FOOD HABITS AND DIETARY OVERLAP OF SOME SHELF ROCKFISHES (GENUS *SEBASTES*) FROM THE NORTHEASTERN PACIFIC OCEAN

RICHARD D. BRODEUR AND WILLIAM G. PEARCY[1]

ABSTRACT

Euphausiids were the major food of five co-occurring species of rockfishes (*Sebastes* spp.) along the west coast of North America from Vancouver Island to northern California. Copepods, decapods, cephalopods, amphipods, fishes, and other pelagic prey were also consumed but were less important to the overall diet. Two species, *S. flavidus* and *S. diploproa*, were relatively euryphagous, utilizing a high number of prey taxa. The other species, *S. pinniger*, *S. alutus*, and *S. crameri*, had a more restricted diet comprised mostly of euphausiids. The numerical composition of prey in the diet of all species was similar due to the preponderance of the two dominant euphausiid species. Diet overlaps based on weight composition were high for *S. pinniger*, *S. diploproa*, and *S. alutus* but were moderate for most comparisons involving *S. flavidus* and *S. crameri*.

The diets of *S. flavidus* and *S. pinniger* were examined in more detail to explain some of the variability associated with their food habits. Both species exhibited peak feeding periods at the same time during the day. They consumed about the same mean size of prey, although *S. flavidus* consumed a wider size range of prey. Size of prey and dietary composition did not vary much with size of fish. There were significant seasonal, geographical, and diel differences in food composition for both species, which may be a function of varying food availability.

Factors that allow coexistence of a large number of morphologically similar species have been the focus of numerous studies and continued debate in the ecological literature. Competition and resource partitioning have been reviewed in general by Schoener (1974), and for fishes by Helfman (1978). Potential competition for resources is thought to be most common in three aspects of the ecological niche in fish communities: habitat, food, and time of activity (Tyler 1972; Bray and Ebeling 1975; Ross 1977; Werner 1979; Larson 1980; McPherson 1981).

Rockfishes (*Sebastes* spp.) of the family Scorpaenidae are, a priori, interesting subjects for examining the various modes of resource partitioning. This genus is extremely speciose, with about 100 species reported from the North Pacific Ocean. At least 69 of these species are known to occur in the eastern North Pacific (Chen 1975). In addition to the large number of species, rockfishes also exhibit a high degree of overlap in their geographical distributions, with as many as 50 species occurring in a narrow latitudinal band (lat. 34°-38° N) off central California (Chen 1971). Several of these congeners are morphologically similar and occupy similar habitats, so the potential for resource overlap and competition is high (Larson 1980).

Many of these species are abundant enough and of sufficient size to contribute substantially to commercial trawl landings in the northeastern Pacific (Alverson et al. 1964; Alton 1972; Gabriel and Tyler 1980; Gunderson and Sample 1980). Despite their abundance in the northeastern Pacific, relatively few quantitative studies exist on rockfish feeding habits. Most of the studies to date have dealt with shallow-water, neritic species often taken in recreational fisheries or accessible to in situ observations and sampling by scuba divers (Gotshall et al. 1965; Larson 1972; Hobson and Chess 1976; Love and Ebeling 1978). Descriptions of the diet of offshore species of *Sebastes* generally either lack taxonomic or quantitative detail (Phillips 1964) or encompass limited geographical area or collection times (Pereyra et al. 1969; Lorz et al. 1983). Skalkin (1964) and Somerton et al. (1978)[2] described food habits of rockfishes from the Bering Sea and Gulf of Alaska, far

[1]School of Oceanography, Oregon State University, Marine Science Center, Newport, OR 97365.

[2]Somerton, D., F. Funk, K. Mesmer, L. J. Bledsoe, and K. Thornburgh. 1978. A comparative study of the diets of Pacific ocean perch (*Sebastes alutus*) and walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. NORFISH Tech. Rep. NPB8, Wash. Sea Grant, 25 p.

Manuscript accepted October 1983.
FISHERY BULLETIN: VOL. 82, NO. 2, 1984.

north of our study area which extends from off northern California to off Vancouver Island, British Columbia.

This study represents the first attempt to examine broad geographical and seasonal patterns in food utilization and overlap by several commercially important species of rockfish on the outer continental shelf. The species considered include the yellowtail rockfish, *Sebastes flavidus*; canary rockfish, *S. pinniger*; Pacific ocean perch, *S. alutus*; splitnose rockfish, *S. diploproa*; and the darkblotched rockfish, *S. crameri*, all important members of the demersal shelf rockfish complex (Gabriel and Tyler 1980). In addition, variability in the diet of two of these species, *S. flavidus* and *S. pinniger*, was examined for the purpose of determining the effects of factors such as season, geographic area, time of capture, and predator size.

MATERIALS AND METHODS

Sampling Methods

The food utilization patterns of the five rockfish species were determined by examining stomach contents. Fishes were obtained by two different survey methods (hereafter referred to as the summer and seasonal surveys). As the collection methods differ, they will be discussed separately. The laboratory methods are similar and will be presented together.

Summer Survey Methods

Collections for the summer survey were made during the National Marine Fisheries Service (NMFS) 1980 West Coast Survey which took place from 12 July to 28 September 1980. The purpose of this survey was to assess the distribution and abundance of commercially important rockfishes. The area encompassed by the survey included much of the continental shelf and inner slope (ranging in depth from 55 to 366 m) between Monterey, Calif., (lat. 36°48′N) and the northern end of Vancouver Island, British Columbia (lat. 50°00′N). Two commercial stern trawlers, the FV *Mary Lou* and the FV *Pat San Marie*, were utilized for the survey. A Nor'Eastern[3] high-opening bottom trawl with an estimated 13.4 m horizontal and an 8.8 m vertical mouth opening was used on both vessels. The main body was constructed of 127 mm stretched mesh with 89 mm mesh in the cod end. The cod end also contained a 32 mm mesh liner. Half-hour tows were made at random depth-stratified stations chosen by a method described in Gunderson and Sample (1980).

The majority of the stomach samples used in this study were collected in August and September from north of lat. 43°N (Table 1, Fig. 1). Complete station data are given in Brodeur (1983).

Stomachs were removed at sea from a random subsample of the catch of the five target species (Table 1). *Sebastes pinniger* and *S. flavidus* were the primary target species, and stomachs of these species were collected first and the other species sampled as time allowed. Altogether, 480 stomachs were collected during the survey, all from adult fish (>200 mm FL). Fork length (measured to the nearest millimeter) and sex were recorded for all fish sampled, and stomachs were then removed, individually wrapped and labeled, and preserved in a 10% Formalin-seawater mixture. The intestinal tracts of many of the fish were examined at sea but few contained any recognizable food and none were retained. Total elapsed time between bringing the fish on board and preserving the stomachs was <1 h. The oral cavities of all fish were examined for signs of stomach eversion and regurgitation; any fish showing such signs were discarded. Individual fish weights were not recorded at sea but were later calculated using the length-weight relationships of Phillips (1964).

TABLE 1.—Number of rockfish stomachs analyzed from the 1980 National Marine Fisheries Service summer survey. The approximate latitudinal ranges covered by each leg were I, lat. 37°-42°N; II, lat. 43°-46°N; III, lat. 46°-50°N.

Leg	Sampling dates	Species	Number
I	12-20 July	*S. pinniger*	9
		S. flavidus	8
			17
II	4-29 Aug.	*S. pinniger*	85
		S. flavidus	127
		S. alutus	54
		S. diploproa	52
		S. crameri	30
			348
III	4-28 Sept.	*S. pinniger*	36
		S. flavidus	50
		S. alutus	19
		S. diploproa	10
			115
		Total number analyzed	480

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

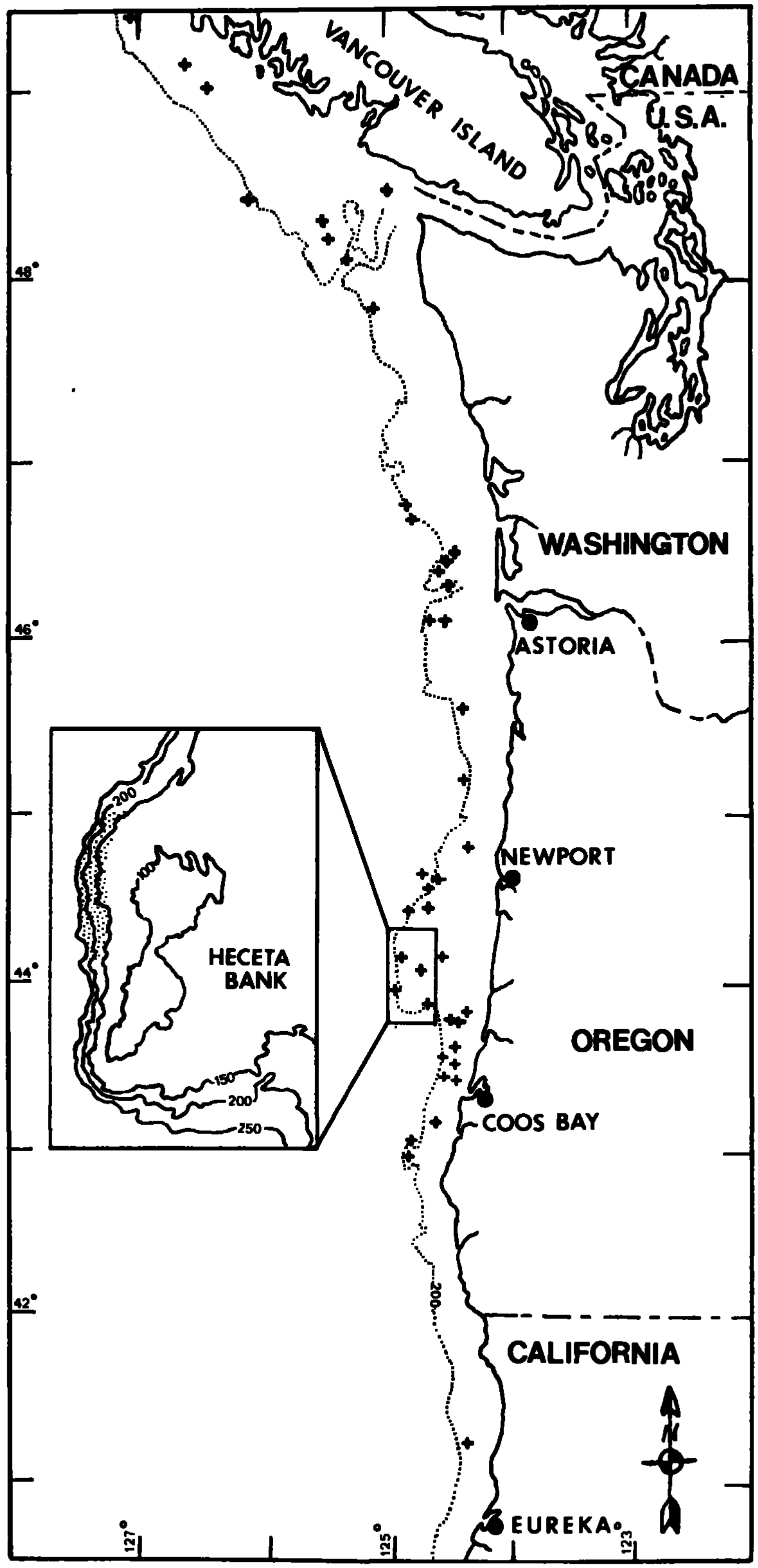

FIGURE 1.—Location of sampling stations from which stomach collections were taken. + sign denotes collections made during the National Marine Fisheries Service's summer survey and the stippled area (inset) shows the sampling area on Heceta Bank of the Oregon Department of Fish and Wildlife's seasonal collections. All depth contours are in meters.

Seasonal Survey Methods

Stomachs for the seasonal study were collected during rockfish surveys conducted by the Oregon Department of Fish and Wildlife (ODFW) on Heceta Bank off the central coast of Oregon. These surveys obtained hydroacoustic and environmental data along with the trawl catches. A total of 317 stomach samples was collected during seven surveys conducted in 1980-81 (Table 2). All surveys used trawling gear similar to that used in the summer surveys.

Locations of the tows were chosen on the basis of high concentrations of fish found during acoustic surveys over the outside edge of Heceta Bank between lat. 44°20′N and 44°00′N between the 128 m and 238 m bathymetric contours (inset, Fig. 1). The duration of tows was variable but averaged <1 h. No tows were attempted at night because of the lack of acoustical targets near the bottom at this time. Stomachs were collected as described earlier.

TABLE 2.—Number of rockfish stomachs analyzed from the seasonal Oregon Department of Fish and Wildlife collections on Heceta Bank. All dates are in 1980 unless otherwise noted.

Vessel	Cruise	Sampling dates	Species	Number
Ronnie C	I	23-24 April	*S. pinniger*	42
Bay Islander	I	17-18 June	*S. pinniger*	24
Queen Victoria	I	15-16 July	*S. pinniger*	47
			S. flavidus	16
Ronnie C	II	26-28 Sept.	*S. pinniger*	60
			S. flavidus	23
New Life	I	27 Oct.	*S. pinniger*	21
			S. flavidus	2
Ronnie C	III	17-18 Dec.	*S. pinniger*	33
			S. flavidus	25
New Life	II	25 Jan. 1981	*S. pinniger*	11
			S. flavidus	13
			Total number analyzed	317

Analysis of Stomach Contents

The stomachs were opened and their contents transferred to 50% isopropyl alcohol in the laboratory. Contents were examined using a variable power dissecting microscope. Individual stomach fullness was estimated according to a subjective rating ranging from 0 (empty) to 5 (stomach fully distended with food). The condition of the contents was assigned a value from 0 (well-digested, barely identifiable to phylum) to 4 (fresh).

Prey were identified to the lowest possible taxon and enumerated. In stomachs containing many small prey, such as euphausiids, any large or rare prey items were removed first. The remaining contents were then subdivided by means of a Folsom plankton splitter (McEwen et al. 1954), and the contents of one subsample were used to estimate the stomach contents of small prey. The digested state of the contents of many stomachs made precise counts of some prey difficult. Some paired parts of prey animals (e.g., eyes of euphausiids, otoliths of teleosts) were more resistant to digestion and total counts of these parts were halved to yield minimum counts of prey ingested. Total lengths or greatest dimensions of intact prey found in the stomach were measured to the nearest 0.1 mm for the total sample (or a subsample of at least 15 individuals) using a stage ruler or ocular micrometer. All prey were blotted dry with absorbent paper and wet weights of each taxon were recorded to the nearest milligram.

