TROPHIC RELATIONS OF THE BLUE ROCKFISH, *SEBASTES MYSTINUS*, IN A COASTAL UPWELLING SYSTEM OFF NORTHERN CALIFORNIA

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ABSTRACT

The planktivorous *Sebastes mystinus* in nearshore habitats off northern California feeds primarily on relatively large, gelatinous zooplankters that originate offshore, including thaliaceans, ctenophores, and pelagic hydrozoans. These prey organisms increase in number during spring and summer when surface waters driven seaward by northerly winds carry upwelled nutrients to diatoms that nourish offshore zooplankton populations. But the resulting increases in zooplankton during this upwelling season become available to *S. mystinus* in the nearshore habitats only when the surface flow turns shoreward during intermittent episodes of downwelling. Although some of this shoreward flow is driven by southerly winds, much of it occurs during calms, or under northerlies lacking the velocities needed to drive surface waters seaward. There is increasing shoreward transport during fall and winter, when downwelling episodes are more frequent, but progressively fewer zooplankters are carried into the nearshore habitats. This is because as less nutrients come into the system with the reduced upwelling, and as available sunlight declines, the offshore zooplankton populations suffer from shortages of diatoms. Although *S. mystinus* compensates for decreased numbers of zooplankters during most of the year with increased consumption of specific plant materials, i.e., *Nereocystis sori*, or the monostromatic epiphytes *Porphyra nereocystis* and *Smithora naidum* (depending on the season), these too are in short supply during winter. In winter, therefore, *S. mystinus* experiences its poorest feeding conditions. Thus, *S. mystinus* is adapted to feeding opportunities created by alternating episodes of strong upwelling and strong downwelling, and is most abundant within its range along the west coast of North America where both conditions are well developed.

Coastal marine fishes in temperate latitudes experience major seasonal changes in their environment. In study off northern California's Mendocino coast (lat. 39°13′N, long, 123°14′W), we studied the effects of seasonal change on the trophic relations of the blue rockfish, *Sebastes mystinus* (Fig. 1). *Sebastes mystinus*, a major species in the recreational fishery off northern and central California (Frey 1971), is a planktivore that feeds on scyphozoans, ctenophores, copepods, amphipods, thaliaceans, fishes, and algae (Gotshall et al. 1965; Love and Ebeling 1978; Hallacher and Roberts 1985). Although its diet is known to vary with the season, relationships involving specific environmental features, and the availability of prey, remain unclear.

The marine environment off California is profoundly affected by seasonal variations in wind-driven movement of the surface water (Reid et al. 1958; Bolin and Abbott 1962; Bakun and Parrish 1980). This force, known as Ekman transport (Ekman 1905), is strongest off the Mendocino coast (Bakun 1973), where it must be a major influence on the trophic relations of *S. mystinus*. Because Ekman transport is the basis of coastal upwelling (e.g., Smith 1968), it is of great importance to biological productivity (e.g., Boje and Tomczak 1978) and, therefore, to the availability of food.

Upwelling develops along the coast of northern California when surface waters driven seaward by northerly winds, such as those characteristic of spring and summer, are replaced by colder subsurface waters from offshore that flow up into the nearshore habitat (Smith 1968; Bakun 1973). On the other hand, an opposing condition develops when surface waters driven shoreward by southerly winds, such as those characteristic of winter storms, flow over the colder nearshore waters to produce the condition sometimes called downwelling (Bakun 1973). But despite the strong seasonality evident in both upwelling and downwelling, short-term reversals lasting just a few days occur throughout the year (see Bakun [1973] and Mason and Bakun [1986]).

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FIGURE 1.—*Sebastes mystinus* next to canopy of bull kelp, *Nereocystis leutkeana*, off Mendocino.

In this paper we consider how the trophic relations of *S. mystinus* respond as seaward and shoreward movements of the surface water produce alternating episodes of upwelling and downwelling. Emphasis is on how the resulting environmental changes alter the relative availability of food. Among studies of marine fishes, this is, to our knowledge, the most comprehensive attempt yet made to integrate data on food, potential food, and environmental variables—all key elements in trophic relations.

METHODS

The study lasted from the winter of 1976–77 to the summer of 1981, with the first 15 months involving exploratory work along about 15 km of the Mendocino coast south of Point Cabrillo. A study site was then established off Salmon Point (Fig. 2) during the spring of 1978, and from that time sampling followed a set regime.

Study Site

The study site (Fig. 3) was in 10–15 m of water, about 300 m from shore. Rocks the size of houses jutted 10–15 m above the water at the seaward perimeter of the site, but despite the shelter offered by these rocks, most of the area was regularly swept by wind and sea. Except for isolated pockets of sand, the site was floored by rock pavement and boulders (some 5–15 m in diameter), largely swept clean by the turbulence and surge that prevailed most of the time.

Environmental Variables

During each sampling session, we noted the gen-

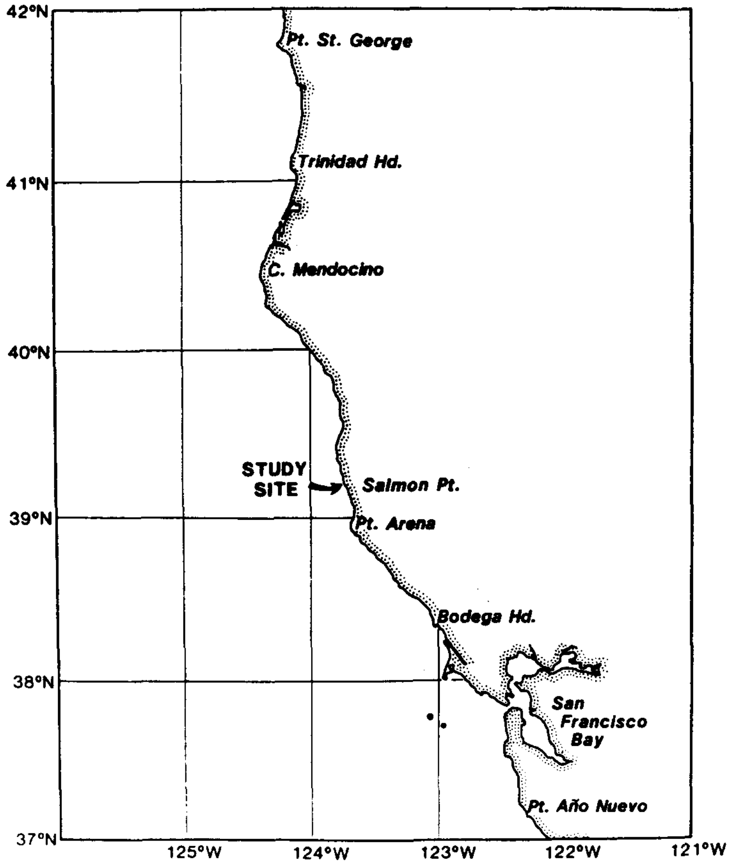

FIGURE 2.—The coast of northern California.

