was calculated as the percentage of total prey numbers consumed in a year, summed over all the individuals examined for stomach contents.

A ranking index, modified from Hobson (1974), was calculated for the major food items. The index (I_r) is the product of proportional frequency of occurrence and percent by number, calculated for all specimens of a species in a year. To quantify dietary overlap among species, the index of Colwell and Futuyma (1971) was used, that is,

$$C_{ih} = 1.0 - 0.5 \left(\sum_{j=1}^{n} p_{ij} - p_{hj} \right),$$

where p_{ij} and p_{hi} are the numerical proportions of prey $j = 1 \ldots N$ found in the diets of species i and h, respectively. The index has a minimum value of zero, when no overlap occurs, and a maximum value of one, when all prey are shared in equal proportions by the two species.

Multivariate analysis of variance (MANOVA) was used to examine relationships among latitude, bottom depth, and the diets of chilipepper, shortbelly, and widow rockfish (Green 1978, SAS 1985). Although only in 1987 were there sufficient data to analyze the diets of all three species, adequate samples of shortbelly rockfish were obtained during all years (1984–87). Thus, examination of overall variation in diet through time, vis-à-vis latitude and depth, was limited to shortbelly rockfish. Analyses were confined to the three prey types of highest frequency of occurrence during the year examined, which varied among the different species and years. The numerical proportions of the three prey types (the dependent variables) were arcsine-transformed (Sokal and Rohlf 1981) prior to MANOVA testing. Latitude, depth, and a latitude-depth interaction term were the independent variables. Station latitude was classified as either north or south of lat. 37°20′N. Similarly, station depth was divided into deep (>100 m) or shallow (<100 m) categories. Data for chilipepper, shortbelly, and widow rockfish sampled in 1987 were also divided into large (>1987 median SL) and small (<1987 median SL) size-classes to examine diet variation as a function of fish size. Shortbelly rockfish were sufficiently numerous during all years to analyze diet variation as a function of predator size. Prey types for this analysis were again limited to the three prey categories with the highest overall frequencies of occurrence in a year, and the dependent variables were the arcsine-transformed numerical proportions in the diet.

Table 2

Summary of stomach contents for five species of pelagic juvenile *Sebastes*, 1984. FO = frequency of occurrence; % = percent by number.

Prey category	Widow rockfish (*n* 15) FO	%	Yellowtail rockfish (*n* 40) FO	%	Chilipepper (*n* 20) FO	%	Shortbelly rockfish (*n* 120) FO	%	Bocaccio (*n* 50) FO	%
EUPHAUSIACEA										
Furcilia	33.3	10.1	50.0	12.3	30.0	6.8	54.2	35.1	36.0	24.1
Calyptopis			2.5	0.3			1.0	0.1	2.0	0.2
Juveniles	20.0	3.2	15.0	3.4	15.0	2.6	14.1	10.2	38.0	25.3
AMPHIPODA										
Hyperiid juveniles							1.0	0.1	4.0	0.3
CUMACEA							1.7	0.1		
DECAPODA										
Natantia juveniles	6.7	0.5					1.0	0.2		
COPEPODA										
Calanus spp.	46.7	41.0	52.5	28.7	40.0	27.2	40.8	15.1	34.0	31.6
Candacia sp.			5.0	0.4			6.7	0.5	2.0	0.2
Copepods (unidentified)	26.7	17.6	47.5	14.7	15.0	10.5	36.7	12.0	30.0	15.8
Juveniles	20.0	27.7	17.5	40.2	40.0	52.9	10.8	26.8	2.0	0.9
OSTEICHTHYES										
Fish larvae (unidentified)									20.0	1.7

Results

Frequency of occurrence and percent number

Stomachs from 1088 pelagic juvenile rockfish collected from midwater trawls during the four survey years (Table 1) were examined. Frequency of occurrence and percent number for specific prey types of each rockfish species varied considerably from year to year (Tables 2–5). In 1984, bocaccio differed from all other rockfish species in the frequency of occurrence of fish larvae as a prey type (Table 2). Euphausiid eggs occurred in the stomachs of all three species in 1985, although there is a disparity in the percent number (Table 3). Euphausiid eggs were much less frequent in the diets of the three rockfish species in 1986 (Table 4), whereas juvenile euphausiids occurred more frequently. Overall, data from 1984–87 show that prey items having a high frequency of occurrence generally had a high percentage by number. Euphausiid eggs and juveniles and unidentified copepods often had high percentages by number relative to their frequencies of

Table 3

Summary of stomach contents for three species of pelagic juvenile *Sebastes*, 1985. FO = frequency of occurrence; % = percent by number.

