

## TROPHIC RELATIONSHIPS OF THE SHORTBELLY ROCKFISH, *SEBASTES JORDANI*, OFF CENTRAL CALIFORNIA

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### ABSTRACT

The shortbelly rockfish, *Sebastes jordani*, the most numerous species of *Sebastes* off central California, feeds primarily on *Euphausia pacifica* and other euphausiids. This rockfish forages in the water column at night, and even more intensively near the bottom during the day. Its major prey, *E. pacifica*, normally inhabits deeper water outside the shelf, where it occurs at depths of 200–400 m during the day. At night, however, *E. pacifica* migrates upward in the water column, and many are transported over the shelf by prevailing currents. In the morning, when they attempt to descend to their normal daytime depths, many become trapped on the relatively shallow shelf, where *S. jordani* probably find these organisms especially vulnerable.

### RESUMEN

*Sebastes jordani*, la especie más numerosa de *Sebastes* en la costa central de California, se alimenta principalmente de *Euphausia pacifica* y otros euphausíidos. Este pez se alimenta en la columna de agua durante la noche, y más intensamente cerca del fondo durante el día. Su presa principal, *E. pacifica*, vive normalmente en aguas profundas fuera de la plataforma continental, en profundidades de 200 a 400 m durante el día. Sin embargo, durante la noche, *E. pacifica* migra hacia la superficie donde numerosos individuos son transportados hacia la costa por las corrientes predominantes. En la mañana, cuando estos organismos intentan completar su migración hacia las profundidades diurnas normales, se encuentran atrapados en las aguas costeras menos profundas donde son particularmente vulnerables a la predación por *S. jordani*.

### INTRODUCTION

The shortbelly rockfish, *Sebastes jordani*, a potentially rich but unfished resource off California (Lenarz 1980), occurs on the continental shelf from

northern Baja California, Mexico (lat. 31°N), to Vancouver, British Columbia, Canada (50°N). It is most numerous off central California, where its biomass between San Francisco and Monterey has been estimated to be 295,000 metric tons—more than 10 times the estimated combined biomass of all other species of *Sebastes* within that area (Gunderson and Sample 1980). The adults of this relatively small scorpaenid (to about 32 cm TL) occur at depths from about 90 to 280 m (Miller and Lea 1972).

In making tentative management recommendations, Lenarz (1980) cautioned that the trophic relationships of this species should be better understood before its exploitation is permitted. The shortbelly is an important prey of chinook salmon, *Oncorhynchus tshawytscha* (Merkel 1957), and current study at the National Marine Fisheries Service Tiburon Laboratory has shown that it is also seasonally important to other coastal predators, including coho salmon (*Oncorhynchus kisutch*) (P.A. Adams, Tiburon Laboratory, pers. comm. Jan. 1983); lingcod (*Ophiodon elongatus*); and black rockfish (*Sebastes melanops*) (E. S. Hobson, J. R. Chess, and D. F. Howard, Tiburon Laboratory, unpubl. data 1985). Little is known about its predatory habits, however, beyond the report that adults feed exclusively on macrozooplankton, primarily euphausiids (Phillips 1964).

Here we describe the diel feeding pattern of the shortbelly relative to variations in the availability of potential prey. We then discuss how the shortbelly's distribution on the coastal shelf off central California is influenced by mechanisms affecting the distribution of its prey.

### METHODS

#### *Study Area*

This study is based on collections and observations made during 10 cruises involving 74 days at sea between 1979 and 1982. Exploratory surveys during November 1979 and March 1980 used hydroacoustics and trawls to locate concentrations of shortbellies in the area between Point Sur (36°18'N) and Point Reyes (38°4'N). These explo-

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[Manuscript received November 5, 1987.]