eral state of the weather, including wind direction and estimated velocity. In this paper (except in Figures 4 and 9, as noted below) we consider winds from between northwest and northeast to be "northerly", and from between SW and SE to be "southerly". We also noted sea conditions and recorded sea-surface temperatures. More precise wind data became available after May 1980, when a NOAA weather station was established at Mendocino. During the same month, we placed recording thermographs at depths of 6 and 20 m in the study area, and although the deeper site was abandoned after 1981 in favor of replicating the record with two instruments at the shallower site, these have given us a continuous record of water temperatures from then until the present (Spring of 1988). Based on these observations and in situ visual assessments of the plankton and water characteristics, usually we could tell whether upwelling or downwelling predominated during a sampling session even though most of the time conditions were to some extent mixed.

Diet and Occurrences of Food

To relate the diet of *S. mystinus* to foods present at the time of feeding, we took concurrent samples of gut contents and plankton, as well as some selective samples of the benthos. Complications from normal diel variability were reduced by taking all samples between the hours of 1100 and 1300. The sampling schedule was strongly influenced by the weather, as much of the time work was prevented by high seas and/or long-period swells and result-

FIGURE 3.—Study site off Salmon Point.

ing turbulence. Although all seasons were sampled, most collections and observations were made when the sea was relatively calm, a condition that generally lasted no more than a few days at a time. Nevertheless, because often the weather turned while observations were under way, turbulent conditions were well represented.

Fish

The *S. mystinus* studied at Mendocino were spatially segregated by size and age. This paper considers only adult fish of more than 200 mm SL, which forage by day in aggregations of up to several hundred individuals in the upper levels of the water column. The analysis of gut-contents involved 247 individuals, 200–350 mm SL, taken from these aggregations using handheld spears. Juveniles and subadults are excluded because they forage at lower levels of the water column and consume organisms not taken by adults.

Plankton

Most sampling sessions included two plankton collections: one at the sea surface, and the other between 1 and 2 m above the sea floor. Only the 27 surface collections are considered here, however, because the others sampled at levels of the water column below where adults usually feed. For each collection we used scuba to push the net (0.333 mm mesh in a 78 cm × 78 cm frame) through the water for 5 minutes. Occasionally the net broke the surface, but usually was kept underwater to avoid fouling the sample with floating debris. (See Hobson and Chess 1976 for additional information on this procedure, and how the samples were processed and analyzed.) We visually assessed the larger zooplankters in the water column during each collection, as well as at other times during each sampling session, and these observations greatly enhanced our ability to interpret the samples.

Benthos

Although *S. mystinus* is a planktivore, it is important to include the benthos when documenting environmental changes that affect its feeding. Many of the actual or potential foods of *S. mystinus* originate on the underlying substrata, and their occurrences in the water column relate to changes in the benthos. Thus, assessments of the benthos done during other studies concurrently under way in the study area, including visual counts and airlift samples, produced data that are incorporated into this report where pertinent.

Ranking Prey Taxa

To estimate the relative importance of the various prey organisms in the diet of *S. mystinus*, we grouped related forms in multispecies categories that were then ranked. The ranking was based on an index calculated as: relative frequency of occurrence in diet × mean number of individuals consumed × percent of total diet volume that was represented by that category. This index is similar to the widely used Index of Relative Importance (IRI) of Pinkas et al. (1971), but puts more weight on numbers consumed. It is important to emphasize numbers consumed in quantifying the feeding activity of *S. mystinus* (and most other planktivores) because the many small prey are ingested individually, making the capture of each a discrete act.

RESULTS

During the four years of this study, spring and (to a lesser extent) summer constituted an upwelling season, while fall and (to a greater extent) winter constituted a downwelling season. The spring transition between downwelling and upwelling seasons occurred over just a few days between late March and early April, whereas the less distinct fall transition between upwelling and downwelling seasons was extended over a month or more between mid-August and late October.

Despite this seasonal pattern, however, there were short-term reversals of just a few days that had profound effects. Reactions of the environment to major wind changes were virtually immediate. Sharply reduced water temperatures signifying the intrusion of upwelled water often followed within hours of increased northerly winds, while warmer water rich in such readily visible zooplankters as ctenophores, hydrozoans, pteropods, thaliaceans, and larvaceans, often flowed into the nearshore habitats within a day after the onset of southerly winds. Conditions during each sampling session are listed in Table 1.

Although downwelling conditions were most intense under southerly winds, they also developed during calms and with weak northerlies. We found that generally it took northerlies of 10 knots (K) or more to produce upwelling conditions, although as little as 5 K were effective if held steady for several days. In the absence of sufficient force, however, upwelling ceased and warmer water rich in offshore zooplankters entered the nearshore habitat, generally moving in a southerly direction along the coast.

The close relation between shifts in prevailing wind and alternations between upwelling and downwelling is illustrated by comparing the wind direction and velocity measured by the nearby NOAA weather station to the sea temperatures recorded by our thermographs. Although these data became available only during the last year of the study, subsequent years have produced similar profiles (except 1982–83, when there was a strong El Niño). Thus, the pattern of sea temperatures and wind during the upwelling season of 1981 and during the downwelling season of 1980–81, recounted in detail below, are representative.

The Upwelling Season

The upwelling season began in late March or early April with a precipitous drop in sea temperatures. It was a drop of about 3°C—typically from 11°–12°C to 8°–9°C—that coincided with the onset of strong, persistent northerly winds characteristic of this time of year. The pattern of sea temperatures and wind during the 1981 upwelling season (Fig. 4) illustrates how upwelling and downwelling related to prevailing winds during that period.