Prey category	Widow rockfish (*n* 75) FO	%	Yellowtail rockfish (*n* 30) FO	%	Shortbelly rockfish (*n* 85) FO	%
EUPHAUSIACEA						
Furcilia	22.7	1.7	30.0	1.2	14.1	0.4
Calyptopis	2.7	0.1	6.7	1.5	1.2	0.1
Juveniles	5.3	0.7	10.0	0.2	16.5	0.4
Euphausiid eggs	18.7	8.2	36.7	59.1	48.2	59.3
AMPHIPODA						
Hyperiid juveniles	6.7	0.1	3.3	0.1	7.1	0.1
LARVACEA	6.7	4.1			7.1	2.4
CHAETOGNATHA	1.3	0.1				
DECAPODA						
Natantia juveniles			3.3	0.1	1.2	0.1
COPEPODA						
Calanus spp.	22.7	1.7	16.7	1.2	25.9	1.2
Candacia sp.	2.7	0.1	3.3	0.1	1.2	0.1
Copepods (unidentified)	13.3	3.7			17.6	2.9
Eucalanus sp.	8.0	1.8			3.5	0.1
Euchirella sp.	2.7	0.2			3.5	0.1
Juveniles	44.0	77.6	56.7	36.5	57.6	33.3
Metridia sp.			3.3	0.1	1.2	0.1
OSTEICHTHYES						
Fish larvae (unidentified)	1.3	0.1				

Table 4

Summary of stomach contents for three species of pelagic juvenile *Sebastes*, 1986. FO = frequency of occurrence; % = percent by number.

Prey category	Yellowtail rockfish (n 10)		Shortbelly rockfish (n 168)		Bocaccio (n 25)	
	FO	%	FO	%	FO	%
EUPHAUSIACEA						
Furcilia	10.0	1.6	13.2	0.9	4.0	0.2
Calyptopis	10.0	0.6	3.6	0.1		
Juveniles	70.0	7.1	59.9	10.0	52.0	22.0
Euphausiid eggs			4.8	1.1		
CUMACEA	10.0	1.0	1.2	0.1		
DECAPODA						
Natantia juveniles	20.0	1.0	0.6	0.1		
COPEPODA						
Calanus spp.			38.3	6.6	64.0	30.5
Copepods (unidentified)			34.1	3.9	28.0	5.9
Epilabidocera sp.	40.0	8.7				
Juveniles	50.0	80.1	71.9	77.3	44.0	41.4