Analysis of Food Habits

The minimum number of stomach samples needed to adequately describe the diet of a species was determined for all five rockfish species, using a cumulative prey species curve. A subset of stomachs of a particular species was randomly chosen and the cumulative number of unique prey taxa were then plotted versus the number of stomachs which produced these taxa. The point on the abscissa where the curve begins to level off is considered the minimum number of stomachs necessary to describe the diet of that species. An example of the cumulative prey curves for the first 28 stomachs of each of the species in this study is shown in Figure 2. Although the curves assume different shapes, all approach an asymptote at sample sizes less than those analyzed.

The contributions of the different prey items to the total diet of the rockfishes were expressed as percent frequency of occurrence, percent numerical composition, and percent gravimetric composition. Breadth and overlap were calculated for the five rockfishes from the summer surveys and for *S. pinniger* and *S. flavidus* from the seasonal surveys, using the pooled p_i's (relative proportion of the total number or biomass of resource i used by each species) for the major taxa. These include all taxa identified to at least generic level that exceeded 0.1% of the total weight or number of all identified foods. Resource breadth was computed for each species using the following formula:

$$B = \frac{1}{\Sigma_i \, p_i^2}$$

where B equals R (the total number of prey taxa

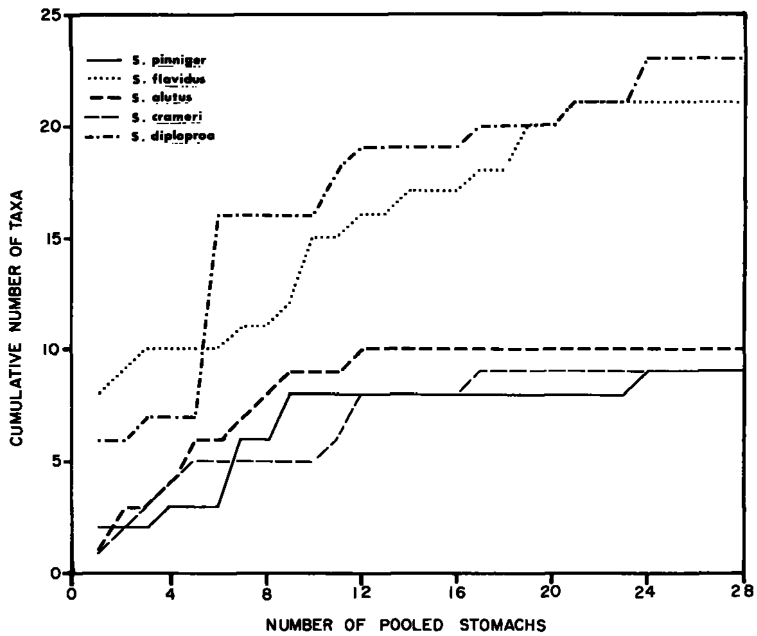

FIGURE 2.—Cumulative prey curves for the first 28 stomachs of each of the 5 rockfish species.

in a food spectrum) when all items are in equal proportion in the diet (Levins 1968). These values were normalized as $B_n = B/R$, which ranges from 0 (most uneven distribution) to 1 (totally even distribution among the prey present). This index assumes equal availabilities of the different prey to all predators.

Several indices of dietary overlap have been proposed and tested with known distributions of prey organisms (see Cailliet and Barry 1979[4]; Linton et al. 1981; Wallace 1981). The coefficient of overlap described by Colwell and Futuyma (1974; identical to Schoener's (1970) index but not expressed as a percentage) was chosen as it was found to be realistic for a wide range of true overlaps (Linton et al. 1981). This coefficient is as follows:

$$C_{ih} = 1.0 - 0.5\,(\Sigma_j | p_{ij} - p_{hj} |)$$

where p_{ij} and p_{hj} are the proportions of prey j found in the diets of species i and h respectively. This coefficient has a minimum of 0 (no overlap of prey) and a maximum of 1 (all items in equal proportions).

[4]Cailliet, G. M., and J. P. Barry. 1979. Comparison of food array overlap measures useful in fish feeding habits analysis. *In* S. J. Lipovsky and C. A. Simenstad (editors), Fish food habits studies, p. 67-79. Proc. 2d Pac. Northwest Tech. Workshop, Wash. Sea Grant.

Analysis of Diet Variations

The sample sizes of *S. pinniger* and *S. flavidus* were sufficient to permit detailed analyses of their food habits, including seasonal, latitudinal, diel, and predator-size variations.

The 368 specimens of *S. pinniger* and 264 of *S. flavidus* were grouped into 10 mm length categories (Fig. 3). The distribution of *S. pinniger* lengths from the two surveys was similar and no significant differences in the means were found (Student's t-test; $P > 0.05$). Specimens of *S. flavidus* collected during the seasonal survey were significantly larger ($P < 0.001$) than those of the summer survey. *Sebastes pinniger* averaged about 40 mm larger than *S. flavidus* for both surveys combined. Corrections were made for this difference where appropriate in the analyses.

To simplify the analysis of dietary variation in *S. pinniger* and *S. flavidus*, eight major types of prey were selected for comparison, based on their gravimetric importance or frequency of occurrence. Numerical abundances were not used because of the great disparity in prey sizes encountered and the problem of making counts on

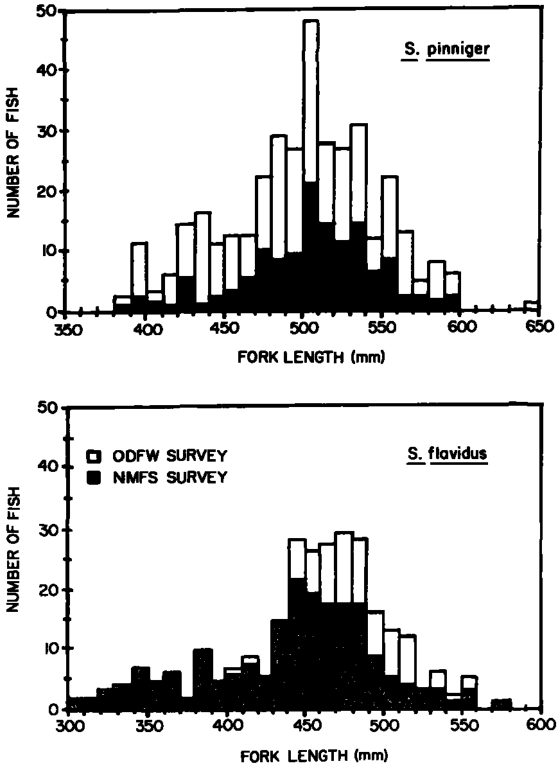

FIGURE 3.—Size distributions of *Sebastes pinniger* and *S. flavidus* from summer (National Marine Fisheries Service) and seasonal (Oregon Department of Fish and Wildlife) surveys.

incomplete animals. These prey categories include the two most important euphausiid species and other major taxonomic groups (Table 3). Other planktonic prey (e.g., copepods, chaetognaths, pteropods) were occasionally present in the diet of one or both species, but their contributions to the overall diets were minor. Cephalopods did not occur in the diet of *S. pinniger*; thus only seven prey categories were used for this species.

TABLE 3.—The major prey categories used in the analysis of diet variations and their respective size ranges found in the stomachs of *S. pinniger* and *S. flavidus*.

Category	Prey size range (mm)	Inclusive taxa or life stages
Euphausia pacifica	8-26	juvenile and adult stages
Thysanoessa spinifera	8-30	juvenile and adult stages
Total euphausiids	8-30	above two and other species, unidentified euphausiids
Decapods	3-87	adult shrimp, crab zoea and megalopae, shrimp mysis
Amphipods	3-30	mostly hyperiid but some gammarid
Cephalopods[1]	18-150+	squid and octopods
Fishes	16-150+	larvae, juvenile and adult stages
Gelatinous zooplankton	10-22	ctenophores, thaliaceans, medusae, and siphonophores

[1]Found in *S. flavidus* stomachs only.

We analyzed four factors that may affect the diet of these two species: season, geographic area, time of day, and size of fish. Each factor was subdivided into four classes to elucidate the general trends within each factor. Stomach content data for all cruises were grouped into four seasons, based on major periods in the hydrographic regime on the continental shelf off Oregon (Huyer et al. 1975; Huyer 1977): spring (March-May), summer (June-August), fall (September-November), and winter (December-February). The collection stations for all cruises were divided into one of four latitudinally defined shelf regions: Northern California-Southern Oregon (lat. 41°00′ to 43°50′N), Heceta Bank-Central Oregon (lat. 43°50′ to 45°00′N), Columbia Region (lat. 45°00′ to 47°00′N), and Northern Washington-Vancouver (lat. 47°00′ to 50°00′N).

For the analysis of diel variation of feeding, the local mean sampling time was adjusted to account for latitudinal, longitudinal, and seasonal differences in daylight. Each collection time was standardized to an equinox day with 12 h between sunrise and sunset, based on solar table values. These adjusted collection times were assigned to one of four time periods: morning (0800-1200 h), early afternoon (1200-1600 h), late afternoon (1600-1800 h), and night (1800-0700 h). Only a small number of *S. pinniger* and *S. flavidus* were collected at night despite extensive nighttime trawling effort on several occasions during the summer survey.

Since the length distributions of the two species were roughly normal (Fig. 3), dividing the length range into four equal size groups would result in disproportionately large sample sizes in the middle size ranges. On the other hand, setting the sample sizes of the four groups equal would result in narrow size ranges around the mode. As neither of these options seemed desirable, compromise groupings were chosen. For *S. pinniger*, we used the following size classes: <45 cm, 45-<50 cm, 50-<55 cm, and ≥55 cm. Similar size classes were selected for *S. flavidus* but were offset 5 cm to reflect the smaller mean size of this species.

To test whether significant within-factor variation occurred in the diet of each species, contingency tables were constructed comparing the occurrence of food or a particular prey category versus the absence of food or that prey category. A variance test for homogeneity of binominally distributed data (Snedecor and Cochran 1967) was used for testing differences among the classes within each factor. Any comparisons which exceeded the tabulated 0.05 χ^2 percentage caused a rejection of the null hypothesis of similar diets.

RESULTS

General Food Habits

The results of the stomach content analysis are presented for both surveys and all five species in Tables 4 through 8. Each species will be discussed in detail in this section.

Sebastes flavidus preyed on a diverse assemblage of planktonic and micronektonic prey (Table 4). Dominating the diet in terms of frequency of occurrence (F.O.), percent by number, and, to a lesser extent, percent by weight were euphausiids, principally *Euphausia pacifica* and *Thysanoessa spinifera*. Many species of hyperiid amphipods were represented in the diet, but these were not numerous and did not comprise a major portion of the food on a weight basis. Decapods and cephalopods were moderately important in stomachs examined from both surveys. Copepods and larval decapods occurred only in the stomachs from the summer survey, while gelatinous zooplankton were found only in the seasonal study, and were common during late fall and winter. Fish were an important component on a weight basis; they were mainly mesopelagic species and juvenile stages of predominantly benthic species, although many adult Pacific herring, *Clupea harengus pallasi*, and some smelts were also found. The mean number of taxa and mean number of myctophids per stomach were higher in fish from the seasonal than those from the summer survey.

Sebastes pinniger had a much more limited diet both in number of prey species and major prey categories consumed than *S. flavidus* (Table 5). Euphausiids were again the dominant prey consumed with proportional abundances and weights exceeding 90% of the total in both surveys. Many stomachs were distended with adult euphausiids (>1,000 individuals). Hyperiid and gammarid amphipods were common but did not appear to be important components of the diet. Mesopelagic fishes, including myctophids and stomiatoids, contributed to the biomass consumed during the fall and winter months of the seasonal survey. There was a low number of taxa represented in each stomach, especially in the summer survey.

Because of the advanced stage of digestion of most of the stomach contents (mean digestion score = 1.05), many taxa were not identified to species in the stomachs of *S. alutus*, although many major prey categories were represented (Table 6). Euphausiids were the principal prey by weight and number. Of the remaining prey species, amphipods were relatively common and numerous. The oceanic shrimp, *Sergestes similis*, appeared in a significant number of stomachs and may constitute an important prey item. Remains of fishes were found in only a few stomachs, a noteworthy difference compared with the other four species examined.

Sebastes diploproa utilized a spectrum of prey items as wide as that of *S. flavidus*, but the smaller mean size of this species is reflected in generally smaller prey taken (Table 7). Euphausiids were less important, and amphipods, copepods, and decapods were more important on a numerical and percentage occurrence basis than for the other species. *Sergestes similis* contributed heavily in all respects and was found in almost half the stomachs examined. The small hyperiid amphipod, *Vibilia propinqua*, was common and numerous but contributed little to the bulk of the diet. The mean number of prey found per stomach was second only to the seasonal number of *S. flavidus*.

The diet of *S. crameri* was characterized by very few prey taxa, perhaps because only 30 stomachs were examined (Table 8). Of these, one-third of the stomachs were empty and only about one-third of the total biomass found in these stomachs was identifiable, resulting in very low mean fullness and digestion scores (1.03 and 1.05, respectively). This identifiable fraction was composed of equal numbers of euphausiids, amphipods, and copepods. Euphausiids contributed a greater share to the total biomass, however, and completely dominated the identifiable contents. Few prey taxa were found, overall, in the stomachs of *S. crameri*.

Diet Breadth and Overlap

In order to quantify the relative food resource used by the various species, niche breadth measures were calculated for all species. The principal prey types (proportional biomasses exceeding 1.0% of the total biomass), and niche breadth values (overall and normalized) are given in Table 9 for all species analyzed from the summer surveys and for *S. pinniger* and *S. flavidus* collected during the seasonal surveys.