TABLE 1  
 Areas Trawled during Each Cruise, Showing Number of Positive *S. jordani* Catches/Total Number of Trawl Sets Taken

	Month/year of cruises										
	11/79	3/80	7/80	11/80	3/81	5/81	9/81	1/82	3/82	9/82	11/82
Pescadero Point	7/14	4/7	2/6	0/3	—	2/5	0/4	0/1	—	—	—
Ascension Canyon	3/6	—	2/3	5/12	2/4	0/5	4/11	4/7	3/8	4/11	0/6
Monterey	—	2/4	—	—	—	0/2	—	—	—	—	—
Point Sur	—	2/4	—	—	2/2	0/1	—	—	—	—	—

rations found the species concentrated where the coastal shelf extended offshore, often near submarine canyons (the same areas where Gunderson and Sample [1980] had found them abundant during a 1977 coastwide rockfish survey). They were most numerous at depths between 120 and 240 m along about 40 km of the coastal shelf's outer edge offshore of Pescadero Point (at approximately 37°13'N), and the areas immediately north of Ascension and Sur canyons (Figure 1 and Table 1). Work was concentrated at these locations following the exploratory cruises of 1979 and 1980, but exploratory surveys were continued elsewhere as opportunities arose. Although these additional surveys located small concentrations at other places, usually on the outer shelf, the more than 340 hours of additional hydroacoustic search and exploratory trawling between Point Sur and Point Reyes failed to locate concentrations that matched those in the primary study areas defined above.

### Collections

The collections were scheduled to define diel and geographical patterns in trophic relationships. The diel feeding patterns discussed below are based on stomach contents of shortbellies trawled from the Ascension area during the hours immediately before sunset and sunrise—times that have been found most effective in defining diel feeding patterns of predatory fish (e.g., Hobson 1974; Hobson and Chess 1976). The geographical patterns are based on shortbellies collected at the various stations during all periods of the diel cycle. Scheduled plankton collections were made during midday (1100–1400 h) and midnight (2200–0100 h) at the Ascension area to define diel variations in prey abundance and distribution.

Shortbellies were collected with a three-bridle midwater trawl that had 30.5-m headropes and footropes. We used a Furuno MkII net monitor with an acoustic link to position the trawl at the depths of the strongest acoustic targets. Often, however, the trawl followed a course offset from that of the ship (due either to the effects of subsurface currents on the trawl, or winds on the ship),

which hampered attempts to position the trawl on specific acoustic targets located by shipboard echosounders. Most sets were made on aggregations that had been located hydroacoustically, but blind sets made where we had found shortbellies earlier were often successful even in the absence of acoustic targets. The standard trawling duration was 20 minutes, but the net was retrieved sooner if there were indications (hydroacoustic or otherwise) that it had passed through a large aggregation of fish. Each catch, or a portion of the catch, was grossly subdivided by size, and from each size group 10 fish were retained for stomach-content analysis. (Fish with any evidence of everted stomachs, an unusual condition, were not included.) A total of 977 specimens were measured (standard length). Their stomachs were removed and preserved, and the contents were analyzed later in the laboratory.

Zooplankton were collected with a messenger-activated, opening-closing 1-m<sup>2</sup> Tucker trawl (Hopkins et al. 1973) fitted with two 0.335-mm mesh nets. Because the net frame was inclined 45° while fishing, its 1 × 1.4-m opening was in effect reduced to 1 m<sup>2</sup>. A total of 84 plankton samples stratified by depth were taken during seven cruises. Each cruise included a series of three plankton collections made on two successive days and nights ( $n = 12$ ). The three collections of each series were replicated at estimated depths of 18, 55, and 119 m along the 137-m (75-fm) isobath. (The ship sometimes drifted off course over depths that varied from about 128 to 145 m.) Sampling depths were determined by wire angle and length, and were standardized by maintaining the wire at 45° (which required a speed of approximately 127 cm sec<sup>-1</sup>) for the 15-minute collection periods. Four test runs using digital flowmeters indicated that this procedure filtered about 1,114 m<sup>3</sup> of water. We used elapsed time and wire angle, rather than a flowmeter, to standardize our samples.

For later analysis in the laboratory, a measured proportion, usually about a 500-ml aliquot of each collection (settled volume) was preserved in 4% buffered formaldehyde. (The entire collection was preserved if smaller than 500 ml.)