occurrence. Euphausiid eggs and juvenile copepods were the smallest significant prey of pelagic juvenile rockfish. It is therefore not surprising that these categories often display high percentages by number. Likewise, the category 'unidentified copepods' typically was based on counts of small items (e.g., head fragments).
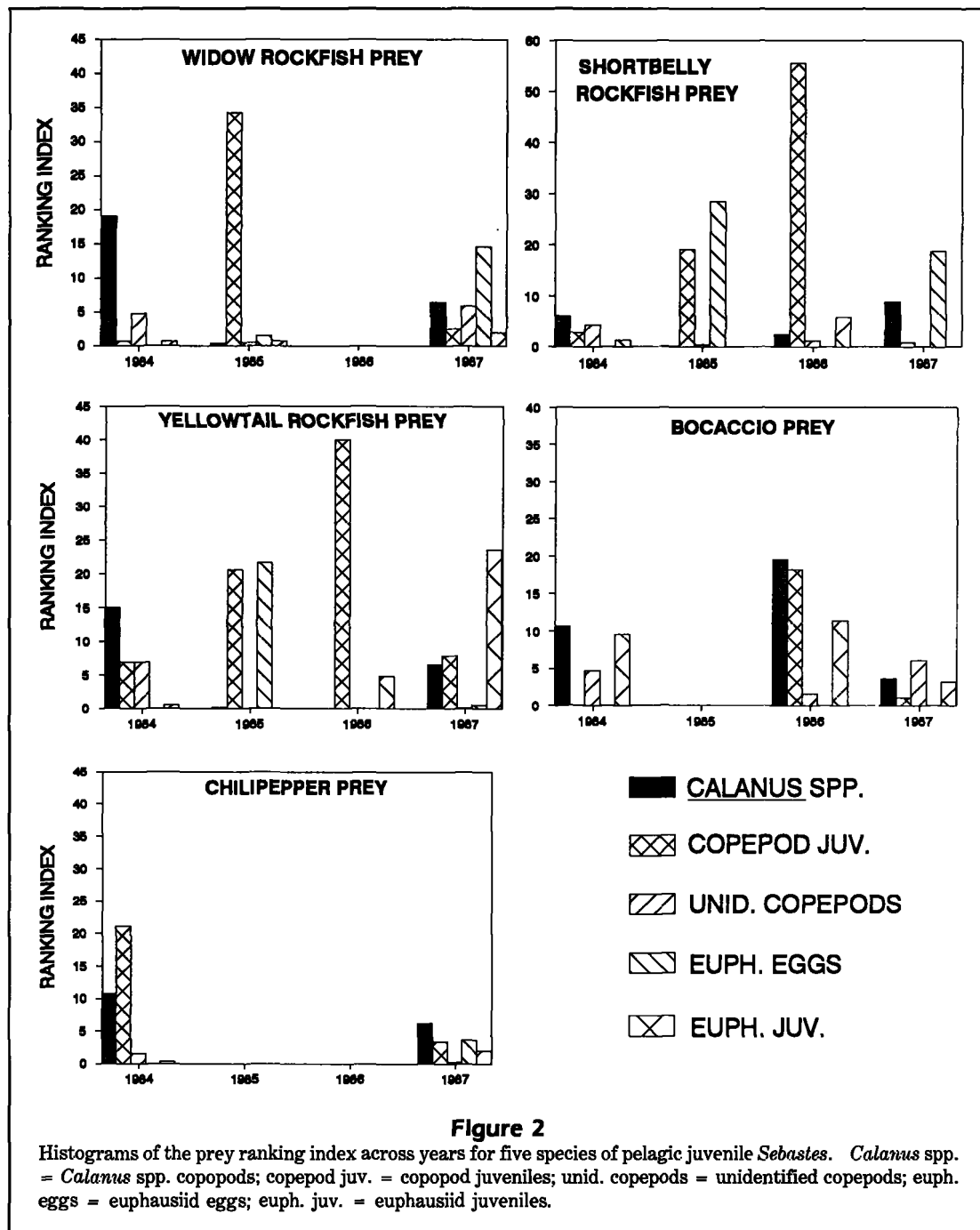
Ranking Index

Prey having both a high frequency of occurrence and percentage by number are the most important items in the diet (Tables 2–5). *Calanus* spp. copepods were particularly important in 1984 when all rockfish species consumed substantial numbers of this

Table 5

Summary of stomach contents for five species of pelagic juvenile *Sebastes*, 1987. FO = frequency of occurrence; % = percent by number.

Prey category	Widow rockfish (n 105)		Yellowtail rockfish (n 17)		Chilipepper (n 125)		Shortbelly rockfish (n 150)		Bocaccio (n 53)	
	FO	%	FO	%	FO	%	FO	%	FO	%
EUPHAUSIACEA										
Furcilia	6.6	0.20	11.8	1.1	8.0	1.30	40.7	4.00	1.9	0.1
Calyptopis	8.5	0.30	5.9	0.4	2.4	0.40	6.7	1.60	1.9	0.1
Juveniles	39.6	9.00	76.5	31.1	19.8	10.30	6.7	0.60	30.2	10.7
Euphausiid eggs	27.4	52.00	5.9	7.7	10.4	35.80	28.7	65.80	1.9	10.5
Euphausiids (unidentified)	8.5	0.30	5.9	0.2	8.0	0.60	8.0	0.20		
Euphausia sp.									3.8	0.2
Thysanoessa sp.	1.0	0.01								
AMPHIPODA										
Hyperiids	1.0	0.01			1.6	0.10	1.0	0.01	1.9	0.1
CUMACEA					1.0	0.04				
DECAPODA										
Natantia juveniles	1.0	0.04			1.0	0.04				
Crab megalopa					3.2	0.20				
Crab zoea					1.6	0.10	1.0	0.01		
CIRRIPEDIA										
Cypris larva							1.0	0.10		
COPEPODA										
Calanus spp.	33.0	19.80	47.1	13.9	28.0	22.80	44.0	20.30	32.1	11.5
Candacia sp.					1.0	0.10			1.9	0.2
Copepods (unidentified)	22.6	7.30	5.9	1.1	8.0	4.10	4.0	1.00	13.2	45.8
Eucalanus sp.	1.9	0.10							1.9	0.1
Euchaeta sp.									1.9	0.8
Rhincalanus sp.	1.0	0.01					1.0	0.01		
Juveniles	24.5	10.00	17.7	44.5	14.4	24.30	16.0	6.30	5.7	19.3
TEUTHOIDEA										
Squid larva									1.9	0.1
OSTEICHTHYES										
Fish larvae									15.1	0.6
Eggs	3.8	1.00					2.0	0.40		