Habitat Conditions

At the start of the upwelling season, the nearshore habitats appeared barren. Storm seas during the previous winter had carried away most of the bull

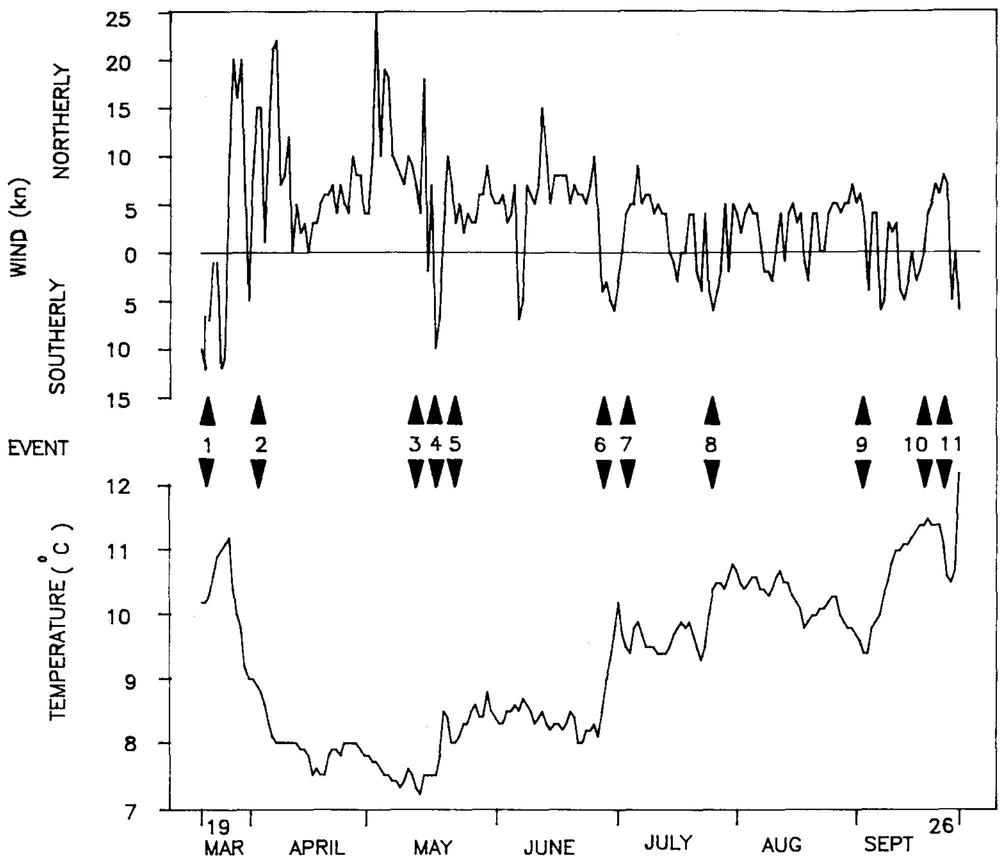

FIGURE 4.—Sea temperatures and wind off Mendocino during the 1981 upwelling season. *Plotted sea temperatures* are estimated daily means from record of continuously recording thermograph. Plotted wind velocities and directions are averages of 2-5 daily readings. Southerly values represent winds from south of east-west axis, northerly values represent winds from north of this axis. The highly infrequent winds from due west or due east were entered as zero. In calculating values for days of both northerlies and southerlies, the former were considered positive, the latter negative. The following accounts of events identified in the figure cite wind velocities that exceed plotted values, which are averages.

EVENT 1—Seven days of southerly winds, 19-25 March, with sea temperatures rising to 11.1°C, represented the last downwelling episode of the 1980-81 downwelling season.

EVENT 2—The 1981 upwelling season began on 26 March, as 2 weeks of strong northerlies (to 4 April) resulted in an abrupt drop of more than 3°C in sea temperature.

EVENT 3—Water temperatures fell to the lowest point of the year, 7.3°C, on 13 May following over 2 weeks of 10-30 K northerlies.

EVENT 4—The first of a series of downwelling episodes during this upwelling season developed as 8-12 K southerlies on 17 and 18 May resulted in a sharp rise in sea temperature to 8.5°C.

EVENT 5—Temperatures dipped when the wind shifted back to the north on 19 May. Over the next month variable northerlies blew at less than 10 K, and although sea temperatures did not vary more than a few tenths of a degree, they were consistently about 1°C warmer than before the 17-18 May downwelling episode.

EVENT 6—On 28 June, the first of 6 consecutive days of 4-10 K southerlies, sea temperatures began a steep climb to above 10°C that marked the upwelling season's second major downwelling episode.

EVENT 7—Northerlies returned on 3 July, and sea temperatures immediately dropped below 10°C again. Despite northerlies of 5-7 K over the next 2 weeks, sea temperatures remained at about 9.5°C, again about 1°C warmer than before the 28 June-2 July downwelling episode.

EVENT 8—With southerlies of 5-10 K on 7 of the 9 days between 12 and 20 July, sea temperatures once again rose above 10°C to mark the season's third major downwelling episode.

TABLE 1.—Conditions during sampling sessions off Salmon Point, Mendocino County, 1978–81.

Date	Sea temp. (°C)	Wind dir. : vel. (knots)	Plankton condition[1]	Fish sampled No.	Size range (mm)	Mean (mm)
I. Upwelling season, upwelling conditions						
5/10/78	8.5	NW: 10	U/M	7	270–312	289.7
8/08/78	10.5	NW: 10	U	6	285–309	293.0
6/12/79	9.0	NW: 15	U/M	7	241–312	239.3
6/24/80	10.0	None	U	9	224–308	250.0
4/09/81	8.1	NW: 15	U	8	235–300	265.6
5/19/81	9.5	WNW: 10	U/M	1	260	260.0
6/17/81	9.0	NNW: 10	U	13	260–336	301.0
II. Upwelling season, downwelling conditions						
6/21/78	9.0	None	D/M	3	228–308	270.3
6/29/78	10.0	SW: 2	D/M	6	240–315	254.7
8/23/78	11.0	None	D	6	230–280	259.0
9/08/78	14.0	None	D	4	240–295	277.5
4/24/79	10.0	None	M	9	225–313	277.7
7/24/79	11.5	None	M	11	208–302	239.5
8/27/79	12.8	NW: 5	M	12	204–335	264.6
5/29/80	9.5	None	D/M	20	213–330	276.4
7/17/80	11.0	NW: 5	D/M	5	240–304	270.8
8/21/80	11.0	S: 5	D	9	230–305	270.6
III. Downwelling season, downwelling conditions, fall						
10/04/78	11.0	WNW: 10	D+	3	270–310	286.7
10/18/78	12.0	S: 5	D+	9	220–350	296.2
12/08/78	9.0	S: 8	D+	17	227–331	281.2
10/16/79	14.0	NW: 8	D	13	218–311	280.1
11/04/80	12.0	N: 6	D	17	230–335	296.6
12/17/80	12.0	NNW: 5	D	14	225–331	276.3
IV. Downwelling season, downwelling conditions, winter						
2/04/79	10	S: 12	D	12	231–320	273.3
3/06/79	11	W: 8	D	2	224–260	242.0
1/31/80	11	None	M	16	200–345	275.3
1/13/81	13	SW: 5	D	8	275–305	286.3

[1]Plankton condition. D = Downwelling condition: zooplankters considered to be offshore species, especially relatively large gelatinous forms, numerous. U = Upwelling condition: offshore zooplankters absent. M = Mixed condition: some offshore zooplankters present.

kelp, *Nereocystis leutkeana*, which is the major component of the kelp forests. These same seas, often heavily laden with sediment, had also scoured the seafloor of much of the algal understory, as well as many of the sedentary invertebrates. Once the upwelling season had been established, however, the habitats changed rapidly.