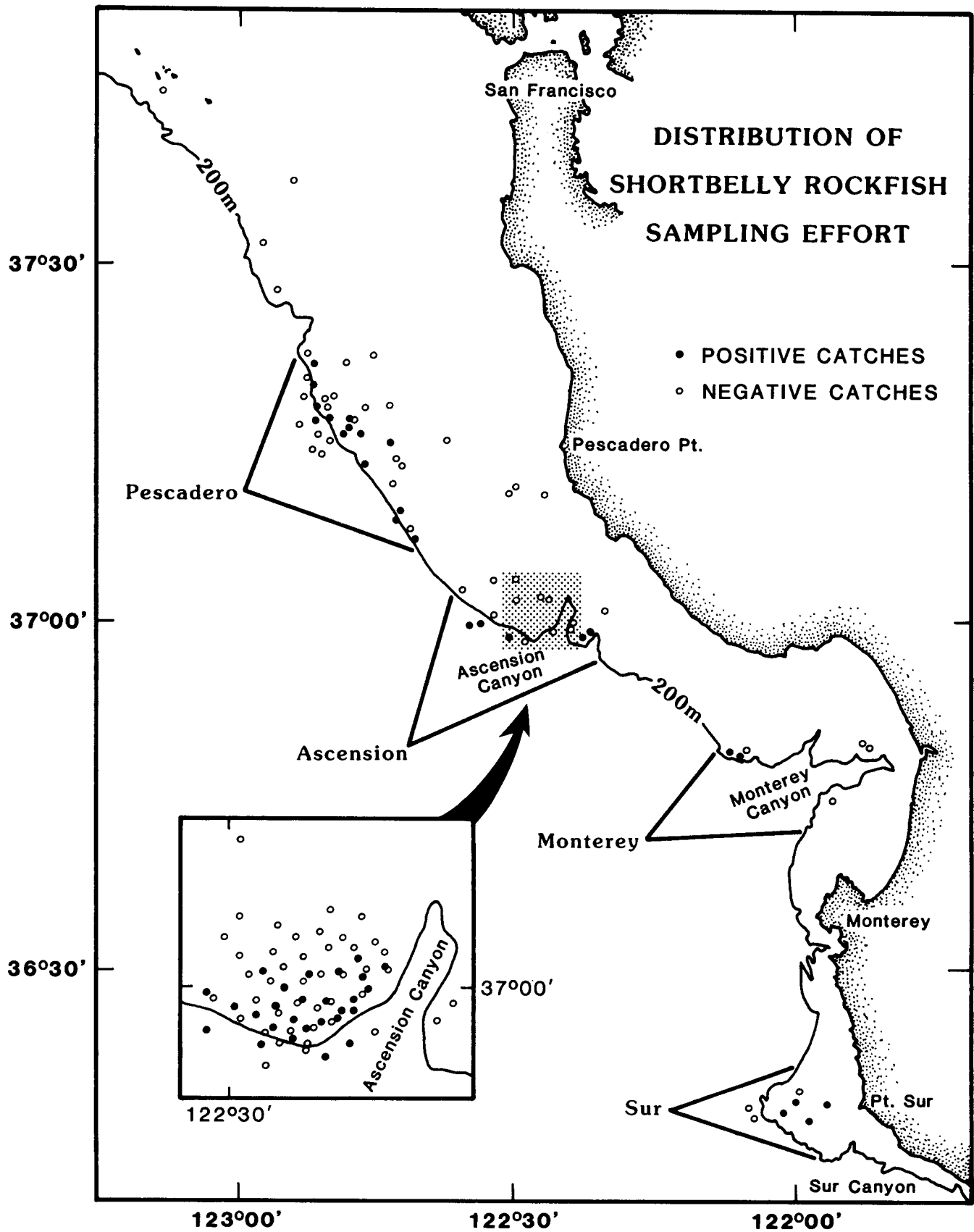


Figure 1. Distribution of shortbelly rockfish sampling effort, giving locations of positive (●) and negative (○) catches.

Additional plankton samples were taken to determine the horizontal distribution of zooplankton within the Ascension study area. These were oblique hauls taken with the Tucker trawl from a depth of 106 m to the surface at specific distances from the canyon. A more complete description of this sample series is presented below.

### Laboratory Procedures

In the laboratory, food items from the stomachs were identified to the lowest taxon feasible. For each taxon the following was noted: number, size range, extent of digestion (on a scale of one to five, with one being fresh), and an estimated proportion of the total volume of stomach contents that it represented. An estimate of fullness also was made, although probably this was of questionable value owing to the elasticity of the stomach.

The settled volumes of the preserved plankton aliquots were again determined after the large gelatinous forms had been removed, and workable aliquots of 7–10 ml (settled volume) were obtained with a Folsom plankton splitter. The remainder of each sample was then searched for taxa absent from the aliquoted portion, and these were included in the analysis. For each taxon the following was noted: abundance, estimated volumetric proportion of total sample, and the range of sizes represented. The numbers of organisms in the aliquots were extrapolated to represent the entire sample.