Figure 2

Histograms of the prey ranking index across years for five species of pelagic juvenile *Sebastes*. *Calanus* spp. = *Calanus* spp. copopods; copepod juv. = copopod juveniles; unid. copepods = unidentified copepods; euph. eggs = euphausiid eggs; euph. juv. = euphausiid juveniles.

prey. Likewise, 1985 was a year in which copepod juveniles and euphausiid eggs dominated the diets of the three species examined (widow, yellowtail, and shortbelly rockfish) and copepod juveniles were again important to all species in 1986.

Interspecific prey utilization patterns were less obvious. There is some indication that widow and chilipepper rockfish consumed more copepod juveniles and *Calanus* spp. copepods than did the other species.

Similarly, shortbelly rockfish appeared to consume more euphausiid eggs, while bocaccio consumed more euphausiid juveniles. Likewise, there was some suggestion that bocaccio fed on larger prey than the other species (e.g., euphausiid adults and fish larvae). Nonetheless, no distinctive separation in primary prey species was evident among the five species examined.

Based on the I_r ranking index, it is apparent that the diet of pelagic juveniles is typically dominated by

a single prey type each year, followed by several prey types with indices at much lower values (Fig. 2). There were few instances in which the two most important prey types were similar in ranking index, e.g., yellowtail rockfish consuming euphausiid eggs (21.7) and juvenile copepods (20.7) in 1985. This result suggests that each year these species, to a large extent, specialize on foods that are intermittently abundant. Also, the ranking index data, together with information on frequency of occurrence and percent by number, indicate the major prey items of pelagic juvenile rockfish were various life stages of copepods and subadult euphausiids.

Dietary overlap

The extent of interspecific dietary similarity was quantified by comparing dietary overlaps among all possible pairs of species within each year (1984–87). Ten species pairs were possible, but not all pairs were observed each year since all five species were not always collected (Table 6). Overlap indices are sensitive to the taxonomic level to which prey items are categorized; thus, statistical tests of significance concerning the data are arbitrary. Therefore, the convention established by Langton (1982) and Brodeur and Pearcy (1984) was invoked. Overlap index values of 0.00–0.29 were considered low, values of 0.30–0.60 were considered medium, and values >0.60 were considered high.

Using these criteria, annual comparisons of the distribution of overlap indices for 1984 indicate that 60% of all comparisons were classified as medium and 40% were classified as high. Results from 1985 and 1986 indicate that 67% of the scores were medium and 33% were high. In contrast, index values during 1987 generally had the lowest amount of overlap: 10% low, 70% medium, and 20% high. Based on these findings we conclude that, although overall patterns of dietary overlap do vary from one year to the next, variations are relatively modest (only in 1987 was any low overlap observed). Moreover, in this study most within-year species pairings showed >30% overlap. The principal exception to this generalization was for yellowtail and shortbelly rockfish sampled in 1987. Their diets were quite dissimilar.

Overlap indices were also calculated for all possible interannual intraspecific combinations. These calculations allow an assessment of the temporal stability of the diet relative to the amount of interspecific dietary overlap displayed during a given year. The frequency distribution of dietary overlap values derived from self-pairing of rockfish species from different years is shifted well to the left (toward zero) of the distribution of interspecific scores obtained within a year (Fig. 3). These findings show that in any particular year the dif-

Table 6

Diet overlap indices for individual pairings of pelagic juvenile Sebastes (1984–87). Wid = widow rockfish; Yel = yellowtail rockfish; Chi = chilipepper; Sho = shortbelly rockfish; Boc = bocaccio.