Sebastes flavidus utilized the greatest number of prey types (R), had the widest niche breadth

TABLE 4.—Summary of yellowtail rockfish, *Sebastes flavidus*, stomach contents from the Oregon Department of Fish and Wildlife's seasonal and the National Marine Fisheries Service's summer samplings. F.O. = frequency of occurrence.

	Seasonal					Summer				
	F.O.	Number		Weight (g)		F.O.	Number		Weight (g)	
Prey organism	(%)	Mean	%	Mean	%	(%)	Mean	%	Mean	%
Euphausiacea										
Euphausia pacifica (juv.)	36.7	24.5	6.4	0.34	2.3	—	—	—	—	—
Euphausia pacifica (adults)	60.8	120.1	52.2	2.57	28.3	40.5	37.4	51.3	1.90	26.4
Thysanoessa spinifera (juv.)	—	—	—	—	—	6.0	11.5	2.3	0.43	0.9
T. spinifera (adults)	68.3	40.6	19.8	1.32	16.7	23.2	8.8	6.8	0.80	6.4
T. longipes	—	—	—	—	—	0.5	1.0	—	0.01	—
Thysanopoda acutifrons	1.3	1.0	—	0.12	—	—	—	—	—	—
Euphausiid unidentified	49.4	56.3	19.9	1.08	9.9	16.7	61.1	34.7	2.60	14.9
Amphipoda										
Phronima sedentaria	7.6	1.2	—	0.11	0.2	3.2	1.8	0.2	0.06	—
Paraphronima gracilis	1.3	1.0	—	0.01	—	1.1	1.0	—	0.01	—
Parathemisto pacifica	1.3	1.0	—	0.01	—	2.7	1.0	0.1	0.01	—
Hyperia medusarum	2.5	1.0	—	0.01	—	2.7	1.2	0.1	0.01	—
Hyperoche medusarum	2.5	4.0	—	0.02	—	4.9	1.7	0.3	0.89	1.5
Streetsia challengeri	3.8	1.3	—	0.03	—	0.5	1.0	—	0.04	—
Vibilia propinqua	1.3	2.0	—	0.16	—	0.5	1.0	—	0.01	—
Primno macropa	3.8	1.0	—	0.02	—	0.5	2.0	—	0.02	—
Hyperiidea unidentified	1.3	2.0	—	0.02	—	—	—	—	—	—
Rhacotropis sp.	1.3	1.0	—	0.01	—	—	—	—	—	—
Decapoda										
Sergestes similis	7.6	2.5	0.1	0.71	1.0	2.7	2.8	0.2	0.75	0.7
Pandalus jordani	1.3	12.0	0.1	3.70	0.9	1.1	1.0	—	5.19	1.9
Munida quadrispina (juv.)	3.8	9.3	0.2	0.22	0.2	2.7	5.6	0.5	0.12	0.1
Pinnotheridae megalopae	—	—	—	—	—	0.5	1.0	—	0.10	—
Cancer sp. megalopae	—	—	—	—	—	4.3	1.9	0.3	0.02	—
Decapod mysis larvae	—	—	—	—	—	1.6	2.7	0.1	0.04	—
Copepoda										
Calanus pacificus	—	—	—	—	—	0.5	1.0	—	0.01	—
C. marshallae	—	—	—	—	—	1.6	5.7	0.3	0.01	—
Neocalanus sp.	—	—	—	—	—	2.7	4.4	0.4	0.01	—
Euchirella sp.	—	—	—	—	—	0.5	1.0	—	0.02	—
Copepod unidentified	—	—	—	—	—	2.2	4.5	0.3	0.01	—
Cephalopoda										
Abraliopsis felis	1.3	1.0	—	0.93	0.2	—	—	—	—	—
Gonatus sp.	1.3	3.0	—	0.68	0.2	1.1	1.0	—	0.57	—
Loligo opalescens	3.8	1.0	—	21.24	14.9	2.2	1.5	0.1	2.26	1.7
Japatella heathi	—	—	—	—	—	1.6	1.0	—	0.68	0.3
Octopus sp. (juv.)	6.3	2.6	0.1	0.71	0.8	6.5	6.5	0.3	1.33	2.1
Cephalopod unidentified	11.4	1.2	0.1	1.82	3.8	2.2	2.2	0.2	2.34	1.7
Miscellaneous invertebrates										
Sagitta elegans	2.5	2.5	—	0.16	—	0.5	1.0	—	0.03	—
Limacina helicina	1.3	1.0	—	0.01	—	5.4	1.5	0.3	0.04	—
Alciopid polychaete	1.3	1.0	—	0.27	—	—	—	—	—	—
Siphonophora	2.5	5.5	0.1	0.54	0.3	—	—	—	—	—
Ctenophora	1.3	8.0	—	1.56	0.3	—	—	—	—	—
Cnidaria	1.3	1.0	—	0.27	—	—	—	—	—	—
Osteichthyes										
Clupea harengus pallasi	—	—	—	—	—	3.8	1.6	0.1	14.17	18.4
Thaleichthys pacificus	1.3	1.0	—	1.22	0.3	—	—	—	—	—
Spirinchus starksi	2.5	2.0	—	1.65	0.7	0.5	1.0	—	0.28	—
Stenobrachius leucopsarus	1.3	1.0	—	0.84	—	0.5	1.0	—	0.99	0.2
Diaphus theta	2.5	1.0	—	1.97	0.9	0.5	2.0	—	9.96	1.8
Tarletonbeania crenularis	5.1	1.7	0.1	4.94	4.6	—	—	—	—	—
Symbolophorus californiensis	1.3	1.0	—	0.07	—	—	—	—	—	—
Protomyctophum crockeri	1.3	1.0	—	0.14	—	—	—	—	—	—
Myctophidae unidentified	11.4	1.3	0.1	1.37	2.9	0.5	1.0	—	0.71	0.1
Argyropelecus aculeatus	1.3	1.0	—	2.49	0.6	—	—	—	—	—
Chauliodus macouni	1.3	1.0	—	3.81	0.8	—	—	—	—	—
Nectoliparis pelagicus	—	—	—	—	—	1.6	1.3	—	0.22	0.1
Liparididae unidentified	1.3	1.0	—	0.17	—	—	—	—	—	—
Stichaeidae unidentified (juv.)	1.3	2.0	—	0.44	0.1	1.1	1.0	—	0.26	0.1
Sebastes sp. (juv.)	2.5	1.0	—	0.37	0.2	1.1	2.0	—	1.07	0.4
Glyptocephalus zachirus	1.3	1.0	—	0.88	0.2	—	—	—	—	—
Lyopsetta exilis (juv.)	—	—	—	—	—	1.1	1.5	—	0.29	0.1
Psettichthys melanostictus (juv.)	—	—	—	—	—	0.5	1.0	—	0.06	—
Unidentified fish larvae	—	—	—	—	—	1.1	1.0	—	0.14	—
Fish remains	15.2	—	—	1.31	3.7	8.1	—	—	4.19	11.6
Unidentified animal remains	30.4	—	—	0.66	3.7	38.4	—	—	0.64	8.4

TABLE 4.—*Continued.*

Predator characteristics		
Number of stomachs examined:	79	185
Number of empty stomachs:	4	38
Mean weight per stomach:	5.192 g ± 7.004 (SD)	2.905 g ± 6.032 (SD)
Mean total length:	478.35 mm ± 29.06 (SD)	444.86 mm ± 51.43 (SD)
Mean fullness score:	2.87	1.92
Mean digestion score:	2.90	1.95
Mean no. prey taxa per fish:	2.81	1.55

TABLE 5.—Summary of canary rockfish, *Sebastes pinniger*, stomach contents from the Oregon Department of Fish and Wildlife's seasonal and the National Marine Fisheries Service's summer samplings. F.O. = frequency of occurrence.

	Seasonal					Summer				
	F.O.	Number		Weight (g)		F.O.	Number		Weight (g)	
Prey organism	(%)	Mean	%	Mean	%	(%)	Mean	%	Mean	%
Euphausiacea										
Euphausia pacifica (juv.)	21.0	88.1	12.1	0.65	4.8	3.8	12.5	0.4	0.09	0.1
E. pacifica (adults)	54.6	141.3	50.3	3.21	62.0	40.8	124.3	51.6	5.74	43.5
Thysanoessa spinifera	22.3	24.0	3.5	0.59	4.6	14.6	64.7	9.6	7.40	20.1
Thysanopoda sp.	0.4	3.4	—	0.03	—	—	—	—	—	—
Euphausiid unidentified	37.4	139.6	34.0	1.54	20.4	26.1	141.5	37.7	5.79	28.1
Mysidacea										
Inusitatomysis sp.	—	—	—	—	—	0.8	2.0	—	0.02	—
Amphipoda										
Parathemisto pacifica	0.8	2.0	—	0.01	—	4.6	1.2	—	0.01	—
Hyperoche medusarum	—	—	—	—	—	0.8	2.0	—	0.01	—
Phronima sedentaria	0.4	1.0	—	0.03	—	—	—	—	—	—
Streetsia challengeri	0.4	2.0	—	0.03	—	—	—	—	—	—
Hyperiidea unidentified	—	—	—	—	—	1.5	1.0	—	0.01	—
Rhacotropis sp.	0.4	4.0	—	0.05	—	1.5	6.0	0.1	0.07	—
Atylus tridens	0.4	1.0	—	0.01	—	—	—	—	—	—
Anonyx sp.	0.8	1.5	—	0.18	—	—	—	—	—	—
Lysianassidae unidentified	—	—	—	—	—	0.8	1.0	—	0.02	—
Decapoda										
Sergestes similis	2.9	1.7	—	0.09	0.1	1.5	14.0	0.2	1.89	0.6
Pandalus jordani	0.4	1.0	—	1.05	0.1	1.5	1.0	—	1.55	0.4
Crangon sp.	—	—	—	—	—	0.8	1.0	—	0.03	—
Munida quadrispina (juv.)	2.5	5.0	0.1	0.06	—	—	—	—	—	—
Chaetognatha										
Sagitta elegans	0.4	6.0	—	0.07	—	—	—	—	—	—
Osteichthyes										
Stenobrachius leucopsarus	0.8	1.5	—	0.78	0.2	0.8	1.0	—	0.59	0.1
Tarletonbeania crenularis	0.4	1.0	—	1.70	0.3	—	—	—	—	—
Myctophidae unidentified	1.3	1.3	—	1.47	0.6	—	—	—	—	—
Tactostoma macropus	0.4	1.0	—	1.73	0.2	—	—	—	—	—
Argyropelecus aculeatus	0.4	1.0	—	0.21	—	—	—	—	—	—
Ammodytes hexapterus	—	—	—	—	—	3.1	4.5	0.1	0.76	0.4
Sebastes jordani	0.8	1.0	—	19.04	5.6	—	—	—	—	—
Fish remains	8.4	—	—	0.39	1.2	10.8	—	—	3.00	6.0
Unidentified animal remains	12.2	—	—	0.03	0.1	42.3	—	—	0.09	0.7
Predator characteristics										
Number of stomachs examined:	238					130				
Number of empty stomachs:	39					18				
Mean weight per stomach:	2.828 g ± 4.440 (SD)					5.385 g ± 11.297 (SD)				
Mean total length:	491.45 mm ± 51.07 (SD)					504.07 mm ± 50.34 (SD)				
Mean fullness score:	2.02					1.68				
Mean digestion score:	1.89					1.55				
Mean no. prey taxa per fish:	1.27					1.00				

TABLE 6.—Summary of Pacific ocean perch, *Sebastes alutus*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey Mean	Number of prey %	Weight of prey (g) Mean	Weight of prey (g) %
Euphausiacea					
Euphausia pacifica	52.1	20.5	62.4	1.12	63.1
Thysanoessa spinifera	19.2	7.1	8.0	0.47	9.8
Euphausiid unidentified	20.6	16.9	20.3	0.55	12.2
Amphipoda					
Phronima sedentaria	2.7	2.0	0.3	0.11	0.3
Paraphronima gracilis	1.4	1.0	—	0.02	—
Parathemisto pacifica	6.8	3.2	1.3	0.03	0.2
Vibilia propinqua	1.4	11.0	0.9	0.12	0.2
Primno macropa	2.7	1.0	0.2	0.02	—
Hyperiidea unidentified	6.8	2.4	1.0	0.01	—
Cyphocaris challengeri	2.7	1.0	0.2	0.03	0.1
Copepoda					
Neocalanus plumchrus	4.1	1.3	0.3	0.01	—
Euchaeta sp.	2.7	3.0	0.4	0.01	—
Decapoda					
Sergestes similis	20.6	3.1	3.7	0.34	7.5
Pasiphaea pacifica	1.4	1.0	—	0.03	—
Decapod mysis larvae	1.4	1.0	—	0.01	—
Crustacea remains	2.7	—	—	0.19	0.6
Cephalopoda					
Loligo opalescens	1.4	1.0	—	0.53	0.8
Cephalopod unidentified	6.8	1.4	0.5	0.22	1.6
Osteichthyes remains	5.5	—	—	0.04	0.1
Predator characteristics					
Number of stomachs examined:	73				
Number of empty stomachs:	26				
Mean weight per stomach:	0.923 g ± 1.954 (SD)				
Mean total length:	365.36 mm ± 60.01 (SD)				
Mean fullness score:	1.49				
Mean digestion score:	1.05				
Mean no. prey taxa per fish:	1.68				

(B), and had the most even distribution among prey types (B_n) of all rockfish examined from the summer survey. *Sebastes diploproa* preyed on fewer taxa than *S. flavidus* but had moderately high overall and normalized food breadth values. *Sebastes pinniger*, *S. crameri*, and *S. alutus* utilized a similar number of distinct prey items and had similar breadth and evenness values with *S. alutus* having a more equitable distribution of prey than the other two.

The seasonal results for the *S. flavidus* and *S. pinniger* were more divergent and represent the extreme values found among the species. Seventeen principal prey types were important in the seasonal diet of *S. flavidus*, contributing toward a high B value. However, the dominance of a few species yielded a low evenness value for this species. *Sebastes pinniger* preyed on few taxa in fairly unequal proportions yielding fairly low niche breadth and evenness values. These low evenness values could be caused by the preponderance of euphausiids found in the guts of both species during the summer months.