Often during early-season upwelling the water was relatively transparent, although after rains visibility often was limited by suspended sediment discharged into the nearshore habitat from coastal streams. By mid-May, however, the numbers of planktonic diatoms (primarily *Chaetoceros* sp. and *Nitzchia* sp.) had greatly increased to depths of

EVENT 9—In the last major upwelling of this upwelling season, sea temperatures fell to 9.4°C on 2 September after 10 consecutive days of 5–8 K northerlies.

EVENT 10—Sea temperatures rose steadily to 11.4°C on 17 September after 1–3 day periods of 4–8 K northerlies had alternated with 1–4 day periods of 4–8 K southerlies through the first half of that month.

EVENT 11—Sea temperatures fell to 10.5°C on 24 September after 7 consecutive days of 5–15 K northerlies. A shift to southerlies on 25 September started another climb, and the transition to the downwelling season clearly was under way. This transition, however, was not nearly so well defined as that which had introduced the upwelling season 6 months before.

10–20 m, which often limited visibility to a few meters. These diatom blooms were most evident during the intermittent episodes of downwelling. The benthos similarly proliferated. Within a few weeks after the initial upwelling, a growth of benthic diatoms (primarily *Isthmia nervosa* and *Tricertium americana*) appeared on the previously baron rocks, and even on sand sheltered from wave surge. Then larger elements of the biota began to increase in size and number. Particularly evident were calcareous sponges (especially *Leucosolenia* spp.), hydroids, and certain bryozoans. Benthic algae, predominantly *Desmarestia ligulata*, rapidly overgrew much of the rock substrata, while young *Nereocystis leutkeana*, which first appeared on the seafloor in May, had grown to the water's surface by mid-June. Swarms of mysids were increasingly numerous near the seafloor in April (they had been prominent for a month or more), and caprellid and gammaridean amphipods on rocky substrata began a sharp increase in numbers.

The bull kelp had formed a dense canopy by mid-July, and at about the same time large numbers of sori (reproductive structures) began falling from the kelp's fronds. (A frond that had recently lost a sorus appears at the left side of Figure 1.) Planktonic diatoms continued to proliferate during periodic blooms, but by this time the benthic diatoms that had carpeted much of the seafloor during the spring were mostly gone. Similarly, the mysid swarms, which had peaked in May and June, usually began to decline by mid-July. Other elements of the biota,

TABLE 2.—Food of adult *Sebastes mystinus* relative to near-surface plankton during upwelling episodes of the upwelling season. $n = 7$.

Food organism		In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	**PLANTS (3751.20)**	**NR[2]**	**72**	**NR**	**52.1**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	15–20	15	1.10	10.6	NR	NR	NR	NR
	Porphyra sp.	NR	15	NR	9.9	NR	NR	NR	NR
	Smithora naidum	NR	21	NR	17.0	NR	NR	NR	NR
	Others	NR	21	NR	14.6	NR	NR	NR	NR
2	**PELAGIC HYDROZOA (1373.30)**	**10–30**	**21**	**4.51**	**14.5**	**<1–4**	**86**	**120.08**	**2.3**
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	<1–2	86	68.65	0.6
	Syphonophora								
	Muggiaea atlantica	—	0	0.00	0.0	—	0	0.00	0.0
	Stephanomia bijuga	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	3–4	14	51.43	1.7
	Chondrophora								
	Velella velella	10–30	21	4.51	14.5	NA[3]	NA	NA	NA
3	**MYSIDACEA (203.15)**	**5–7**	**3**	**10.26**	**6.6**	**—**	**0**	**0.00**	**0.0**
	Acanthomysis spp.[4]	5–7	3	10.26	6.6	—	0	0.00	0.0
	Others	—	0	0.00	0.0	—	0	0.00	0.0
4	**SCYPHOZOA (61.60)[5]**	**NR**	**8**	**NR**	**7.7**	**NR**	**NR**	**NR**	**NR**
	Fragments	NR	8	NR	7.7	NR	NR	NR	NR
5	**EUPHAUSIACEA (35.10)**	**5–8**	**15**	**1.95**	**1.2**	**<1–4**	**57**	**363.60**	**3.1**
	Larvae	—	0	0.00	0.0	<1–4	57	363.60	3.1
	Thysanoessa spp.	5–8	15	1.95	1.2	—	0	0.00	0.0
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	**GAMMARIDEA (1.80)**	**1–8**	**8**	**0.75**	**0.3**	**1–8**	**86**	**10.31**	**5.3**
	Atylus tridens	—	0	0.00	0.0	2–8	29	4.63	5.0
	Ishyrocerus n. sp.	4	3	0.31	0.1	—	0	0.00	0.0
	Jassa falcata[6]	1–3	8	0.28	0.1	<1–3	14	0.78	NR
	Polycheria osbourni	—	0	0.00	0.0	—	0	0.00	0.0
	Others	2–8	5	0.16	0.1	1–2	57	4.90	0.3
7	**CALANOIDA (0.90)**	**5–6**	**8**	**0.16**	**0.7**	**<1–7**	**100**	**2454.09**	**38.6**
	Nauplii	—	0	0.00	0.0	<1	14	72.00	0.1
	Acartia spp.	—	0	0.00	0.0	1–2	52	224.23	4.4
	Calanus pacificus	—	0	0.00	0.0	2–3	57	24.68	5.3
	Eucalanus californicus	6	8	0.13	0.6	4–7	71	35.48	1.4
	Rhincalanus nasutus	—	0	0.00	0.0	—	0	0.00	0.0
	Others[7]	5	3	0.03	0.1	<1–3	1	2097.70	27.4

however, reached maximum development during the summer. Prominent among them were benthic algae, e.g., *Desmarestia ligulata* and *Laminaria setchelli*, as well as certain sedentary animals including various sponges, e.g., *Leucilla nuttingi*; ascidians, e.g., *Trididemnum opacum*; hydroids, e.g., *Obelia* spp.; and bryozoans, e.g., *Bugula* spp. The benthic caprellids and gammarideans attained peak numbers during early summer, when they literally carpeted some areas of the seafloor. Samples taken with an airlift during July 1978 measured densities of over 10,000 caprellids (mostly *Metacaprella kennerleyi*), and 108,000 gammarids (mostly *Jassa* spp.) in m^2 quadrats. Their numbers declined sharply during August, however, and by September they occurred only in scattered patches.