Species pair	Year			
	1984	1985	1986	1987
Wid–Yel	0.84	0.53	—	0.39
Wid–Chi	0.58	—	—	0.69
Wid–Sho	0.52	0.46	—	0.77
Wid–Boc	0.57	—	—	0.50
Yel–Chi	0.61	—	—	0.52
Yel–Sho	0.58	0.90	0.91	0.22
Yel–Boc	0.64	—	0.46	0.48
Chi–Sho	0.38	—	—	0.56
Chi–Boc	0.41	—	—	0.49
Sho–Boc	0.61	—	0.51	0.30
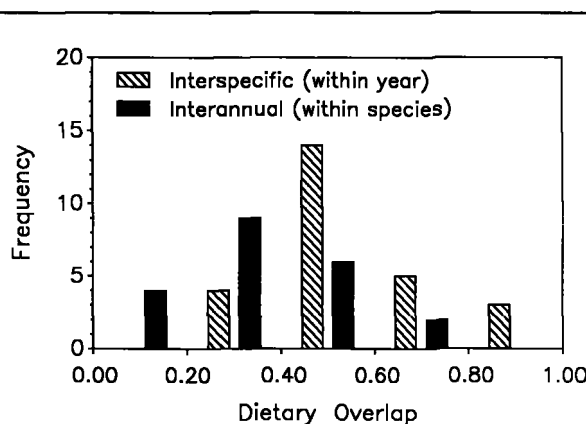
Figure 3

Frequency of dietary overlap indices among all interspecific Sebastes pairs within years, compared with frequency of overlap indices calculated for each Sebastes species self-paired across years.

ferent species of rockfish are opportunistic feeders that utilize relatively similar prey items, but substantial dietary change can occur from year to year.

Latitude and depth effects

Dietary variation with respect to station latitude (north or south of lat. 37°20′N), station depth (deeper or shallower than 100m), and the interaction of these variables were analyzed using MANOVA (Table 7). The statistical significance of each analysis depended on the particular combination of species and year examined. In 1987, highly significant (P<0.001) diet variations occurred with depth for shortbelly and widow rockfish.

Table 7

Results of MANOVA of depth, latitude, and depth by latitude effects on three principal prey types of pelagic juvenile *Sebastes*. Cal = *Calanus* spp.; CoJv = copepod juveniles; EJv = euphausiid juveniles; EuEg = euphausiid eggs; ELv = euphausiid larvae; UnCo = unidentified copepods; Fur = furcilia.

| | | Prey type | | | MANOVA model effects | | | | | |
| | | | | | Depth | | Latitude | | Depth * latitude | |
Species	Year	I	II	III	Wilks' λ	P	Wilks' λ	P	Wilks' λ	P
Chilipepper	87	Cal	CoJv	EJv	0.9019	0.0580[b]	0.9186	0.1044	0.9715	0.5525
Widow	87	Cal	EuEg	EJv	0.6638	0.0001**	0.9536	0.2813	0.9805	0.6632
Shortbelly	87	Cal	EuEg	ELv	0.7649	0.0001**	0.9805	0.5059	0.9243	0.0252*
Shortbelly	86	Cal	CoJv	EJv	0.8917	0.0005**	0.7522	0.0001**	0.9404	0.0234*
Shortbelly	85	Cal	EuEg	CoJv	0.8934	0.0472*	0.9293	0.1600	0.9185	0.1121
Shortbelly	84	Cal	UnCo	Fur	0.9647	0.3110	0.9213	0.0429*	0.9095	0.0240*

Significance levels:
  [b]borderline
  *$P<0.05$
  **$P<0.01$

In that year, latitude had no discernible influence on the diet of these two species, although for shortbelly rockfish a significant interaction between depth and latitude was evident. These findings strongly suggest that spatial variability in the environment (i.e., latitude and depth of the water column) can influence, to some extent, the diets of pelagic juvenile rockfish in a species-specific manner.

Results for the full time-series of shortbelly rockfish data (1984–87) also show that spatial patterns change over time. Although depth had a highly significant effect on diet in 1986 and 1987, it was not significant in 1984 or 1985. Similarly, latitude had no appreciable relationship to the diet of shortbelly rockfish in 1985 and 1987, but it had a highly significant effect in 1986. Importantly, whenever a latitude correlation with diet was present, the interaction term (depth * latitude) was significant as well. We believe that the erratic influence of spatial structure on the shortbelly diet is likely due to the dynamic nature of the nearshore pelagic/neritic physical environment.