The individual overlap coefficients and the mean overlap for each species are presented for

TABLE 7.—Summary of splitnose rockfish, *Sebastes diploproa*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey Mean	Number of prey %	Weight of prey (g) Mean	Weight of prey (g) %
Euphausiacea					
Euphausia pacifica	46.8	26.5	41.2	1.53	42.1
Thysanoessa spinifera	14.5	2.9	1.4	0.16	1.4
Euphausiid remains	29.0	34.9	33.7	1.79	30.6
Amphipoda					
Parathemisto pacifica	1.6	1.0	—	0.01	—
Hyperoche medusarum	3.2	1.0	—	0.01	—
Paraphronima gracilis	3.2	1.0	—	0.02	—
Streetsia challengeri	1.6	1.0	—	0.02	—
Vibilia propinqua	32.3	10.3	11.1	0.10	1.9
Primno macropa	3.2	1.0	—	0.01	—
Hyperiidea unidentified	9.7	1.5	0.4	0.02	0.1
Cyphocaris challengeri	4.8	1.7	0.3	0.02	—
Lysianassidae unidentified	1.6	1.0	—	0.03	—
Gammaridea unidentified	1.6	1.0	—	0.03	—
Isopoda unidentified	1.6	1.0	—	0.02	—
Copepoda					
Neocalanus cristatus	6.5	3.2	0.7	0.02	0.1
Euchaeta elongata	4.8	3.3	0.5	0.03	0.1
Euchirella sp.	3.2	1.5	0.2	0.01	—
Candacia bipinnata	4.8	3.6	0.6	0.01	—
Metridia sp.	3.2	1.0	0.1	0.01	—
Decapoda					
Sergestes similis	46.8	4.4	6.8	0.60	16.5
Pasaphaea pacifica	1.6	1.0	—	0.59	0.6
Benthogenema burkenroadi	1.6	1.0	—	0.12	0.1
Munida quadrispina	1.6	6.0	0.3	0.12	0.1
Cancer sp. megalopae	9.7	1.3	0.4	0.02	0.1
Decapod mysis larvae	1.6	1.0	—	0.01	—
Mollusca					
Pteropoda unidentified	1.6	1.0	—	0.03	—
Gonatus sp.	1.6	1.0	—	0.07	—
Octopus sp. (juv.)	1.6	1.0	—	0.17	0.2
Osteichthyes					
Stenobrachius leucopsarus	1.6	1.0	—	0.36	0.3
Myctophidae unidentified	6.5	1.0	0.2	0.13	0.5
Tactostoma macropus	1.6	1.0	—	2.28	2.2
Liparididae unidentified	1.6	1.0	—	0.15	0.1
Fish remains	9.7	—	—	0.38	0.1
Unidentified animal remains	17.7	—	—	0.03	0.3
Predator characteristics					
Number of stomachs examined:	62				
Number of empty stomachs:	15				
Mean weight per stomach:	1.698 g ± 3.449 (SD)				
Mean total length:	264.82 mm ± 41.82 (SD)				
Mean fullness score:	2.50				
Mean digestion score:	1.25				
Mean no. prey taxa per fish:	2.48				

both the weight and numerical abundance of prey in Table 10 for the summer surveys. As overlap indices are affected by the level of taxonomic specificity at which the prey have been identified, no unbiased means for testing the significance of these values are available. We adopted the convention that overlap values from 0.00 to 0.29 are considered low, 0.30 to 0.60 considered medium, and those above 0.60 show highly similar diets (Langton 1982).

The coefficients for numerical composition show high values for all possible combinations except those involving *S. crameri*. Very similar proportions of the major euphausiid prey groups resulted in an extremely high overlap value (0.93) between

TABLE 8.—Summary of darkblotched rockfish, *Sebastes crameri*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey Mean	Number of prey %	Weight of prey (g) Mean	Weight of prey (g) %
Euphausiacea					
Euphausia pacifica	13.3	8.0	37.2	0.42	26.2
Thysanoessa spinifera	3.3	1.0	1.2	0.06	0.9
Euphausiid remains	3.3	1.0	1.2	0.01	0.2
Amphipoda					
Parathemisto pacifica	16.7	4.4	25.6	0.01	1.0
Cyphocaris challengeri	6.7	1.0	2.3	0.01	0.3
Lysianassidae unidentified	3.3	1.0	1.2	0.04	0.8
Copepoda					
Neocalanus cristatus	3.3	1.0	1.2	0.01	0.2
Euchaeta elongata	10.0	3.0	10.5	0.01	0.5
Copepod unidentified	16.7	3.0	17.4	0.01	0.8
Decapoda					
Sergestes similis	3.3	1.0	1.2	0.07	1.1
Osteichthyes					
Ammodytes hexapterus	3.3	1.0	1.2	0.28	4.3
Unidentified animal remains	53.3	—	—	0.25	62.5
Predator characteristics					
Number of stomachs examined:	30				
Number of empty stomachs:	10				
Mean weight per stomach:	0.246 g ± 0.389 (SD)				
Mean total length:	330.36 mm ± 77.17 (SD)				
Mean fullness score:	1.03				
Mean digestion score:	1.05				
Mean no. prey taxa per fish:	1.26				

TABLE 9.—Principal prey types making up >1.0% of the diet and food breadths of the five species of *Sebastes*. *R* is the total number of distinct prey items identified to at least genus level and that make up 0.1% ($p_i > 0.001$) of the identified fraction of the total weight. These prey were used to calculate the overall diet breadth (B) and the evenness of distribution of the prey items in the diet (B_n). The seasonal values for *S. flavidus* and *S. pinniger* are given in parentheses.

Species	Sample size	Principal prey types (p_i's > 0.01)	Pooled species values R	B	B_n
S. flavidus	185 (79)	*Euphausia pacifica*, *Thysanoessa spinifera*, hyperiid amphipods, *Sergestes similis*, *Loligo opalescens*, myctophids, *Clupea harengus pallasi*	12 (17)	3.64 (3.77)	0.303 (0.222)
S. diploproa	62	*E. pacifica*, *T. spinifera*, *S. similis*, *Vibilia propinqua*	8	2.28	0.285
S. pinniger	130 (238)	*E. pacifica*, *T. spinifera*, *Sebastes jordani*	8 (6)	1.86 (1.33)	0.232 (0.222)
S. crameri	30	*E. pacifica*, calanoid copepods, hyperiid amphipods, *Ammodytes hexapterus*	8	1.80	0.225
S. alutus	73	*E. pacifica*, *T. spinifera*, *S. similis*	7	1.73	0.247

S. pinniger and *S. flavidus*, although the diets are not similar for other prey items.

Overlap on the basis of weight, which may be a better measure of the energy obtained from the various food items, indicates high overlap between *S. pinniger* and *S. diploproa* and between *S. alutus* and *S. pinniger*, *S. diploproa*, and *S. crameri*. The rest of the values were <0.60, including *S. pinniger* with *S. flavidus* (C_{ih} = 0.48). The diet of *S. flavidus* overlaps the least with the other species ($\overline{C}_{ih}$ = 0.42) mainly due to its more piscivorous habits. The mean overlap values of *S. pinniger*, *S. diploproa*, and *S. alutus* are all relatively high (0.58, 0.56, and 0.61, respectively).

Overlaps between *S. pinniger* and *S. flavidus* for the seasonal cruises are similar to the results of the summer surveys (C_{ih} = 0.80 by number; 0.46 by weight). A possible explanation for the lower values may be changes in availability of both predator and prey (i.e., no *S. flavidus* stomachs were collected during spring and early summer when the euphausiid populations are generally the highest). The variability associated with the different cruises was examined by calculating the overlaps between these two species for the four seasonal cruises that contained at least 10 specimens of each species. The July cruise had the highest overlap of all on a weight basis (C_{ih} = 0.88) and the September cruise had the lowest (C_{ih} = 0.32), while the December and January cruises had intermediate overlaps (C_{ih} = 0.52 and 0.46), suggesting seasonal variations in prey availability for these species.

For comparative purposes, the dietary composition of the five most important prey categories for each of the rockfish species is presented by percent number and percent weight in Figures 4 and 5. Both figures show the importance of euphausiids in all five species. The stomachs of *S. crameri* contained a more equitable distribution of numbers of the major prey groups than the other species of rockfishes, with higher proportions of amphipods and copepods. Some of this difference may be ascribed to the smaller sample size. On a weight basis, *S. flavidus* was unique in that fishes and cephalopods were of greater importance in the

TABLE 10.—Overlap matrix for the five species of *Sebastes*. Only those prey that have proportional abundances exceeding 0.1% were used in the analysis. Values above the rules are for proportional weight overlap and values below are for proportional abundance. The mean overlap for each species by weight and number is given in parentheses directly above and below the rules.

	S. pinniger	*S. flavidus*	*S. diploproa*	*S. crameri*	*S. alutus*	
S. pinniger	(0.58) / (0.71)	0.48	0.72	0.47	0.66	W
S. flavidus	0.93	(0.42) / (0.70)	0.44	0.30	0.46	E I
S. diploproa	0.76	0.78	(0.56) / (0.65)	0.48	0.63	G
S. crameri	0.40	0.40	0.42	(0.48) / (0.41)	0.69	H T
S. alutus	0.74	0.70	0.63	0.42	(0.61) / (0.62)	
			NUMBER			

diet of this species than any of the other rockfish. Decapods were of moderate importance to *S. diploproa* and, to a lesser extent, *S. alutus*. Fishes were an important food source by weight for all rockfishes but *S. alutus*.

Seasonal Variation

Differences in the diet of *S. pinniger* and *S. flavidus* are summarized in Table 11 for the four seasons. The spring cruise shows an extreme dominance of one prey item, *Euphausia pacifica*, in the diet of *S. pinniger*. This prey species was found in about three-quarters of the stomachs and made up almost all the prey biomass. Decapod shrimp and fishes were rarely found in the diet at this time. Euphausiids also dominated the diet in the sum-

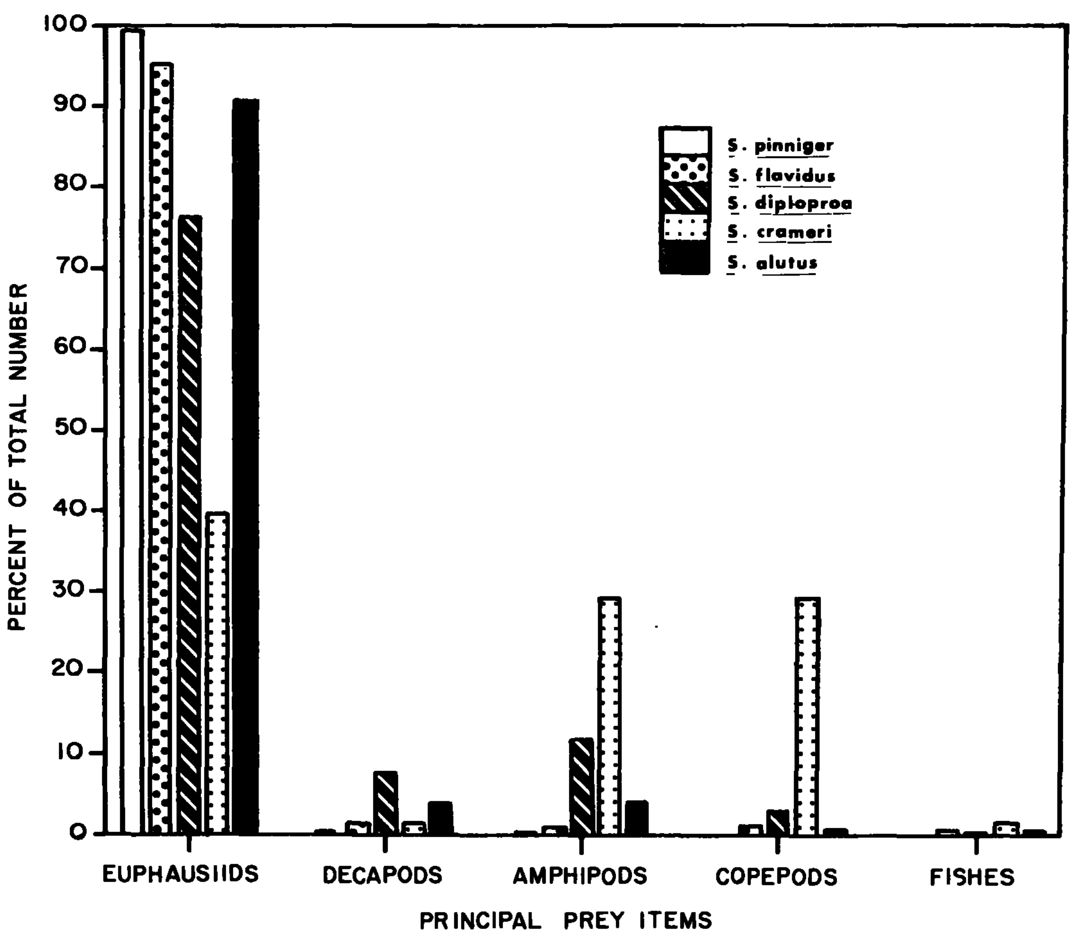

FIGURE 4.—The proportions of the five major prey taxa found in the five rockfish species based on numerical composition.

TABLE 11.—Variation in major prey taxa composition with season for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % W = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Species and season	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Spring[1] (Mar.-May)	42 (14.3)	73.8	99.6	—	—	73.8	99.6	2.4	+	—	—	—	—	2.4	0.4	—	—
Summer (June-Aug.)	165 (10.9)	61.2	75.1	7.9	0.5	68.5	94.7	3.6	1.1	2.4	+	—	—	6.7	4.2	3.6	+
Fall (Sept.-Nov.)	117 (20.5)	35.9	13.8	32.5	37.8	55.6	84.2	9.4	0.2	12.0	0.1	—	—	17.9	15.1	22.2	0.3
Winter (Dec.-Feb.)	44 (22.7)	50.0	25.9	47.7	12.0	81.8	94.2	—	—	6.8	0.4	—	—	13.6	5.5	4.5	+
Sebastes flavidus																	
Spring[2] (Mar.-May)	0																
Summer (June-Aug.)	151 (16.6)	52.3	37.2	23.2	0.5	58.3	66.7	9.9	0.8	13.2	0.1	15.2	6.5	13.9	25.6	3.3	0.4
Fall (Sept.-Nov.)	75 (22.7)	34.7	6.1	42.7	29.6	54.7	42.2	9.3	13.8	26.7	0.8	6.7	1.8	28.0	40.5	10.7	0.8
Winter (Dec.-Feb.)	38 (0.0)	81.6	19.5	92.1	15.3	94.7	46.7	0.5	0.7	10.5	+	28.9	30.6	52.6	15.4	21.1	6.6

[1]All collections taken during one cruise. All other seasons represent the means of at least two cruises spaced a minimum of 1 mo apart (Tables 1 and 2 give the exact dates and samples collected on each cruise).