## RESULTS

### Distribution of *Sebastes jordani*

Of 126 trawl sets made at depths from 70 to 275 m between Point Sur and Point Reyes, 48 (38.1%) caught shortbellies. Most of the successful sets were near the outer margin of the shelf at depths of about 150 m, on the north sides of submarine canyons (Figure 1).

During the day, shortbellies were found near the bottom in dense aggregations that often extended 15 m and more into the water column (Figure 2, upper). At night, however, they were more dispersed—20 to 70 m above the bottom—but still 30 m or more below the water's surface (Figure 2, lower). Consistent with this pattern of nocturnal dispersion, our catches after dark took shortbellies more frequently, but in smaller numbers than during the day. At the Ascension Canyon site, for example, 14 (64%) of 22 nocturnal hauls took  $\bar{x} = 122.9$  kg (SE 58.2) of *S. jordani*, whereas 10 (30%) of 33 diurnal hauls took  $\bar{x} = 1,904.0$  kg (SE 687.5).

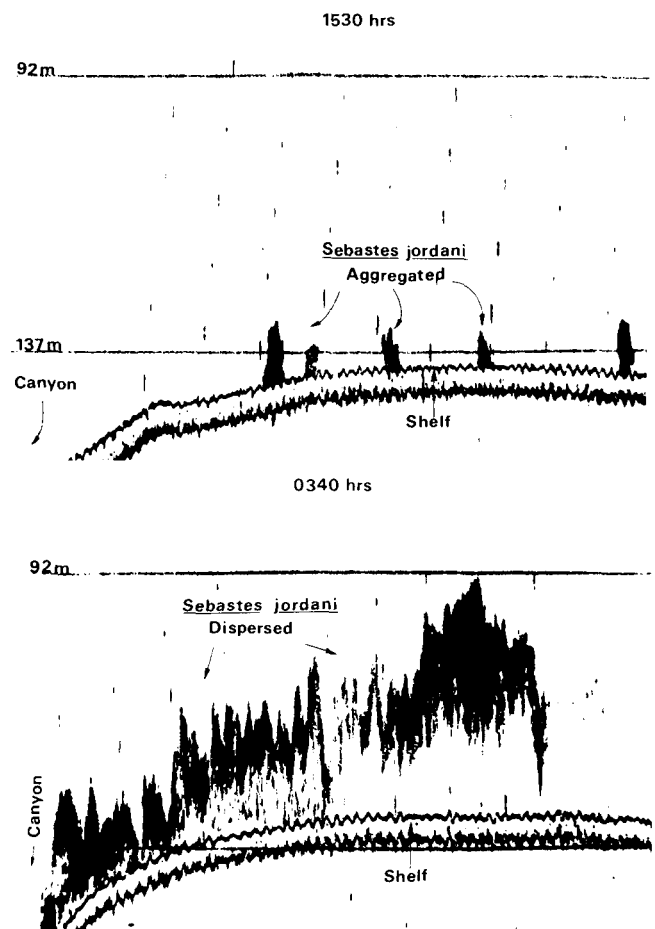


Figure 2. Distribution of shortbellies in the water column during the day (upper) and night (lower) on the shelf adjacent to Ascension Canyon, January 1982.

### Diet of *Sebastes jordani*

Of the 977 shortbellies (99–272 mm SL,  $\bar{x} = 175$  mm) collected for gut analysis (under the wide variety of circumstances sampled during this study), 694 (71%) contained food. Although 87 prey taxa were consumed, only 24 of them occurred in 14 or more ( $\geq 2\%$ ) of the shortbellies examined (Table 2). The primary prey species was *Euphausia pacifica*, but another euphausiid, *Thysanoessa spinifera*, was also important. Most of the prey were relatively large: 68% of the items exceeded 10 mm, and only 7.7% were less than 2 mm (this fact reflected the prominence of euphausiids in the diet). Some minor items, however, were as small as 0.5 mm (e.g., fish eggs). The size and species composition of prey taken by any given shortbelly was influenced by that fish's size. Although the relative importance of euphausiids was greater in larger fish (Table 3), euphausiids and calanoid copepods were the first- and second-ranked prey in all size groups examined.