Using the 1987 data, we examined the least-squares means (Searle et al. 1980) of the transformed numerical proportions of the individual prey types to learn exactly how dietary composition varied when statistically-significant model effects occurred. In that year, the diet of chilipepper showed borderline significance with depth ($P = 0.058$); the least-squares means revealed that chilipepper consumed more *Calanus* spp. copepods in shallow water, and more juvenile copepods and juvenile euphausiids at bottom depths >100m. Likewise, all three prey types (*Calanus* spp., euphausiid eggs, and juvenile euphausiids) of widow rockfish were consumed in greater proportion in deep water, especially euphau-

siid eggs. For shortbelly rockfish, which displayed a significant interaction term, consumption of *Calanus* spp. copepods was noticeably depressed at shallow southern stations. Euphausiid eggs were consumed in much greater quantities at deep stations, both north and south, while fewer larval euphausiids (furcilia and calyptopis) were found in fish from northern deep stations.

Predator size

Results were inconsistent when these same data (i.e., numerical proportions in the diet of the three most frequently occurring prey items for 1984–87 shortbelly rockfish, 1987 chilipepper, and 1987 widow rockfish) were also explored with MANOVA to assess the effect of fish size on composition of the diet. In each instance, fish were assigned to either small or large size-classes, based on whether standard lengths were smaller or larger than the annual median of that species.

Of the six cases examined (Table 8) two yielded significant ($P<0.05$) results. Large shortbelly rockfish sampled in 1986 tended to eat a higher proportion of *Calanus* spp. copepods, whereas small fish had a higher fraction of juvenile euphausiids and juvenile copepods in their diet. Results from that year, therefore, support the view that large fish tend to consume large prey. Even so, a significant size effect was demonstrated for 1985 shortbelly rockfish, which was exactly the opposite of 1986; large fish consumed fewer *Calanus* spp. copepods and a greater percentage of euphausiid eggs than did small fish. Sample size was not adequate to statistically analyze fish length jointly with distributional patterns. However, in 1985, 34 of

Table 8

Results of MANOVA of fish size on three principal prey types of pelagic juvenile *Sebastes*. Cal = *Calanus* spp.; CoJv = copepod juveniles; EJv = euphausiid juveniles; EuEg = euphausiid eggs; ELv = euphausiid larvae; UnCo = unidentified copepods; Fur = furcilia.

| Species | Year | Prey type | | | Fish size | |
		I	II	III	Wilks' λ	P
Chilipepper	87	Cal	CoJv	EJv	0.9927	0.9088
Widow	87	Cal	EuEg	EJv	0.9678	0.4407
Shortbelly	87	Cal	EuEg	ELv	0.9634	0.2132
Shortbelly	86	Cal	CoJv	EJv	0.9362	0.0161*
Shortbelly	85	Cal	EuEg	CoJv	0.8801	0.0261*
Shortbelly	84	Cal	UnCo	Fur	0.9928	0.8654

*$P<0.05$

the 42 shortbelly rockfish that were classified as small came from deep stations. Results presented earlier (Table 7) showed that the diet of shortbelly rockfish varied significantly with depth in 1985 (i.e., fewer euphausiid eggs and copepod juveniles at deep stations). Thus, the conclusion that small fish consumed large prey in 1985 is, to some degree, confounded with this spatial effect.

Discussion

The five species of pelagic juvenile rockfish examined in this study consumed pelagic zooplankton almost exclusively. Relatively few prey types made up the major portion of the diet each year. Various life history stages of calanoid copepods and euphausiids dominated. Carlson and Haight (1976) reported that copepods and euphausiids were important in the diet of pelagic juvenile Pacific ocean perch *S. alutus*. Singer (1985) recently reported that settled juveniles of several rockfish species consumed copepods and zoea larvae in a central California kelp forest. Other studies (Robb and Hislop 1980, Bowman 1981, Conway 1980) have also demonstrated that calanoid copepods and euphausiids are extremely important foods to pelagic juvenile fishes in the northeastern Pacific Ocean. These studies demonstrate that the diets of pelagic juvenile rockfishes are similar to those of other species possessing pelagic juvenile life stages.