Feeding Conditions

The diet of *S. mystinus* relative to foods present during the upwelling season was assessed with samples of gut contents and near-surface plankton taken during 7 upwelling episodes (Table 2) and 10 downwelling episodes (Table 3).

More prey were consumed during the downwelling episodes (e.g., $\bar{x}$ no. prey taken = 110.8, vs. 20.1 during upwelling episodes). Thaliacians (Fig. 6) were the primary food during the upwelling season, but all were taken during downwelling episodes—the only times when the guts were packed with food. These relatively large, gelatinous zooplankters did not occur either in the plankton or in the diet of *S. mystinus* during upwelling episodes.

TABLE 2.—*Continued.*

Food organism		In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
8	**CAPRELLIDEA (0.54)**	**10**	**5**	**1.08**	**0.1**	**6**	**14**	**2.25**	**0.4**
	Metacaprella kennerlyi	10	5	1.08	0.1	—	0	0.00	0.0
	Others	—	0	0.00	0.0	6	14	2.25	0.4
9	**CHAETOGNATHA (0.09)**	**23**	**3**	**0.03**	**1.0**	**3–12**	**57**	**20.80**	**2.1**
	Undetermined species	23	3	0.03	1.0	3–12	57	20.80	2.1
10	**FISHES (0.02)**	**12**	**3**	**0.05**	**0.1**	**2–14**	**57**	**14.92**	**1.1**
	Larvae	12	3	0.05	0.1	2–14	57	14.92	1.1
OTHER CATEGORIES									
Polychaeta		—	0	0.00	0.0	<1–12	86	74.83	1.4
Molluscan larvae		—	0	0.00	0.0	<1–1	57	149.92	1.7
Pelagic gastropoda		—	0	0.00	0.0	1–5	29	2.32	8.6
Cladocera		—	0	0.00	0.0	1	29	64.28	0.7
Harpacticoida		—	0	0.00	0.0	1–2	1	54.77	0.7
Cyclopoidea		—	0	0.00	0.0	1	71	75.08	0.9
Cirripedean larvae		—	0	0.00	0.0	<1–1	1	1850.92	15.0
Reptantian larvae		—	0	0.00	0.0	<1–2	86	134.48	1.9
Natantian larvae		—	0	0.00	0.0	2–3	43	72.00	1.4
Larvacea		—	0	0.00	0.0	3–8	43	53.48	1.1
Eggs, undetermined		—	0	0.00	0.0	<1	43	3024.00	9.7
Eggs, fish		—	0	0.00	0.0	<1–2	71	312.68	1.7
UNIDENTIFIABLE MATERIAL[8]		—	—	—	15.9	—	—	—	—

No. fish examined: 51
224–336, $\bar{x}$ = 284.3 mm SL
No. empty = 13
$\bar{x}$ no. prey: individuals = 20.13
taxa = 2.03

No. plankton collections: 7
$\bar{x}$ no. zooplankters: 4940.57

[1]Value is estimated mean number per 100 m^3 of water, based on water filtered (54.8 m^3) during the 5-min collection.
[2]NR = not recorded. The enumeration was either omitted or unfeasible.
[3]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[4]Most mysids sampled were *Acanthomysis sculpta*.
[5]Adult *S. mystinus* often were seen feeding on large individuals of *Cyanea capillata* (Fig. 5), which were avoided by us during plankton collections because they would have made collections unmanageable.
[6]According to Kathleen Conlan (National Museum of Canada, P.O. Box 3443, Station D, Ottawa, Canada K1P 6P4, pers. commun. 26 May 1987), *Jassa falcata* does not occur in California, and forms along the coast considered to be this species (including the form(s) referred to here) are undescribed.
[7]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[8]Foods digested beyond recognition.

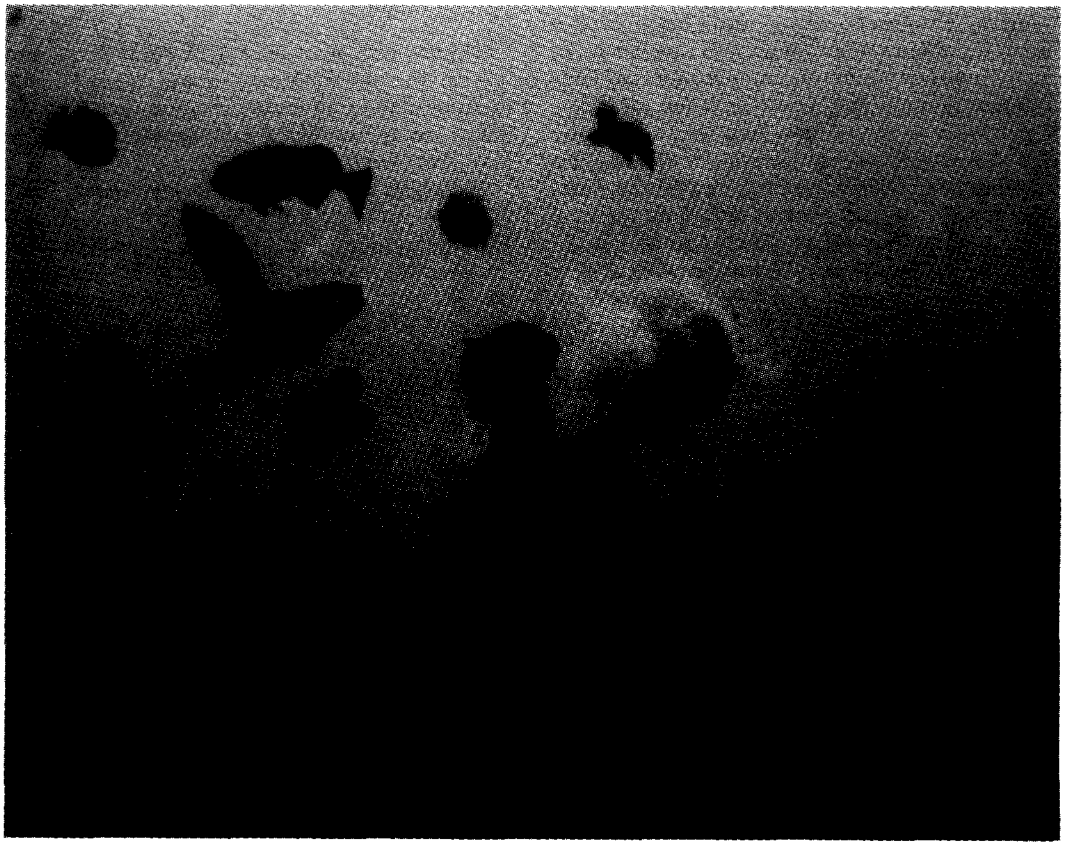

FIGURE 5.—Adult *Sebastes mystinus* feeding on a scyphozoan, *Cyanea capillata*.