TABLE 2  
**Important Prey of *Sebastes jordani*: Taxa Occurring in at Least 2% of the Stomachs That Contained Food**

Prey taxa	Freq. occur.	$\bar{x}$ n stom.	Mean % volume	Size range (mm)
Polychaeta				
<i>Tomopteris</i> spp.	.02	0.08	0.385	7.0–15.0
Ostracoda				
Halocypridae	.07	0.14	0.281	1.5–4.0
Calanoida				
<i>Calanus pacificus</i>	.25	1.79	1.590	2.1–2.8
<i>Candacia bipinnata</i>	.03	0.06	0.072	2.5–4.0
<i>Candacia</i> spp.	.02	0.02	0.062	2.8–4.0
Eucalanidae	.05	1.14	1.050	3.0–9.0
<i>Eucalanus californicus</i>	.06	0.24	0.704	3.5–7.0
<i>Euchirella rostrata</i>	.12	0.55	0.859	2.3–5.0
<i>Metridia pacifica</i>	.17	6.17	2.091	1.4–3.5
<i>Pleuromamma abdominalis</i>	.04	0.09	0.084	3.0–4.5
<i>Pleuromamma</i> spp.	.14	0.65	0.899	1.5–4.5
<i>Rhincalanus nasutus</i>	.08	0.36	0.555	1.4–7.0
<i>Undeuchaeta bispinosa</i>	.02	0.03	0.157	4.0–6.0
Undetermined	.20	1.28	3.165	0.9–6.3
Hyperiidia				
<i>Paraphronima</i> spp.	.02	0.04	0.196	5.0–12.5
Hyperiididae	.04	0.12	0.050	4.0–5.5
Undetermined	.06	0.09	0.768	1.0–15.0
Euphausiacea				
<i>Euphausia pacifica</i>	.49	10.48	25.228	10.0–24.0
<i>Nematoscelis difficilis</i>	.05	0.34	1.284	6.0–22.0
<i>Nyctiphanes simplex</i>	.07	0.22	0.845	7.0–19.0
<i>Thysanoessa spinifera</i>	.25	4.15	11.821	8.0–29.0
Fragments (digested)	.71	—	36.923	9.0–23.0
Chaetognatha				
Undetermined	.02	0.08	0.034	2.0–25.0
Other				
Undetermined digested material	.14	—	4.13	—

The shortbellies fed during both day and night. This was demonstrated by fresh prey in gut content samples taken late in the day and shortly before dawn. The 182 individuals (112–261 mm SL,  $\bar{x}$  = 167 mm) examined from among those collected at the Ascension Canyon site during the three hours immediately before sunset had consumed  $\bar{x}$  = 37.8

TABLE 3  
**Dietary Proportions of Euphausiacea and Calanoida in Three Size Groups of *Sebastes jordani***

Size of fish (mm)	Mean % diet volume		
	Euphausiacea	Calanoida	Other
99–160 (n = 305)	68.5	17.2	14.3
161–200 (n = 199)	78.6	10.5	10.9
201–272 (n = 190)	86.3	4.5	9.2

prey of  $\bar{x}$  = 4.6 taxa, whereas the 237 fish (99–253 mm SL,  $\bar{x}$  = 155 mm) collected in the same area during the three hours immediately before sunrise had consumed  $\bar{x}$  = 10.2 prey of  $\bar{x}$  = 2.1 taxa. Numbers of prey and numbers of taxa are both significantly different (t-test— $\bar{x}$  no. prey:  $P \leq 0.01$ ;  $\bar{x}$  no. taxa:  $P \leq 0.01$ ). The incidence of empty stomachs was consistent with these data, because only 12.1% of the day feeders were empty, compared to 26.6% of the night feeders ( $2 \times 2$  contingency table,  $\chi^2 = 12.4$ , 11 df,  $P = 0.005$ ). Stomach fullness showed the same pattern: the mean fullness of the day feeders was 35.6% (means of individual estimated percent), whereas the night feeders were 28.4% full (Wilcoxon sign rank test,  $z = 2.58$ ,  $P \leq 0.001$ ). Thus although feeding occurred during both day and night, it was more intensive by day.