A significant finding of this study is that *Sebastes* spp. juveniles periodically forage heavily on euphausiid eggs. Euphausiid eggs have not been previously reported as a prey item of pelagic juvenile rockfish and yet they were a very important dietary component both in 1985 and 1987. During those years, euphausiid eggs averaged over 37% of the prey items consumed by the five species studied. However, euphausiid eggs were absent from samples collected in 1984 and were a minor component in 1986.

Some species of euphausiids brood their eggs prior to hatching (e.g., *Nyctiphanes* spp.), whereas other species release eggs upon fertilization (e.g., *Euphausia pacifica* and *Thysanoessa spinifera*). Since adult euphausiids were not found in any stomachs in 1985 (Table 3), and since only the latter genera were encountered in large swarms in the study area in 1987 (Smith and Adams 1988), rockfish must have consumed eggs after release. It was not expected that a non-motile prey would constitute such an important food resource to pelagic juvenile rockfish. The appearance of eggs in clumped masses in guts suggests that eggs were not individually picked from the plankton.

Another interesting finding was the consumption of fish larvae by bocaccio juveniles. A total 15–20% of all bocaccio sampled in 1984 and 1987 contained larval fish. In our surveys, bocaccio grow faster and reach larger sizes as pelagic juveniles (≥ 100 mm SL) than do other species (Woodbury and Ralston 1991). They are also distributed at shallower depths (Lenarz et al. 1991).

We used the I_r statistic to rank the importance of individual prey items in the diet. This statistic differs from a similar statistic used by Hobson (1974) in that it is the product of proportional frequency of occurrence and percent by number, rather than percent by volume. Use of this statistic allowed us to characterize the prey types consumed by *Sebastes* in each of the 4 years studied. No obvious species-specific patterns emerged in the absence of a temporal component.

Our results indicate that pelagic juvenile *Sebastes* tend to respond similarly to environmental fluctuations in their food base, suggesting an opportunistic feeding strategy. Intraspecific dietary overlap between interannual pairings was much lower than were interspecific interannual pairings. On a relative basis, interannual differences in diet were tracked similarly among the five species we examined. Annual changes in diet are likely to reflect annual differences in the composition, availability, and abundance of prey.

It was not possible to infer from our results whether or not food is limiting to pelagic juvenile rockfishes, given the relatively large interannual variation in the diet among these species and the likelihood that variation in the availability of prey is likely responsible.

Even so, high dietary overlap observed among co-occurring pelagic juvenile rockfishes suggests that similar recruitment dynamics must exist if the distribution and abundance of foods has a major impact on recruitment.

Intraspecific spatial variation was observed (Table 7), even though substantial interspecific overlap exists in patterns of food utilization. In some instances, parallel spatial differences were observed for different species. For example, in 1987 both widow and short-belly rockfish fed on euphausiid eggs to a much greater extent in deep water (>100 m) than in shallow water. In other cases, however, species-specific differences in diet due to depth were reversed. In 1987, for example, the consumption of *Calanus* spp. copepods by chilipepper was higher in shallow water, while consumption by widow rockfish was higher in deep water.

With the exception of the predator-size MANOVA discussed previously (i.e., shortbelly rockfish in 1985), sample sizes for each treatment combination in all MANOVA tests were reasonably well balanced. Therefore, it is unlikely that our conclusions were compromised by our choice of statistical tests.

The spatial incongruity of within-year dietary patterns among species also extended to interannual within-species comparisons. For example, shortbelly rockfish sampled in 1984 and 1987 consumed substantially fewer *Calanus* spp. copepods in the shallow southern quadrant than anywhere else. However, in 1986 consumption of this prey was greatest in fish taken in this region.

These interspecific (within-year) and interannual (within-species) comparisons demonstrate a lack of stability in the specifics of how spatial dietary effects are expressed. It is likely that the complex nearshore pattern of circulation that characterizes the study area (frontal structures, mesoscale eddies, turbulent jets, and upwelling plumes are common recurrent features; Mooers and Robinson 1984, Flament et al. 1985, Njoku et al. 1985, Schwing et al. 1990) defines the spatial distribution of the zooplanktonic animals upon which these rockfish feed. Thus, the dynamic nature of the physical environment off central California generates spatial instabilities in the distribution and abundance of prey.

Acknowledgments

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