[2]No stomachs of *S. flavidus* were collected during this season.

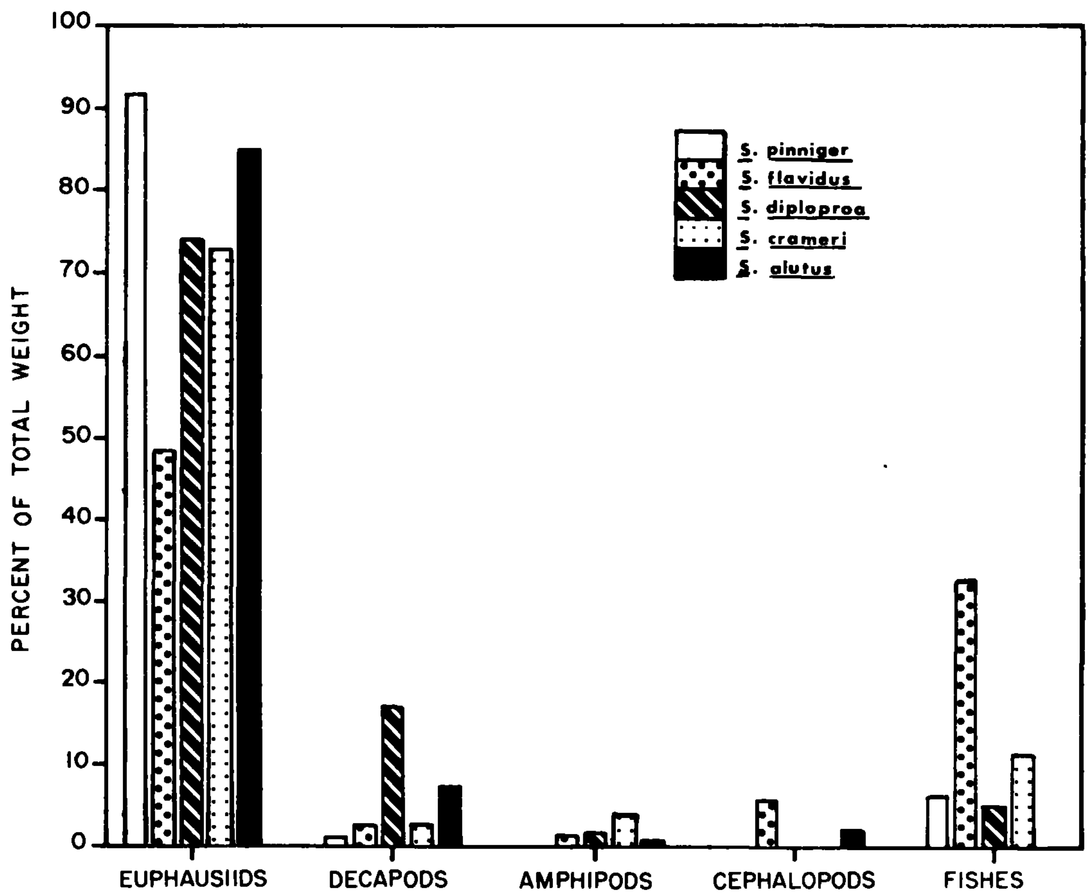

FIGURE 5.—The proportions of the five major prey taxa found in the five rockfish species based on gravimetric composition.

mer but to a lesser degree. *Thysanoessa spinifera* appeared in the stomachs at this time, but *E. pacifica* continued to be the most important euphausiid consumed. Shrimp and fishes were slightly more important but together made up only a minor portion of the diet. A low percentage of empty stomachs occurred in the summer.

The diet of *S. pinniger* in the fall showed substantial shifts in prey composition. Although the frequencies of occurrence were about equal for the two species of euphausiids, *T. spinifera* greatly exceeded *E. pacifica* by weight. Decapods were common but were represented mainly by small shrimp (*Sergestes similis*) and juvenile pelagic crabs (*Munida quadrispina*), which contributed little on a weight basis. Amphipods and gelatinous zooplankton occurred frequently but were not important by weight. Fishes were important by occurrence and weight and consisted mostly of mesopelagic species and several adult *Sebastes jordani* which made a large contribution to the biomass consumed.

Almost one-quarter of the fish collected in the winter had empty stomachs and contained much digested material. *Euphausia pacifica* and *T. spinifera* occurred in about the same number of stomachs, but *E. pacifica* contributed over twice as much of the total weight as *T. spinifera*. Subadult *E. pacifica* were very numerous at this time. The fishes consumed were mostly mesopelagic species.

Sebastes flavidus showed similar trends in food resource utilization among the three seasons from which collections were made (Table 11). Euphausiids, consisting mostly of *E. pacifica*, made up two-thirds of the diet by weight in the summer. Fishes were common and contributed heavily to the total biomass. Cephalopods were next in importance by either occurrence or weight. The diet in the fall showed the same shift in euphausiid species as was apparent for *S. pinniger*, with *T. spinifera* the dominant species. Fishes were almost as important by weight as euphausiids, but their weight total was mostly composed of adult clupeids. Cephalopods were least important in the fall months.

Euphausiids represented about half the diet during the winter, but the remainder was shared mostly by cephalopods and fishes. Both species of euphausiids were commonly found, but *E. pacifica* (mostly subadults) were slightly more important in the overall diet. Cephalopods (mostly adult *Loligo opalescens* and juvenile copepods) did show a substantial increase in weight and occurrence during these months. Fishes were found in over half the stomachs but were mainly juveniles of relatively small myctophids. Gelatinous zooplankton were most common, and decapods were least common, during this season. In contrast to *S. pinniger*, all stomachs of this species contained some food and many stomachs were full during this season.

Geographic Variation

Several trends were evident when comparing the diet of *S. pinniger* between regions (Table 12). The two southernmost regions had similar diets dominated by *E. pacifica* with *T. spinifera* representing only a minor portion of the diet. Meso-

TABLE 12.—Variation in major prey taxa composition with geographic area for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % *W* = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Area taken	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Southern Oregon	51 (13.7)	52.9	63.1	9.8	0.6	54.9	93.1	5.8	0.8	7.8	+	—	—	5.8	6.2	5.8	+
Heceta-Central	281 (16.0)	56.9	67.1	19.6	4.4	61.2	91.3	5.3	0.8	3.2	0.1	—	—	11.7	7.6	6.4	0.1
Columbia Region[1]	0																
Washington-Vancouver	36 (16.7)	22.2	4.6	27.8	57.7	36.1	92.8	2.8	+	22.2	0.1	—	—	25.0	6.7	36.1	0.4
Sebastes flavidus																	
Southern Oregon	70 (17.1)	58.6	47.6	30.0	9.2	65.7	84.9	10.0	+	14.3	0.8	24.3	13.7	8.6	0.6	5.7	0.1
Heceta-Central	122 (11.5)	61.5	27.9	49.2	14.1	70.5	50.6	11.4	2.2	18.0	0.3	16.4	16.9	32.8	27.6	13.1	2.3
Columbia Region	22 (13.6)	27.3	3.2	9.1	0.6	36.4	12.1	18.2	1.0	4.6	+	9.1	0.3	45.5	86.5	—	—
Washington-Vancouver	50 (26.0)	28.0	7.3	34.0	12.0	48.0	20.7	12.0	17.2	16.0	0.6	2.0	1.0	26.0	60.5	4.0	+

[1]No stomachs of *S. pinniger* were collected from this region.

pelagic fishes and sergestid shrimps were common but generally contributed little to the diet on a weight basis.

The northernmost region showed reduced occurrences of euphausiids, overall, but they still composed a percent weight equivalent to the two southern areas. This could have resulted from a shift to *T. spinifera*, which is generally larger than *E. pacifica*, as the main euphausiid consumed. Decapods were of lesser importance, but gelatinous zooplankton were very common in the stomachs of fish from this region. This may explain the high abundances of hyperiid amphipods known to be associated with gelatinous zooplankton. Fishes were common, especially juvenile Pacific sand lance, *Ammodytes hexapterus*, a prey species found only in the stomachs collected from this area.

Sebastes flavidus showed a different pattern in food utilization. A general decrease in euphausiid abundance was observed with increasing latitude (Table 12). The euphausiids from the southernmost regions were mostly *E. pacifica*, although many were unidentified. The only other important prey groups in these southern regions were cephalopods (mostly *Loligo opalescens*) and relatively large fishes such as Pacific herring and myctophids (*Diaphus theta*). All other prey groups were common but made little contribution to the diet.

Specimens of *S. flavidus* collected in the northernmost regions consumed substantial amounts of fish (mainly clupeids and myctophids). Euphausiids were relatively unimportant in these regions. As was the case with *S. pinniger*, *T. spinifera* was the dominant euphausiid eaten in the Washington-Vancouver region. Decapods, consisting mostly of *Pandalus jordani*, reached their highest proportion of the diet in the northernmost region.

Diel Variation

Both species showed variation in prey composition with the diel period (Table 13). *Sebastes pinniger* contained high percentages of euphausiids by weight during all four diel periods, with highest percentages occurring in the afternoon periods. Fishes, mostly non-mesopelagic species, were most important on a weight basis during morning and night when they occurred least frequently. Euphausiids were relatively more important by weight in the two afternoon periods. A high proportion of the fishes found in the stomachs during the afternoon periods were mesopelagic species.

Sebastes flavidus exhibited the opposite trends in food consumption with respect to time of day. Euphausiids were found in the highest proportions by weight during the morning and night periods while proportions of fish were substan-

TABLE 13.—Variation in major prey taxa composition with time of day for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % *W* = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Time of day (h)	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Morning (0800-1200)	68 (19.1)	25.0	32.1	19.1	5.7	51.5	83.1	7.3	0.2	13.2	0.1	—	—	8.8	15.9	23.5	0.6
Early aft. (1200-1600)	128 (10.2)	62.5	51.2	21.1	20.5	69.5	95.9	4.7	0.5	6.2	+	—	—	14.1	3.4	7.8	+
Late aft. (1600-1800)	79 (17.7)	50.6	80.2	1.6	1.8	70.9	96.3	3.8	0.7	—	—	—	—	13.9	2.9	5.1	+
Night (1800-0700)	93 (18.3)	52.7	56.8	20.4	5.9	69.9	83.4	4.3	1.4	4.3	0.2	—	—	9.7	14.8	7.5	0.1
Sebastes flavidus																	
Morning (0800-1200)	81 (18.5)	43.2	38.1	35.8	9.1	58.0	76.7	2.5	0.1	3.7	+	6.2	5.3	12.4	17.1	4.9	0.9
Early aft. (1200-1600)	71 (14.5)	54.9	25.5	28.2	7.5	57.7	48.8	14.1	4.4	19.7	0.2	15.5	7.6	25.3	37.4	7.0	1.3
Late aft. (1600-1800)	57 (17.7)	50.9	16.4	43.9	18.5	63.2	46.2	7.0	0.1	22.6	0.3	21.0	6.6	33.3	46.3	7.0	0.3
Night (1800-0700)	55 (12.7)	60.0	31.8	43.6	11.8	69.1	50.6	18.2	4.8	16.4	0.2	21.8	24.9	27.3	15.8	16.4	3.4

tially lower during these periods. Collections taken around late afternoon had equal amounts of fishes and euphausiids, while those taken at night had high occurrences and biomass of cephalopods (mostly *Loligo opalescens*) and gelatinous zooplankton.

The mean fullness score, mean digestion score, mean weight ratio (equal to the weight of stomach contents divided by weight of fish), and the percentage of empty stomachs were plotted for each adjusted collection time for both species. *Sebastes pinniger* had a distinct periodicity in its feeding cycle (Fig. 6). Peak periods of feeding intensity occurred midday and shortly after dusk. One collection (eight stomachs) taken at 0400 h had low values for fullness score and weight ratio but average values for digestion score and percentage of empty stomachs. The fullness and digestion scores (Fig. 6A) follow each other fairly well except that the midday digestion peak was several hours later than the fullness peak. A very distinct peak in the weight ratio at 1200 h and a smaller one shortly after dusk are evident (Fig. 6B).

Sebastes flavidus also appears to show a diel periodicity in its feeding pattern (Fig. 7). The fullness and digestion scores track each other very closely and show distinct peaks of feeding intensity around noon and shortly after dusk, although the number of samples in the latter period was limited (Fig. 7A). The actual mean weight ratio showed similar trends, but the noon peak is somewhat obscured (Fig. 7B). The percentage of empty stomachs was highest in the morning and remained low through the remainder of the day unlike that found for *S. pinniger.*

A high degree of variability in the mean weight ratio was found several times, especially during periods of peak feeding when both totally distended and almost empty stomachs were often found together. The differences in the weight

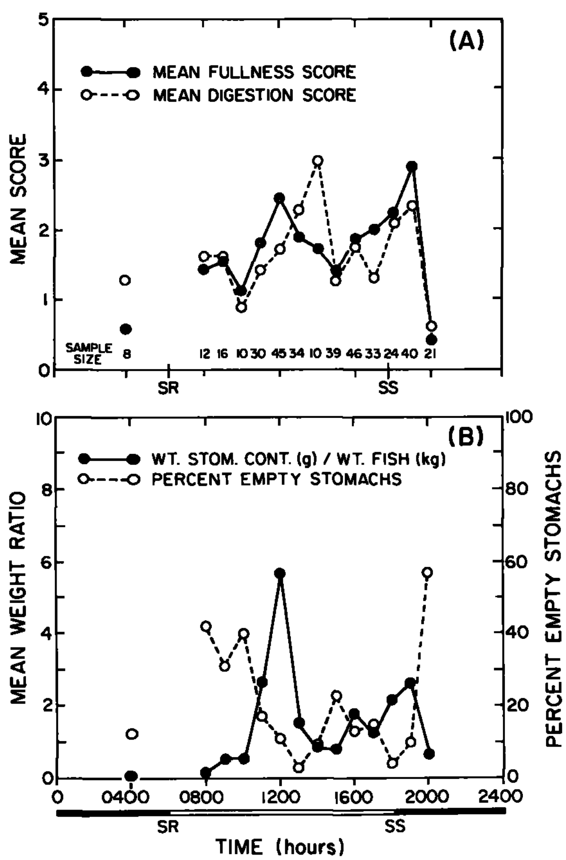

FIGURE 6.—Feeding intensity indices for *Sebastes pinniger* at adjusted times of the day. See text for explanation of indices.