In relating diel feeding patterns of shortbellies to available prey organisms in the environment, we limited our list of prey taxa to those that occurred in at least 5% of the stomachs examined. We determined that each of these taxa was taken in numbers that differed between day and night (Table 4). While the primary prey, *Euphausia pacifica*, was most numerous in fish collected during the day, two other euphausiids—*Thysanoessa spinifera* and *Nyctiphanes simplex*—were most numerous in fish collected at night.

TABLE 4  
**Diel Variations in the Major Prey Taxa\* in Stomachs of *Sebastes jordani* Collected at the Ascension Study Area within the 3 Hours Preceding Sunset and Sunrise**

Major prey taxa	Day (N = 158)			Night (N = 174)		
	Freq. occur.	$\bar{x}$ n stom.	Mean % diet vol.	Freq. occur.	$\bar{x}$ n stom.	Mean % diet vol.
Halocyprid ostracods	.17	0.39	0.93	.01	0.02	0.02
<i>Calanus pacificus</i>	.33	2.61	3.17	.14	1.42	1.38
<i>Eucalanus californicus</i>	.16	0.66	2.18	.01	0.01	0.01
<i>Euchirella</i> spp.	.22	1.27	3.06	—	—	—
<i>Metridia pacifica</i>	.30	3.61	2.19	.04	0.06	0.04
<i>Pleuromamma</i> spp.	.32	0.85	1.03	.01	0.02	1.05
<i>Rhincalanus nasutus</i>	.15	0.94	1.11	.03	0.03	0.63
<i>Euphausia pacifica</i>	.54	18.43	27.24	.39	2.90	19.16
<i>Nyctiphanes simplex</i>	.09	0.13	0.64	.06	0.33	1.20
<i>Thysanoessa spinifera</i>	.14	0.47	1.85	.21	2.97	11.22
Other Euphausiacea	.04	0.05	0.36	.04	0.44	1.30
Euphausiacea (digested)	.83	—	37.78	.75	—	47.67

\*Taxa that occurred in  $\geq 5\%$  of all stomachs examined.