TABLE 3.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of the upwelling season. $n = 10$.

Food organism		In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	**THALIACEA (124990.86)**	**1–10**	**47**	**76.20**	**34.9**	**3–45**	**30**	**130.70**	**8.9**
	Undetermined species	1–10	47	76.20	34.9	3–45	30	130.70	8.9
2	**PLANTS (2030.40)**	**NR[2]**	**54**	**NR**	**37.6**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	18	NR	9.7	NR	NR	NR	NR
	Porphyra sp.	NR	22	NR	11.5	NR	NR	NR	NR
	Smithora naidum	NR	15	NR	5.5	NR	NR	NR	NR
	Others	NR	28	NR	10.9	NR	NR	NR	NR

TABLE 3.—*Continued.*

Food organism		In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
3	CALANOIDA (778.78)	3–6	20	16.93	2.3	<1–8	100	5557.10	31.9
	Nauplii	—	0	0.00	0.0	<1–1	50	594.00	1.8
	Acartia spp.	—	0	0.00	0.0	1–2	1	1121.00	4.6
	Calanus pacificus	—	0	0.00	0.0	2–5	70	105.84	2.4
	Eucalanus californicus	4–6	20	16.92	2.3	1–8	70	796.68	14.6
	Rhincalanus nasutus	—	0	0.00	0.0	5–6	10	92.88	2.7
	Others[3]	3	1	0.01	<0.1	<1–3	1	2846.70	5.8
4	HYPERIIDEA (405.13)	2–13	49	6.36	1.3	1–7	60	17.10	0.6
	Hyperoche medusarum	2–6	5	0.38	0.1	1–7	20	9.72	0.3
	Vibilia spp.	5	24	4.35	0.7	—	0	0	0
	Others	2–13	23	1.63	0.5	1–3	40	7.38	0.3
5	PELAGIC GASTROPODA (334.66)	1–20	16	5.81	3.6	1–18	20	37.44	1.1
	Heteropoda								
	Carinaria japonica	10–20	8	2.35	2.0	—	0	0.00	0.0
	Pteropoda								
	Corolla spectabilis	10–15	11	3.45	1.6	15–18	10	4.32	0.8
	Limacina helicina	3	1	0.01	<0.1	1–2	20	33.12	0.3
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	PELAGIC HYDROZOA (318.24)	2–35	30	1.56	6.8	1–20	70	240.66	8.8
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	10–20	10	0.54	0.3
	Others	—	0	0.00	0.0	1–5	50	187.56	5.8
	Syphonophora								
	Muggiaea atlantica	8–9	5	0.27	0.2	6–9	10	2.88	0.6
	Stephanomia bijuga	NR	5	0.31	0.2	—	0	0.00	0.0
	Others	2–16	14	0.51	2.7	2–6	20	49.68	2.1
	Chondrophora								
	Velella velella[4]	25–35	7	0.47	3.7	NA[4]	NA	NA	NA
7	LARVACEA (1.12)	2–7	8	0.70	0.2	2–6	70	142.74	2.2
	Undetermined	2–7	8	0.70	0.2	2–6	70	142.74	2.2
8	POLYCHAETA (0.87)	4–25	19	0.46	0.1	<1–7	70	103.50	0.7
	Larvae	—	0	0.00	0.0	<1–4	70	90.36	0.3
	Postlarvae	4–25	19	0.46	0.1	7	10	13.14	0.4
9	FISHES (0.73)	8–45	4	0.14	1.3	2–11	50	4.50	0.4
	Larvae	8–45	4	0.14	1.3	2–11	50	4.50	0.4
10	SCYPHOZOA (0.02)	NR	3	0.01	0.5	NR	NR	NR	NR
	Fragments	NR	3	0.01	0.5	NR	NR	NR	NR
OTHER CATEGORIES									
	Molluscan larvae	NR	1	0.01	<0.1	<<1–<1	70	631.08	4.9
	Cladocera	—	0	0.00	0.0	<<1–<1	40	115.92	1.7
	Harpacticoida	NR	3	0.03	NR	<1–2	70	55.25	1.1
	Cirripedean larvae	—	0	0.00	0.0	<1–2	100	1372.44	11.8
	Gammaridea	1–8	12	0.32	0.5	<1–3	90	12.24	0.6
	Euphausiacea	2–12	9	0.11	0.7	<1–11	60	229.86	1.0
	Reptantian larvae	—	0	0.00	0.0	<1–3	70	119.52	2.1
	Natantian larvae	—	0	0.00	0.0	1–6	60	43.20	0.7
	Chaetognatha	—	0	0.00	0.0	6–18	50	18.54	1.2
	Eggs, undetermined	NR	12	0.74	0.3	<<1–<1	50	2921.40	5.0
	Eggs, fish	—	0	0.00	0.0	<1–2	60	48.96	0.9
UNIDENTIFIABLE MATERIAL[5]		—	—	—	11.0	—	—	—	—

No. fish examined: 85
204–335, $\bar{x}$ = 266.2 mm SL
No. empty = 8
$\bar{x}$ no. prey: individuals = 110.84
taxa = 3.35

No. plankton collections: 10
$\bar{x}$ no. zooplankters: 6622.50

[1]Value is estimated mean number per 100 m^3 of water, based on water filtered (54.8 m^3) during the 5-min collection.
[2]NR = not recorded. The enumeration was either omitted or unfeasible.
[3]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[4]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[5]Foods digested beyond recognition.