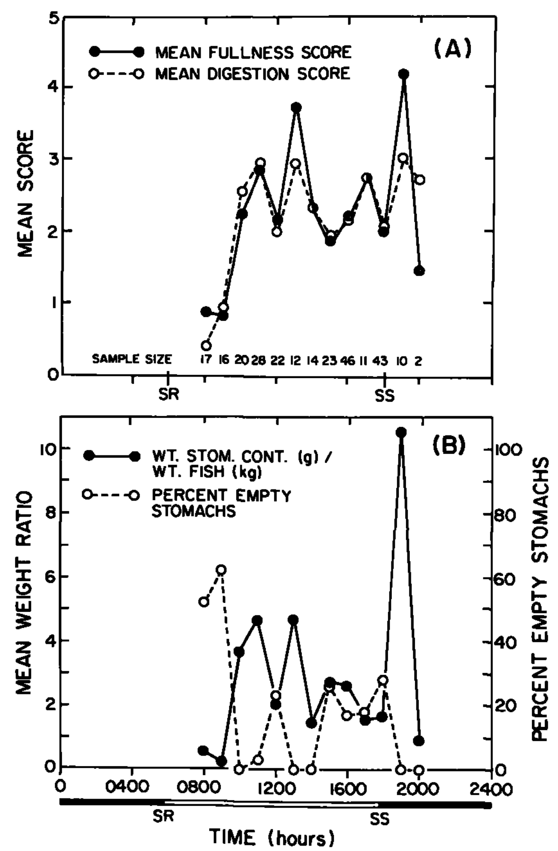

FIGURE 7.—Feeding intensity indices for *Sebastes flavidus* at adjusted times of the day. See text for explanation of indices.

ratios at the individual times were subjected to an analysis of covariance which compared the weight ratios adjusted for fish size (Jenkins and Green 1977). Both *S. pinniger* ($F_{(12,354)}$ = 5.68, P < 0.001) and *S. flavidus* ($F_{(11,262)}$ = 6.51, P < 0.001) showed significant differences in the mean weight ratios over the times tested, implying that feeding varied during the diel period. No significant differences (P > 0.05) in stomach fullness were associated with size or sex of the predator for either species.

Predator-Size Variation

The proportion of empty *S. pinniger* stomachs as well as the percent frequency of occurrence and percent weight of prey taxa were remarkably invariant among the four predator size classes (Table 14). Only the largest size class (≥55+ cm) shows any substantial variation with a larger proportion by weight of fishes and a commensurate decrease in weight of euphausiids consumed. Much of this fish weight was contributed by a few individual fish of large relative size (mostly adult *S. jordani*); the frequency of occurrence of fishes is only slightly higher for this largest size class.

Few obvious size-related trends were apparent for *S. flavidus*. The two smallest size classes consumed the largest proportion of euphausiids. *Euphausia pacifica* were less important for large fish. Decapods and cephalopods showed similar trends except that the frequencies of occurrence were highest for cephalopods but lowest for decapods in the largest size class. Fishes were consistent in their weight and occurrence proportions except that one size class (40-<45 cm) had much lower proportions than the others. Few trends were apparent for either amphipods or gelatinous zooplankton although both groups were commonly found.

To determine if different sizes of rockfish selected different sizes of prey, all fish that contained measurable prey were grouped into 10 mm length intervals and the means and ranges of their prey were plotted against fish size (Fig. 8). Although some exceptions exist, the majority of the prey of *S. pinniger* are found within a narrow range of prey sizes, a range (15-27 mm) largely determined by adult euphausiids, the dominant prey category (Fig. 8). Fishes of the largest two size classes consumed larger prey on average, and their prey had the largest variation in size due to high numbers of both small and large prey consumed by these fish. No significant relationship was found between length of fish and either overall size of prey or size of euphausiid prey.

Sebastes flavidus showed a much greater range in the sizes of prey consumed with the variation and range in prey length increasing with size of predator (Fig. 8). The mean size of prey eaten did not appreciably increase until the very largest size classes. Although the maximum prey size increases with fish size, the minimum size varies little throughout the length ranges examined. Again for this species, no relationship was found between fish length and overall or euphausiid prey lengths.

The size distribution of prey is shown for both species in Figure 9. The prey-size spectrum of *S. pinniger* was distributed fairly normally with the

TABLE 14.—Variation in major prey taxa composition with size of predator for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % W = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Size range (cm)	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
<45	64 (17.2)	48.4	43.2	21.9	9.7	68.7	91.4	4.7	3.1	6.2	0.3	—	—	14.1	4.8	4.7	0.4
45-<50	102 (17.6)	51.8	46.1	17.6	18.6	67.6	92.5	4.9	0.9	4.9	0.1	—	—	13.7	6.5	5.9	0.1
50-<55	146 (14.4)	47.3	65.6	21.2	12.0	61.1	94.9	5.5	0.2	4.1	+	—	—	11.0	4.7	8.9	0.1
≥55	56 (14.3)	58.9	49.3	12.5	7.6	67.9	83.4	5.4	0.2	7.1	+	—	—	16.1	16.3	14.3	0.2
Sebastes flavidus																	
<40	35 (0.0)	88.6	44.7	57.1	11.7	94.3	61.3	11.4	0.1	14.3	0.1	14.3	2.8	31.4	34.6	2.9	0.1
40-<45	61 (22.9)	45.9	50.2	29.5	12.4	52.5	83.9	13.1	1.2	24.6	0.2	13.1	8.4	9.8	5.8	4.9	0.4
45-<50	126 (21.4)	47.6	22.9	38.1	13.7	57.1	46.8	11.1	3.7	12.0	0.1	12.7	17.4	29.3	29.3	7.9	2.4
≥50	42 (2.4)	47.6	25.8	30.9	8.3	54.7	51.9	7.1	2.6	23.8	0.3	21.4	13.6	45.2	30.3	21.4	0.1

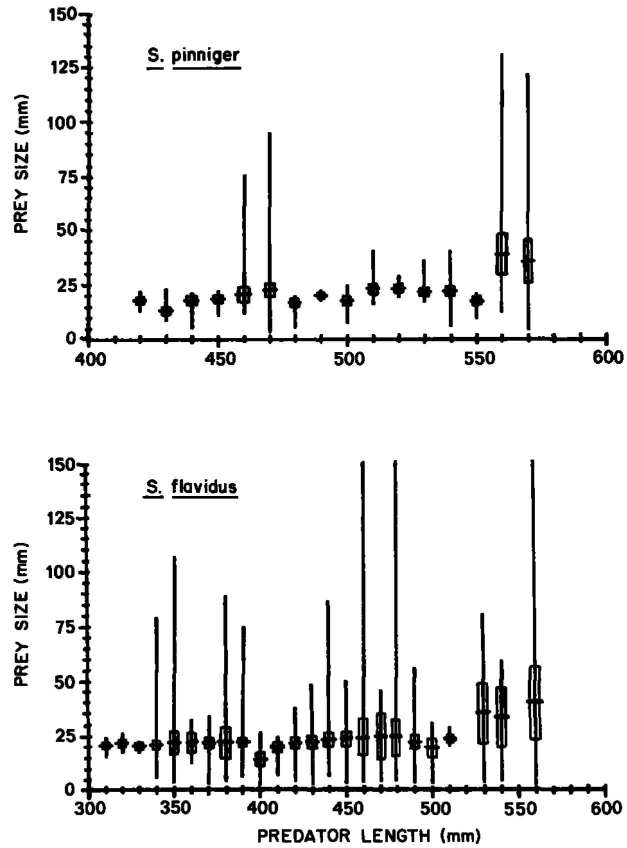

FIGURE 8.—Mean (horizontal lines) ±95% confidence limits (boxes) and ranges (vertical lines) of prey sizes found for each 10 mm interval of *Sebastes pinniger* and *S. flavidus*.

mode coinciding with the mean ($\bar{x}$ = 10.38 mm), although disjunct groups of small and large prey were found (Fig. 9). The prey-size spectrum of *S. flavidus* was slightly skewed toward the larger sized prey with the mean size ($\bar{x}$ = 18.44 mm) less than the mode. A smaller peak also appeared around 25 mm. No significant differences were found in the mean prey sizes utilized by the two species (Student's *t*-test, $P > 0.05$).

Analysis of Variation

The results of the chi-square analyses for *S. pinniger* showed that none of the factors analyzed had a significant effect on the occurrence of food in the stomachs (Table 15). At least one of the factors was related to the occurrences of all seven prey categories examined. Seasonal effects were the most significant (all $P \leq 0.01$) and were due to the higher occurrences of hyperiid amphipods, fishes, and gelatinous zooplankton in fall and winter. Area and time of capture showed both highly significant ($P \leq 0.001$) and insignificant effects depending on the prey category, but most comparisons were significant at the 0.05 level. In none of the prey categories examined did the size of the predator have a significant effect on the relative proportions consumed.

For *S. flavidus*, season of capture and size of predator affected the proportion of empty stomachs found (Table 15). Again season had the most significant influence on prey occurrence and was significant in all eight prey categories. Highly significant differences were found in area of capture and size of predator especially in the euphausiid and fish categories. Differences in occurrence of prey with time of capture deviated from expected the least of all the factors analyzed.

DISCUSSION

The five species of rockfishes examined rely heavily, if not exclusively, on pelagic macrozooplankton and micronekton. Although some benthic species appear in the prey lists (e.g., *Lyopsetta exilis*, *Munida quadrispina*, *Psettichthys melan-*

TABLE 15.—Results of chi-square analyses testing for differences in the occurrence of food and specific prey categories within the various factors. All significances are with three degrees of freedom except where noted.

Factor analyzed	Occurrence of food	*Euphausia pacifica*	*Thysanoessa spinifera*	Total euphausiids	Decapods	Amphipods	Cephalopods	Fishes	Gelatinous zooplankton
Sebastes pinniger									
Season	6.59	23.09***	72.48***	11.26**	113.28***	16.76***	—	15.87***	39.96***
Area[1]	0.19	8.61*	5.22	11.42***	0.46	22.44***	—	7.95*	35.66***
Time	4.32	28.18***	53.77***	11.86**	1.37	13.05***	—	1.43	19.21***
Size	0.67	3.12	3.24	6.26	0.04	0.98	—	1.26	4.35
Sebastes flavidus									
Season[1]	9.79**	13.32***	51.33***	10.02**	30.27***	11.15***	6.65*	21.43***	11.67***
Area	5.76	20.83***	15.81***	14.23***	1.21	2.76	11.62**	22.41***	6.43
Time	1.12	3.21	5.42	2.38	10.43*	12.30**	8.25*	9.33*	5.60
Size	17.50***	13.78***	6.35	14.17***	2.02	11.69**	0.94	12.92***	8.86*

* = $P \le 0.05$, ** = $P \le 0.01$, *** = $P \le 0.001$.
[1]Significance with two degrees of freedom.

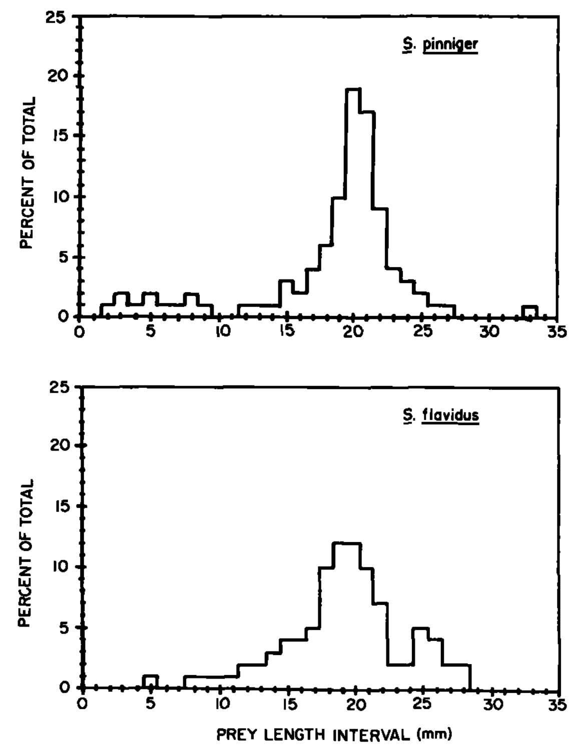

FIGURE 9.—Prey size spectra in percent for *Sebastes pinniger* and *S. flavidus*.

ostictus), they were represented by postlarval or juvenile forms commonly found in the plankton. Several comparatively large nektonic fishes and cephalopods (e.g., *Clupea harengus pallasi*, *Sebastes jordani*, *Loligo opalescens*) were eaten, but their occurrences were relatively rare. Conversely, the virtual absence of many common benthic and epibenthic organisms of appropriate size such as mysids, cumaceans, and gammaridean amphipods further implies that these fish do not normally feed on benthic animals.

These findings concur with the limited number of previous studies dealing with food habits of offshore rockfish. Phillips (1964) reported on the diet of all the species included here except *S. alutus*. Although little taxonomic detail and no quantitative data on prey consumption were given, euphausiids were listed as important forage items for all four species. Fishes were also important prey for several species, especially *S. flavidus*. Skalkin (1964), in a study of *S. alutus* in the Bering Sea, found mostly euphausiids and copepods in the stomachs, but also stated that a few nektobenthic species and "fragments" of benthic echinoderms were present.