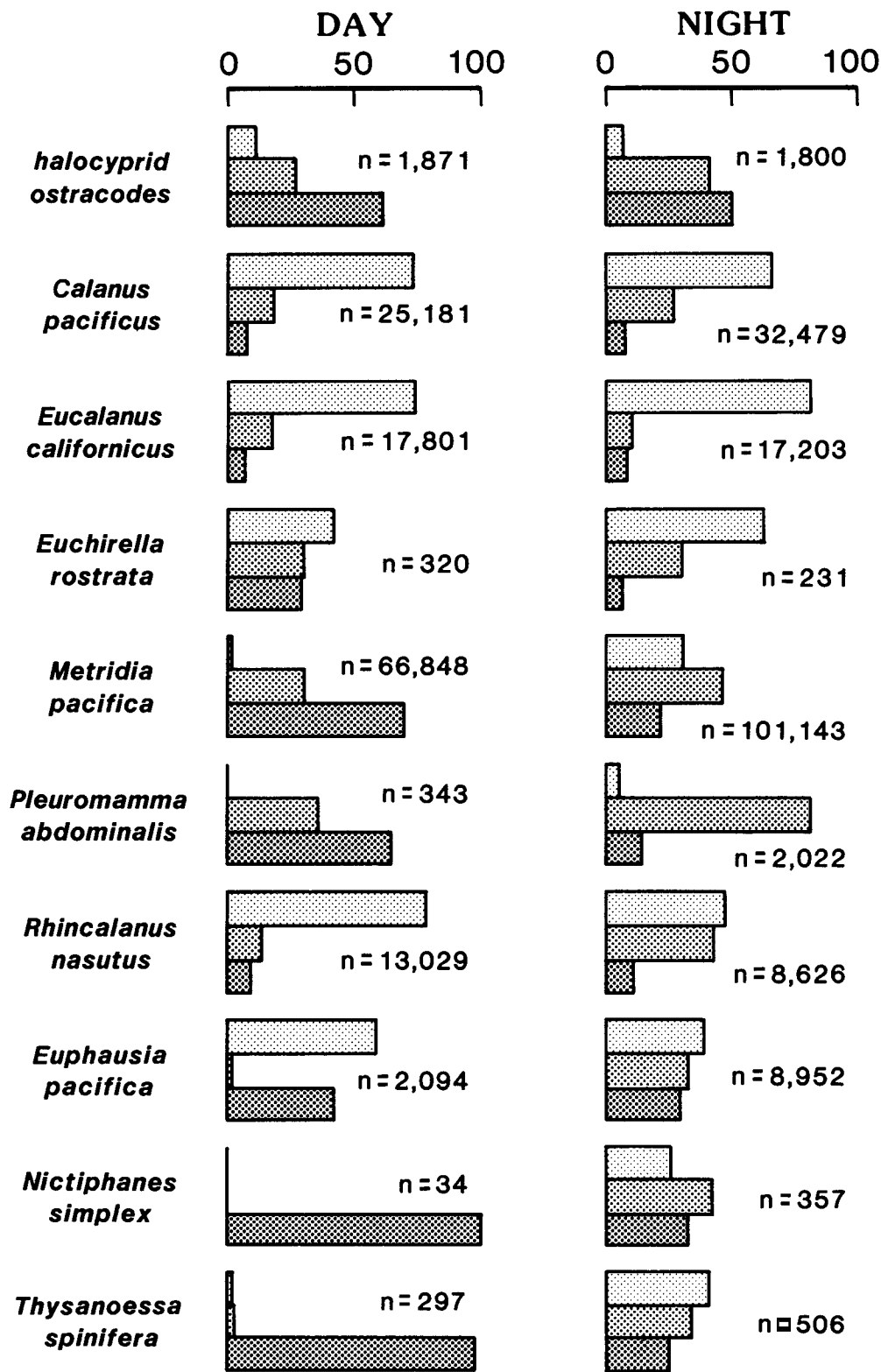


Figure 3. Diel vertical distribution patterns of the major prey taxa (those taxa occurring in  $\geq 5\%$  of the *S. jordani* that contained food). Values are the percentage of mean numbers of each taxon collected from each depth: upper (light), 18 m; mid (medium), 55 m; and lower (dark), 119 m. *n* = the sum of the mean numbers collected from each depth.

#### Distribution of Prey

Most of the major prey taxa were more numerous at higher levels of the water column at night than during the day (Figure 3). (The many *E. pa-*

*cifica* in the upper level by day, shown in Figure 3, resulted from a single large collection of 5–11-mm juveniles; those shown at the lower levels were 5–24-mm juveniles and adults.) Although net avoid-

ance may have contributed to the discrepancy between day and night *n* values in Figure 3, we have no evidence of this. Most collections were taken at least 18 m above the bottom, but one plankton collection taken over the shelf during midday (15 min. at a depth of 218 m) inadvertently sampled close to the bottom (striking it at least once, as evidenced by a variety of strictly benthonic organisms in the catch). This collection, which included 46,720 *E. pacifica* (nearly four times the number we took in any other plankton collection) suggests that members of this species and perhaps others are more abundant close to the seafloor on the shelf during the day.

A series of collections at the Ascension Canyon site provided some detail on the nocturnal horizontal distribution of *E. pacifica* and other euphausiids over the shelf in relation to the canyon. During seven cruises between November 1980 and September 1982 we made 10 series of four successive oblique hauls, including 3 series that were replicated (all collections were taken between 2300 and 0330 h). Each haul was from a depth of 106 m to the surface and lasted 10 minutes; the first haul of each series sampled over the canyon; the next three sampled at 3.7-km intervals away from the northern rim of the canyon along the 137-m depth contour on the adjacent shelf.

The numerical proportion of *E. pacifica* collected above the canyon was significantly greater than that from any of the stations above the shelf. The mean proportions were: above canyon—46.77%; at 3.7 km—22.87%; at 7.4 km—18.02%; and at 11.1 km—18.68% (analysis of variance of arc sin transformations of percentages  $F = 3.96$ ,  $P = 0.02$ ,  $df\ 3,24$ ; Newman-Keuls multiple comparison of means for gap order 2, difference = 19.95; for gap order 3, difference = 24.14; and for gap order 4, difference = 26.66). But although the proportions of *E. pacifica* collected from the shelf stations tended to be progressively less with distance from the canyon, the differences were not significant. In contrast, *Thysanoessa spinifera*, the euphausiid second in importance in the diet of *S. jordani*, was more evenly distributed over both the canyon and shelf, because there was no significant difference in its abundance among these collections ( $F = 1.16$ ,  $df = 3,24$ ).