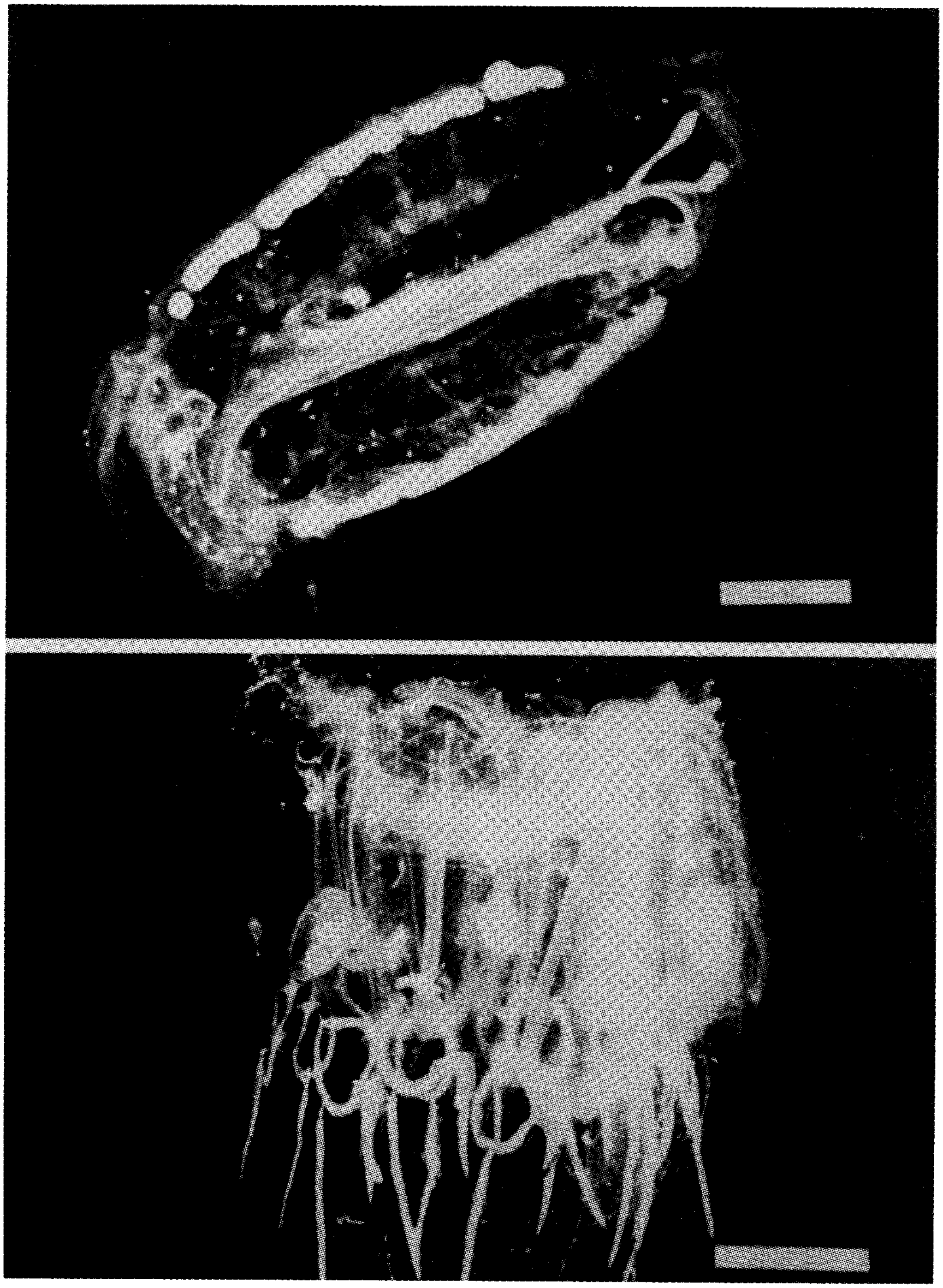

FIGURE 6.—Thaliacean, *Cyclosalpa bakeri*, off Mendocino. Solitary individual (upper) and aggregate of individuals (below). Scale indicator = 1 cm.

Plant material ranked as the top food-category during upwelling episodes (Table 2) and as the second-ranked food during downwelling episodes (Table 3). In both cases, certain algae dominated the diet on days when offshore zooplankters were in short supply during the latter part of the upwelling season (upwelling episodes on 8 August 1978, 12 June 1979, and 17 June 1981; downwelling episodes on 24 July 1979 and 27 August 1979; see Table 1). Algae were not taken earlier in the season, however. Thus, while the six individuals collected during a plankton-poor upwelling episode of 8 August 1978 (Table 1) were full of algae (90% of gut contents) and epibenthic crustaceans (10%), all eight collected during a plankton-poor upwelling episode of 9 April 1981 (Table 1) were empty. Similarly, the occurrence of algae in the diet during downwelling episodes (Table 3) is based mostly on 20 adults collected during two days (24 and 27 August 1979) when environmental conditions indicated downwelling but an absence of offshore zooplankters was noted (Table 1). There was no indication of plants being ingested for epiphytic animals.

Of the wide variety of plant materials in the diet, only the three most frequently ingested forms appeared to some extent digested. These were the sori of *N. leutkeana*, *Porphyra nereocystis* (an epiphyte on *N. leutkeana*), and *Smithora naidum* (an epiphyte on certain seagrasses). The sori of *N. leutkeana* developed as variably sized areas (typically about 50–150 mm long) in fronds near the water's surface. They dropped from the fronds when mature, and we saw several ingested by *S. mystinus* as they drifted toward the bottom. Sori recovered from the intestines of *S. mystinus* were more translucent than sori from the stomach, but comparison under magnification of sectioned material from both regions of the gut (Fig. 7) indicated that only zoospores were digested. Ingested fragments of *P. nereocystis* and *S. naidum*, both species having monostromatic thalli, ranged from intact, but flaccid and blanched, to disintegrating. Ingested *S. naidum* often were attached to pieces of *Zostera marina* or *Phyllospadix torreyi*, but these seagrasses never evidenced digestion. Nor did other plant forms present among the gut contents appear to be digested, including *D. ligulata* and *N. leutkeana* (vegetative tissue), along with various unidentified phaeophytes and rhodophytes. Thus, plants contributed less food than is indicated by the tables and histograms, where their rank is inflated by undigested materials.

Zooplankters taken during upwelling episodes differed from early to late in the season, whereas those taken during downwelling episodes remained much the same throughout (as listed in Table 3). Thus, of the food categories listed for the upwelling condition (Table 2), pelagic hydrozoans, mysids, and scyphozoans were taken only during the spring, whereas euphausiids and caprellids were taken only in summer. The only notable departure from the downwelling condition depicted in Table 3 occurred on 24 April 1979 (Table 1), when conditions were at the time judged to be mixed. Upwelling had been unusually weak during the first month of that upwelling season, and there was no wind at the time of sampling. The sea was calm and, at 10°C, warm for April. Although these conditions usually indicate downwelling (which is why the data are assigned to that category), we neither collected nor saw organisms typical of downwelling conditions. Furthermore, of the nine adult *S. mystinus* (224–313, $\bar{x}$ = 277.7 mm SL) collected, eight (89%) were empty. The ninth contained one sorus from *N. leutkeana* (an unusually large number of *N. leutkeana* had persisted through the previous winter, which had been exceptionally mild) and also organisms not seen or collected by us in the environment at the time: two *Corolla spectabilis* (a pelagic gastropod typical of downwelling conditions) and six *Velella velella* (a pelagic hydrozoan typical of upwelling conditions). The latter float on the water's surface (Fig. 8), and often we saw adult *S. mystinus* break the surface to feed on them.