The food habits of *S. flavidus* have been described in several studies off Oregon and Washington. Pereyra et al. (1969) found unusually high abundances and volumes of the mesopelagic fish, *Stenobrachius leucopsarus*, in *S. flavidus* stomachs collected near Astoria Canyon and hypothesized that local hydrographic conditions may have aggregated these prey at high densities. Gunderson et al. (1980)[5] reported that *S. flavidus* off the coast of Washington fed mostly on fishes, including some pleuronectid fishes possibly eaten near the bottom along with benthic polychaetes. Lorz et al. (1983) found euphausiids dominating the diet of *S. flavidus* off Washington and Queen Charlotte Sound, with fishes of greater importance in the latter region. Another deepwater species, *S. marinus*, found in the North Atlantic Ocean, also fed chiefly on pelagic prey (Lambert 1960). Euphausiids, hyperiid amphipods, and copepods were the most abundant prey, but mesopelagic fishes were also found in large numbers.

Among the species considered here, two divergent feeding patterns are apparent, assuming that

[5]Gunderson, D. R., G. L. Thomas, P. Cullenberg, D. M. Eggers, and R. Thorne. 1980. Rockfish investigations off the Washington coast. Ann. Rep., prep. for NMFS, Univ. Wash., 68 p.

the same prey items are equally available to all species. These can be seen most clearly in the divergence of the cumulative curves of the number of prey species (Fig. 2). Three species (*S. pinniger*, *S. alutus*, and *S. crameri*) tend to be stenophagous, with very few prey items represented in large volumes of prey organisms. Euphausiids appear to be the most sought after or available prey, and other prey taxa occur in low numbers. These three species show similar low food breadth values.

Sebastes flavidus and *S. diploproa*, on the other hand, have steadily rising prey curves that continue to rise and approach an asymptote beyond the limits of the figure. These curves are characteristic of euryphagous predators which show high overall prey diversity as well as high within-stomach diversity. This high prey diversity can be seen in the greater food breadth values attained by these two species. Although euphausiids predominate in these stomachs, high abundances of other prey, which may be preferred but have lower abundances and availabilities than euphausiids, also occur.

The diet overlap measurements calculated here may be useful in comparing how similar the food habits of two species are but may be of limited use when interpreted in an ecological sense. The interaction of factors that affect or determine the diet of a particular species is complex and may include such factors as temporal and spatial distribution of prey, behavioral adaptations of predator and prey, prey detection capabilities, and feeding morphologies of predators (Hyatt 1979). Caution should be exercised when inferences are made about possible species interactions based on diet overlap measurements alone. Two species may have broadly overlapping diets in terms of prey composition but segregate with respect to prey sizes selected, time of feeding, or habitat utilization (Schoener 1974; Ross 1977; Werner 1979; Macpherson 1981).

Sebastes pinniger and *S. flavidus* are two of the most abundant rockfish species within the geographical confines of this study. They inhabit similar depth ranges, latitudinal ranges, and show broadly overlapping areas of peak abundances according to trawl survey data (Alverson et al. 1964; Richardson and Laroche 1979; Gunderson and Sample 1980). Adams (1980) found that these two species had the highest positive association in trawl catches using presence-absence data of the seven abundant species he examined. Little is known, however, about their small-scale horizontal and vertical distribution. Although they may occupy similar bottom habitat, *S. flavidus* may be more pelagic (Alton 1972).

Seasonal, geographical, and diel variations in the abundance and availability of the important prey of *S. pinniger* and *S. flavidus* could be a major cause of the variations in the diet of these species. These variations may be the result of intrinsic prey population fluctuations with season, behavioral adaptations such as diel and ontogenetic vertical migration, or may stem from the prevailing oceanographic conditions either concentrating, dispersing, or transporting prey so that all prey are not equally available in the limited time and space frame of the individual predator. Current patterns alone are known to vary with season, depth, and geographic area (Huyer et al. 1975; Ingraham and Love 1978) and may affect the availability and concentration of prey.

Quantitative estimates of the seasonal and areal distributions of the total prey spectrum consumed by these rockfishes are limited. Day (1971) sampled macrozooplankton and micronekton from the northern part of the range of this study (lat. 46°45′-50°02′N) using a 0.9 m Isaacs-Kidd midwater trawl in the upper 150 m of the water column during the spring and fall. He found a peak in the biomass of catches at the outer edge of the continental shelf. Euphausiids dominated the catch at most stations, and *E. pacifica* and *T. spinifera* together accounted for 90% of the total abundance of all organisms collected, which is similar to the abundances found in the stomachs of several species examined here. Although the proportional abundance of *E. pacifica* varied greatly relative to *T. spinifera*, *E. pacifica* dominated the catches and was most concentrated during the spring when it comprised the largest proportion of the stomach weights in our study. Mesopelagic fishes were commonly collected in Day's sampling, but mostly at the offshore stations.

Pearcy (1972) reviewed the species composition, vertical and horizontal distribution, and variations in abundance of the macrozooplanktonic and nektonic fauna derived from 8 yr of sampling off Oregon. Annual and seasonal changes in the abundance and distribution of many species could be correlated with changes in oceanographic conditions. Following the cessation of upwelling in fall, surface waters flow predominantly inshore and northward, transporting shrimps and myctophids onto the shelf. We found that shrimp and myctophids became more important in the diets of

S. pinniger and *S. flavidus* at this time. An inshore-offshore peak in the biomass of midwater collections occurred on the edge of the continental slope off the central Oregon coast (lat. 44°39′N), a zone where oceanic macrozooplankton and micronekton may be concentrated by advection (Pearcy 1976). This is the region where pelagic-feeding rockfishes are often concentrated (Gabriel and Tyler 1980).

The majority of the prey species found in the stomachs of the rockfish species examined are pelagic species that undertake extensive diel vertical migrations and are important components of the biological sound scattering layer in the Northeast Pacific (Pearcy and Laurs 1966; Brinton 1967; Pearcy and Mesecar 1971; Pearcy 1972; Alton and Blackburn 1972). In this study, both of the euphausiid species of interest, *E. pacifica* and *T. spinifera*, have been found to have substantially different daytime and nighttime vertical distributions. According to Alton and Blackburn (1972), catch rates of *T. spinifera* off the coast of Washington were the highest near the bottom during the early evening hours (1800-2000 h) and at the surface a few hours later (2100-2300 h).

The diurnal downward migration of these organisms over the continental shelf may result in a substantial biomass in close proximity to near-bottom predators, such as rockfishes, which feed on pelagic prey during the day. Deeper migration to daytime depths typical of their more open ocean conspecifics is restricted by the shelf, especially in shoaler areas such as Heceta Bank. Isaacs and Schwartzlose (1965) found dense populations of predators, including many rockfishes, on shallow banks off California; these predators presumably take advantage of net inshore transport by currents of oceanic organisms over the bank. Pereyra et al. (1969) reported high incidences of predation on mesopelagic organisms by aggregations of *S. flavidus* residing on the shelf edge near a deep canyon. Vertically migrating mesopelagic organisms may also constitute an important food source for many species of slope fishes (Sedberry and Musick 1978).

Diel vertical distribution patterns of offshore rockfishes are not well documented. Based on acoustic observations, Westrheim (1970) concluded that schools of Pacific ocean perch move off bottom at night. Pereyra et al. (1969) and Love (1981) caught rockfishes that were apparently feeding well off the bottom at night. Lorz et al. (1983) concluded that *S. flavidus* off Washington fed on euphausiids during night or early morning hours, when these euphausiids would be expected to be in surface waters. Similar migrations were seen on Heceta Bank during this study. Figure 10 shows an acoustic 33 kHz transect taken across Heceta Bank during the late morning (about 1023-1050 h PST). Many large "spikes" of fish aggregations were apparent extending over 100 m above bottom. Some of these were probably caused by rockfish ascending in the water column to feed. Figure 11 is a 33 kHz echogram on Heceta Bank made around 1800 h PST. The "haystacks" shown are characteristic of tight aggregations of *S. pinniger* just above bottom (Barss[6]) and may represent feeding aggregations. Also visible in this echogram is more diffuse scattering in the water column (20 m off bottom) probably caused by euphausiids. The tow made concurrently with this trace did yield a large catch of rockfish (97% *S. pinniger*), most of which had stomachs full of fresh euphausiids. This stratification of large sound scatterers below diffuse midwater scattering prey was often observed during the acoustic surveys. Atlantic cod appear to interact with pelagic prey in a similar fashion (Brunel 1965; Pearcy et al. 1979; Falk-Peterson and Hopkins 1981).

The two primary species examined in detail in this study appear to forage mainly during the midday and evening dusk periods, although sampling was limited during nighttime. The similar diel patterns of feeding intensity suggest that temporal partitioning of feeding time is not occurring between *S. pinniger* and *S. flavidus*. The differing utilization patterns of euphausiids and fishes seen for the two species (Table 13) may be related to the vertical positioning of the two species in the water column. *Sebastes flavidus* may feed high in the water column, prey upon adult herring and pelagic juvenile fishes during the daytime, and intercept euphausiids during crepuscular periods, whereas *S. pinniger* may stay nearer the bottom where they may feed almost exclusively on increased daytime aggregations of euphausiids.

The occurrence of a high percentage of empty stomachs and generally low feeding intensity indices in *S. alutus*, which were caught mainly in late afternoon in our study, suggests that this species is more nocturnal in its feeding patterns, assuming that this species has similar regurgita-

[6]W. Barss, fishery biologist, Oregon Department of Fish and Wildlife, Newport, OR 97365, pers. commun. December 1980.

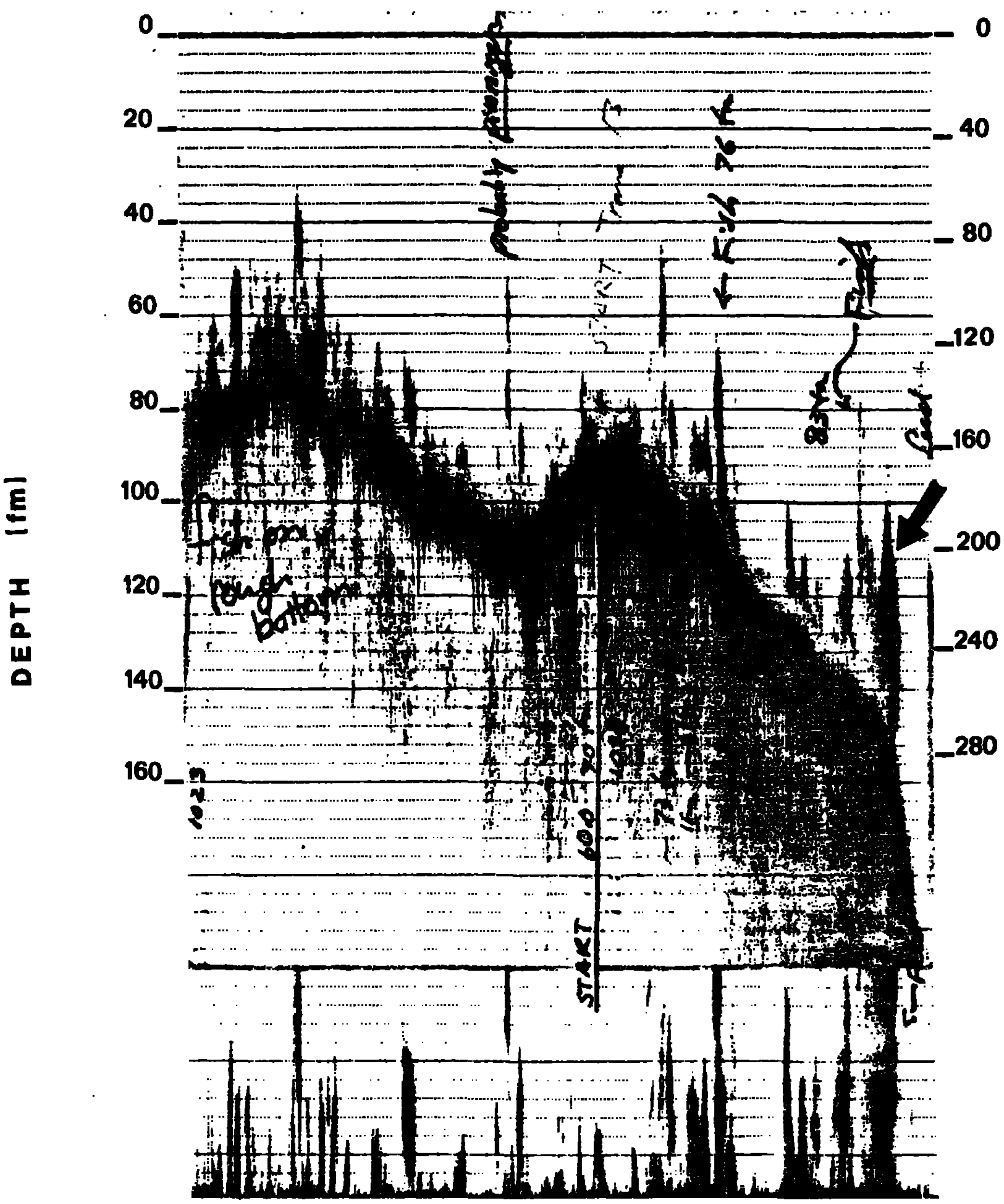

FIGURE 10.—Echo sounder (Krupp-Atlas Elektronik Model 611, 33 kHz) transect across Heceta Bank showing characteristic rough topography and schools of fish in the water column. The larger signal at the extreme right (arrow) is believed to be a large concentration of forage fish, possibly myctophids. The bottom section of the figure shows an expanded version of the layer just above the seabed.

tion and digestion rates as the other species studied. Skalkin (1964) found that the feeding intensity of immature *S. alutus* in the Bering Sea was highest around midday with a smaller peak shortly after dusk as found for *S. pinniger* and *S. flavidus* in this study. He also hypothesized that larger fish may feed higher in the water column at night on euphausiids, but his nighttime sampling was also limited. Similar pelagic feeding by *S. alutus* at night may be occurring in our study area, but these fish would not be available to bottom trawls at this time.