Additional information on the distribution of prey species comes from comparing the diet of *S. jordani* between different areas. For example, the generally oceanic *E. pacifica* (Brinton 1962) dominated the diet of shortbellies taken near Ascension and Sur canyons, but the more neritic *T. spinifera*

TABLE 5  
 Mean Numbers of *Euphausia pacifica* and *Thysanoessa spinifera* in Gut Contents of *Sebastes jordani* from Different Areas

	Ascension Canyon ( <i>n</i> = 516)	Sur Canyon ( <i>n</i> = 18)	Pescadero Point ( <i>n</i> = 104)	Monterey Bay ( <i>n</i> = 56)
<i>E. pacifica</i>	13.93	13.56	4.91	1.99
<i>T. spinifera</i>	0.78	0.05	14.13	3.47

was more important to the diet of shortbellies taken off Pescadero Point and near Monterey Canyon (Table 5).

## DISCUSSION

It is evident that *S. jordani* was distributed on the coastal shelf in relation to the distribution of its prey. This appeared true even though the normal habitat of its major prey, *Euphausia pacifica*, is beyond the shelf break at depths below 200 m (Brinton 1976). This could explain why shortbelly rockfish were concentrated along the shelf margin, especially adjacent to certain submarine canyons (Figure 1). Certain other shelf predators are known to feed heavily on deepwater organisms when these intermittently enter the shelf habitat. For example, *Sebastes pinniger* and *S. flavidus* off central Oregon feed primarily on *E. pacifica* above the outer shelf, with the former foraging mainly by day near the bottom (Brodeur and Pearcy 1984).

It is known that some oceanic organisms that perform diel vertical migrations are carried or disperse over the coastal shelf when in the surface waters at night. It has been suggested that when these organisms attempt to regain their normal daytime depths in the morning, many become trapped on the relatively shallow shelftop, where they are vulnerable to shelf-dwelling predators (Isaacs and Schwartzlose 1965; Pereyra et al. 1969; Clarke 1984). Apparently this mechanism is important in the trophic dynamics of *S. jordani*, because despite foraging at night on a variety of organisms in the water column, members of this species that were examined during this study had fed most intensively by day near the bottom—primarily on *E. pacifica* (Table 4). Clearly *E. pacifica* is especially vulnerable in this setting, probably because it is an open-water species that is maladapted to conditions close to or on the seafloor. On the other hand, *Thysanoessa spinifera* and *Nyctiphanes simplex*, which appear to be more neritic, did not share the diurnal vulnerability of *E. pacifica*. (*S. jordani* preyed most intensively on these two species in the water column at night; Table 4.) As shelf residents, they would be expected to possess adap-

tive defenses against threats characteristic of that habitat.

Probably *E. pacifica* is transported above the shelf at night by the coastal undercurrent. This current flows poleward above the shelf or upper continental slope throughout the year, but during most years reaches the surface only during fall and winter. At other times of year it is usually submerged, reportedly at depths of 200 to 500 m during the summer (Wyllie 1966; McLain and Thomas 1983). Chelton et al. (1987) found the undercurrent's velocities to be poleward at depths between 70 and 470 m throughout an 18-month period. So most of the time, at least, this current should be expected to impinge most directly on and flow over those parts of the shelf that extend offshore. This would account for the concentrations of *E. pacifica* at the Ascension and Sur canyon sites (Table 5). The dominance of *E. pacifica* near the northern rims of the canyons is consistent with this view. Because these locations are prominent projections in the path of the undercurrent (Figure 1), euphausiids ascending from the depths of adjacent canyons or downstream offshore areas would be expected to be carried over the shelf.

#### ACKNOWLEDGMENTS

This study incorporated the combined efforts of all members of the Groundfish Communities Investigation at the Tiburon Laboratory. Edmund Hobson made numerous contributions in discussing the data, and in preparing the manuscript. Peter Adams provided counsel on statistical analysis, and also helped make the collections. Dan Howard assisted with the statistical analysis and also was an invaluable member of the field party. We are grateful to Edward Brinton, Scripps Institution of Oceanography; Geoff Moser, National Marine Fisheries Service Southwest Fisheries Center; and William Percy, Oregon State University, for helpful comments on the manuscript. We also thank the officers and crew of the NOAA ship

*David Starr Jordan* for their cooperation and assistance. Roy Allen, Southwest Fisheries Center, prepared the figures, and Rahel Fischer typed the manuscript.

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