The rockfishes considered here are just a few species in an extensive guild (sensu Root 1967)

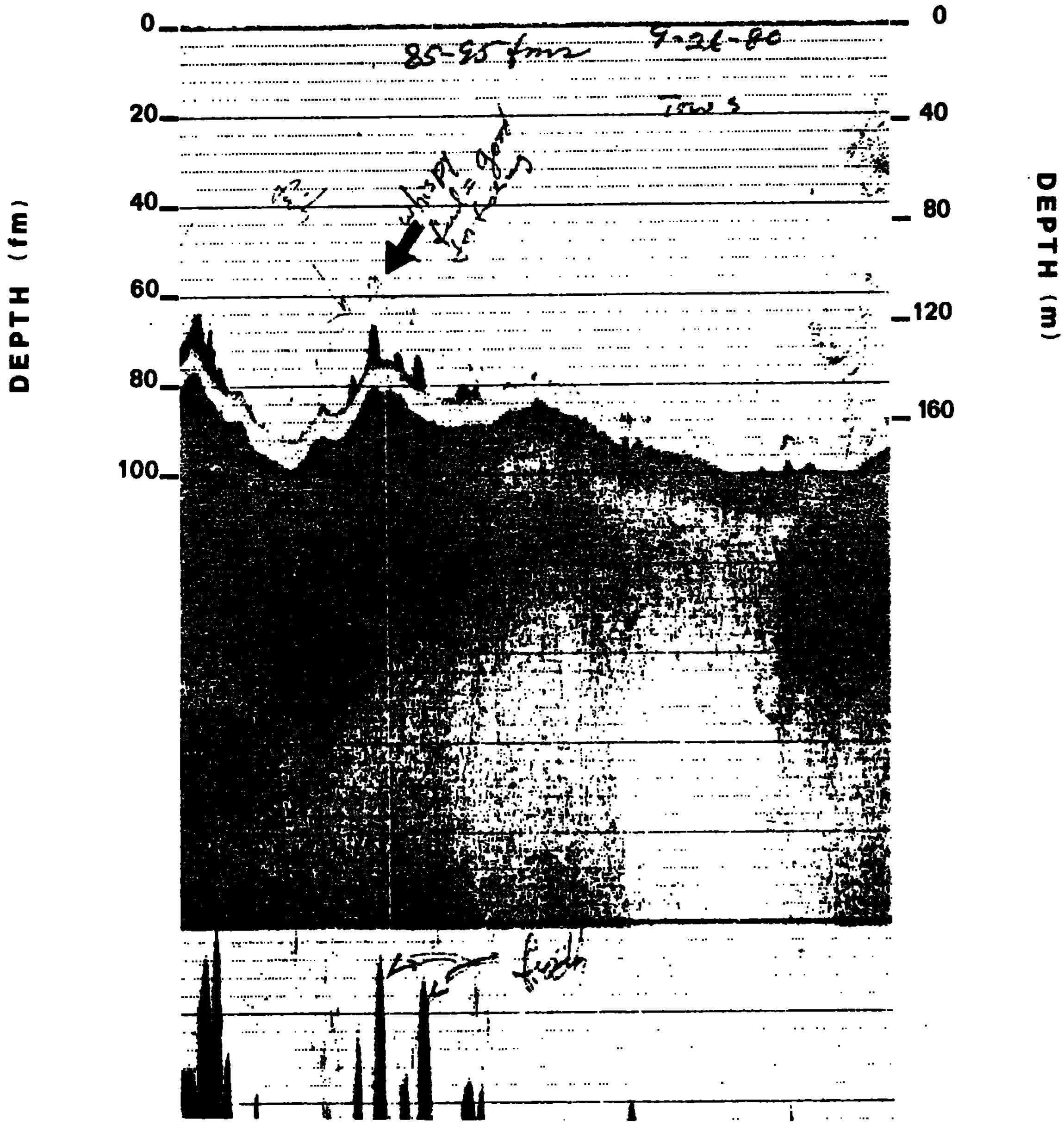

FIGURE 11.—Smoother bottom profile made during a tow showing the "haystacks" of rockfish in close association with the bottom and possibly preying upon the food organisms (arrow) directly above them.

of organisms which feed in varying degrees on euphausiids. Other pelagic predators in this study area known to feed intensively on euphausiids include Pacific hake (Alton and Nelson 1970), myctophids (Tyler and Pearcy 1975), juvenile salmon (Peterson et al. 1982), and squid (Karpov and Cailliet 1978). Standing stocks and production rates of euphausiids in northern latitudes may be of such magnitude that many predators often subsist on them in coexistence rather than compete for other more limited resources. More research is needed on the biology and distribution of these abundant prey species and their importance to fishery resources. In complex, multispecies fisheries such as those utilizing rockfishes, it may be possible to treat several species with similar life histories and which prey on similar resources as a biological unit for management purposes.

ACKNOWLEDGMENTS

We are indebted to the many individuals who assisted with the collection of the stomach samples and in particular to Mary Yoklavich and Ray Taylor of Oregon State University, Bill Barss and Steve Johnson of the Oregon Department of Fish and Wildlife (ODFW), and numerous scientists at the Northwest and Alaska Fisheries Center (NWAFC) Seattle Laboratory. We thank Bob Demory of ODFW and Tom Dark of NWAFC for allowing us to participate on their research cruises and George Boehlert, Carl Bond, and an anonymous reviewer for their helpful criticisms on the manuscript. This study was funded by Contract No. 81-ABC-00192 from the NWAFC, National Marine Fisheries Service.

LITERATURE CITED

ADAMS, P. B.
1980. Morphology and distribution patterns of several important species of rockfish (Genus *Sebastes*). Mar. Fish. Rev. 42(3-4):80-82.

ALTON, M. S.
1972. Characteristics of the demersal fish fauna inhabiting the outer continental shelf and slope off the northern Oregon Coast. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River Estuary and adjacent ocean waters, p. 583-634. Univ. Wash. Press, Seattle.

ALTON, M., AND M. O. NELSON.
1970. Food of the Pacific hake, *Merluccius productus*, in Washington and northern Oregon coastal waters. *In* Pacific hake, p. 35-42. U.S. Fish Wildl. Serv., Circ. 332.

ALTON, M. S., AND C. J. BLACKBURN.
1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen, in coastal waters of Washington. Calif. Fish Game 58:179-190.

ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT.
1964. A study of the demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lectures in Fisheries, 190 p. Institute of Fisheries, University of British Columbia, Vancouver.

BRAY, R. N., AND A. W. EBELING.
1975. Food, activity, and habitat of three "picker-type" microcarnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

BRINTON, E.
1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

BRODEUR, R. D.
1983. Food habits, dietary overlap and gastric evacuation rates of rockfishes (Genus *Sebastes*). M.S. Thesis, Oregon State Univ., Corvallis, 102 p.

BRUNEL, P.
1965. Food as a factor or indicator of vertical migrations of cod in the western Gulf of St. Lawrence. Int. Comm. Northw. Atl. Fish., Spec. Publ. 6:439-448.

CHEN, L.-C.
1971. Systematics, variation, distribution, and biology of rockfishes of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr. 18, 115 p.
1975. The rockfishes, genus *Sebastes* (Scorpaenidae), of the Gulf of California, including three new species, with a discussion of their origin. Proc. Calif. Acad. Sci. 40: 109-141.

COLWELL, R. K., AND D. J. FUTUYMA.
1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

DAY, D. S.
1971. Macrozooplankton and small nekton in the coastal waters off Vancouver Island (Canada) and Washington, spring and fall of 1963. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 619, 94 p.

FALK-PETERSON, S., AND C. C. E. HOPKINS.
1981. Zooplankton sound scattering layers in North Norwegian fjords: Interactions between fish and krill shoals in a winter situation in Ullsfjorden and Øksfjorden. Kieler Meeresforsch. 5:191-201.

GABRIEL, W. L., AND A. V. TYLER.
1980. Preliminary analysis of Pacific Coast demersal fish assemblages. Mar. Fish. Rev. 42(3-4):83-88.

GOTSHALL, D. W., J. G. SMITH, AND A. HOLBERT.
1965. Food of the blue rockfish *Sebastodes mystinus*. Calif. Fish Game 51:147-162.

GUNDERSON, D. R., AND T. M. SAMPLE.
1980. Distribution and abundance of rockfish off Washington, Oregon and California during 1977. Mar. Fish. Rev. 42(3-4):2-16.

HELFMAN, G. S.
1978. Patterns of community structure in fishes: summary and overview. Environ. Biol. Fish 3:129-148.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

HUYER, A.
1977. Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. Limnol. Oceanogr. 22:442-453.

HUYER, A., R. D. PILLSBURY, AND R. L. SMITH.
1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90-95.

HYATT, K. D.
1979. Feeding strategy. Chap. 2. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology. Vol. VIII. Bioenergetics and growth, p. 71-119. Academic Press, N.Y.

INGRAHAM, W. J., JR., AND C. M. LOVE.
1978. Oceanographic conditions off California to Vancouver Island in the summer of 1977. Mar. Fish. Rev. 40(2):24-28.

ISAACS, J. D., AND R. A. SCHWARTZLOSE.
1965. Migrant sound scatterers: interaction with the sea floor. Science (Wash., D.C.) 150:1810-1813.

JENKINS, B. W., AND J. M. GREEN.
1977. A critique of field methodology for determining fish feeding periodicity. Environ. Biol. Fish 1:209-214.

KARPOV, K. A., AND G. M. CAILLIET.
1978. Feeding dynamics of *Loligo opalescens*. Calif. Dep. Fish Game, Fish Bull. 169, p. 45-65.

LAMBERT, D. G.
1960. The food of the redfish *Sebastes marinus* (L.) in the Newfoundland area. J. Fish. Res. Board Can. 17: 235-243.

LANGTON, R. W.
1982. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other Northwest Atlantic finfish. Fish. Bull., U.S. 80:745-759.

LARSON, R. J.
1972. The food habits of four kelp-bed rockfishes (Scorpaenidae, *Sebastes*) off Santa Barbara, California. M.S. Thesis, Univ. California, Santa Barbara, 57 p.
1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50:221-239.

LEVINS, R.
1968. Evolution in changing environments. Princeton Univ. Press, Princeton, 120 p.

LINTON, L. R., R. W. DAVIES, AND F. J. WRONA.
1981. Resource utilization indices: an assessment. J. Anim. Ecol. 50:283-292.

LORZ, H. V., W. G. PEARCY, AND M. FRAIDENBURG.
1983. Notes on the feeding habits of the yellowtail rockfish, *Sebastes flavidus*, off Washington and in Queen Charlotte Sound. Calif. Fish Game 69:33-38.

LOVE, M. S.
1981. Evidence of movements of some deepwater rockfishes (Scorpaenidae: Genus *Sebastes*) off Southern California. Calif. Fish Game 67:246-249.

LOVE, M. S., AND A. W. EBELING.
1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 76:257-271.

MACPHERSON, E.
1981. Resource partitioning in a Mediterranean demersal fish community. Mar. Ecol. Prog. Ser. 4:183-193.

MCEWEN, G. F., M. W. JOHNSON, AND T. R. FOLSOM.
1954. A statistical analysis of the performance of the Folsom plankton sample splitter, based on test observations. Arch. Meteorol. Geophys. Bioklimatol., Ser. A, 7:502-527.

PEARCY, W. G.
1972. Distribution and ecology of oceanic animals off Oregon. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 351-377. Univ. Wash. Press, Seattle.
1976. Seasonal and inshore-offshore variations in the standing stocks of micronekton and macrozooplankton off Oregon. Fish. Bull., U.S. 74:70-80.

PEARCY, W. G., C. C. E. HOPKINS, S. GRØNVIK, AND R. A. EVANS.
1979. Feeding habits of cod, capelin, and herring in Balsfjorden, northern Norway, July-August 1978: the importance of euphausiids. Sarsia 64:269-277.

PEARCY, W. G., AND R. M. LAURS.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

PEARCY, W. G., AND R. S. MESECAR.
1971. Scattering layers and vertical distribution of oceanic animals off Oregon. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 381-394. Maury Center for Ocean Science, Wash., D.C.

PEREYRA, W. T., W. G. PEARCY, AND F. E. CARVEY, JR.
1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Can. 26:2211-2215.

PETERSON, W. T., R. D. BRODEUR, AND W. G. PEARCY.
1982. Food habits of juvenile salmon in the Oregon coastal zone, June 1979. Fish. Bull., U.S. 80:841-851.

PHILLIPS, J. B.
1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

RICHARDSON, S. L., AND W. A. LAROCHE.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1-46.

ROOT, R. B.
1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr. 37:317-350.

ROSS, S. T.
1977. Patterns of resource partitioning in searobins (Pisces: Triglidae). Copeia 1977:561-571.

SCHOENER, T. W.
1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408-418.
1974. Resource partitioning in ecological communities. Science (Wash., D.C.) 185:27-39.

SEDBERRY, G. R., AND J. A. MUSICK.
1978. Feeding strategies of some demersal fishes of the continental slope and rise off the Mid-Atlantic Coast of the USA. Mar. Biol. (Berl.) 44:357-375.

SKALKIN, V. A.
1964. Diet of rockfish in the Bering Sea. *In* P. A. Moiseev (editor), Soviet fisheries investigations in the Northeast Pacific, Part II, p. 159-174. (Transl. Isr. Program Sci. Transl.; available U.S. Dep. Commer., Clearinghouse Fed. Sci. Tech. Inf., Springfield, VA 22151.)

SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

TYLER, A. V.
1972. Food resource division among northern, marine, demersal fishes. J. Fish. Res. Board Can. 29:997-1003.

TYLER, H. R., JR., AND W. G. PEARCY.
1975. The feeding habits of three species of lanternfishes (family Myctophidae) off Oregon, USA. Mar. Biol. (Berl.) 32:7-11.

WALLACE, R. K., JR.
1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110:72-76.

WERNER, E. E.
1979. Niche partitioning by food size in fish communities. *In* H. Clepper (editor), Predator-prey systems in fisheries management, p. 311-322. Sport Fish. Inst., Wash., D.C.

WESTRHEIM, S. J.
1970. Survey of rockfishes, especially Pacific ocean perch, in the northeast Pacific Ocean, 1963-66. J. Fish. Res. Board Can. 27:1781-1809.