The Downwelling Season

Between late August and mid-September it became evident that transition to the downwelling season was under way. Winds had become light and variable (but generally remained either northerly or southerly), and for a growing number of days at a time, the water was notably blue and transparent. Records of sea temperatures and wind for the 1980–81 downwelling season illustrate how occurrences of downwelling and upwelling related to prevailing wind during that period (Fig. 9).

Habitat Conditions

The downwelling season developed with less wind from the north and more wind from the south, but either way with winds that tended to be light, so that relatively tranquil conditions prevailed. Flowing into the nearshore habitat with offshore surface waters was a rich supply of relatively large, mostly gelatinous zooplankters that were major prey of *S.*

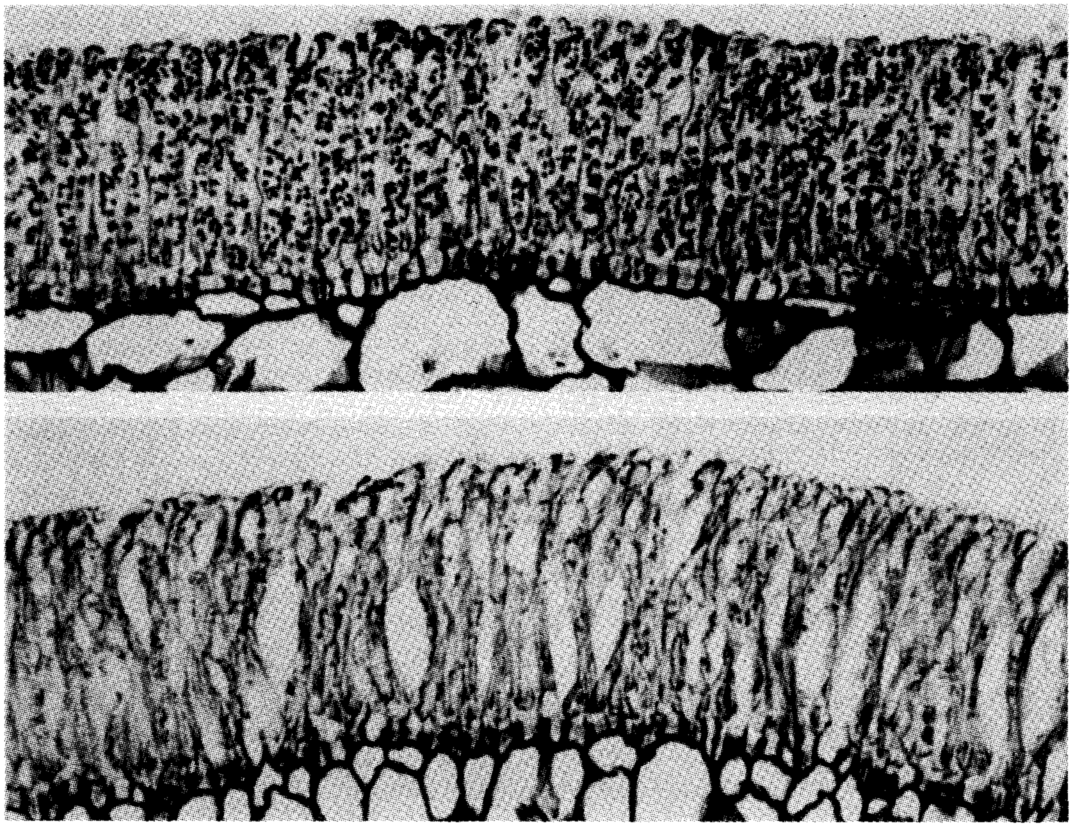

FIGURE 7.—Sections through surface region of sori (stained with hematoxylin) from gut of *Sebastes mystinus*. Upper section is from the stomach, lower is from the intestine. Granular objects in upper section but largely absent in lower section are zoospores in zoosporangia.

mystinus. But, whereas the predominant of such forms during spring and summer usually were thaliaceans, during the fall they were usually ctenophores (Fig. 10), pelagic hydrozoans—mostly siphonophores (Fig. 11), and hydromedusae. The pelagic hydrozoan *Velella velella*, which had been prominent during the upwelling season, was not seen. Pelagic gastropods (Fig. 12), pteropods at least, also were more abundant during fall downwelling. On the other hand, these waters were poor in the pelagic diatoms that had bloomed periodically during spring and summer. Furthermore, the nearshore habitat had by this time lost much of its benthos. Many of the more insecurely anchored *Nereocystis* plants, for example, had been carried away by strong wave surge that frequently swept through the nearshore habitat even during relatively tranquil periods. Although the loss of these plants greatly increased interplant distances, *Nereocystis* beds remained dominant features. This was because the plants still in place continued to grow, to produce sori, and to thicken the surface canopy. Probably at least partly because the canopy's increased thickness blocked sunlight from the seafloor below, the algal understory, *Desmarestia lingulata* in particular, was greatly reduced. Similarly, many benthic animals that proliferated during the previous upwelling season had become scarce, including the amphipods and mysids noted above to be declining during late summer.

As the downwelling season progressed through fall toward winter, there were major transformations of the nearshore habitat that, to at least some extent, resulted from southwesterly storms. The

FIGURE 8.—*Velella velella* being driven shoreward by a northwest wind off the coast of northern California.

major effects of storms on the nearshore habitats came from 1) physical force of waves and surge, and 2) suspended sediments carried by coastal runoff into the nearshore habitats after heavy rains. The first of these was the more apparent, at least in exposed locations where often many of the benthic algae and sessile invertebrates were swept away. This force, intensified when the water carried abrasive sediments, swept away most of the *Nereocystis*, although some plants survived the winter in sheltered places where they continued to produce sori. Suspended sediments had their most obvious effects in locations sheltered from water movement, where they frequently settled to blanket the benthos. Probably a more profound effect of materials in suspension, however, was reduced transparency of the water that limited the amount of light (already at low levels owing to the shorter days and low sun angle) reaching phototrophic organisms.

As a general result of these, and probably other forces in combination, the nearshore habitat appeared relatively barren during the latter stages of the downwelling season. That storms were a major factor in reducing the vitality of this habitat was apparent during the relatively mild winter of 1978–79, when the effects described above were reduced. That was the only year, for example, when mysids were noted to be conspicuous in the nearshore habitat throughout the winter.

Feeding Conditions

The diet of *S. mystinus* relative to foods available during the downwelling season was assessed during 10 days of sampling under downwelling condi-

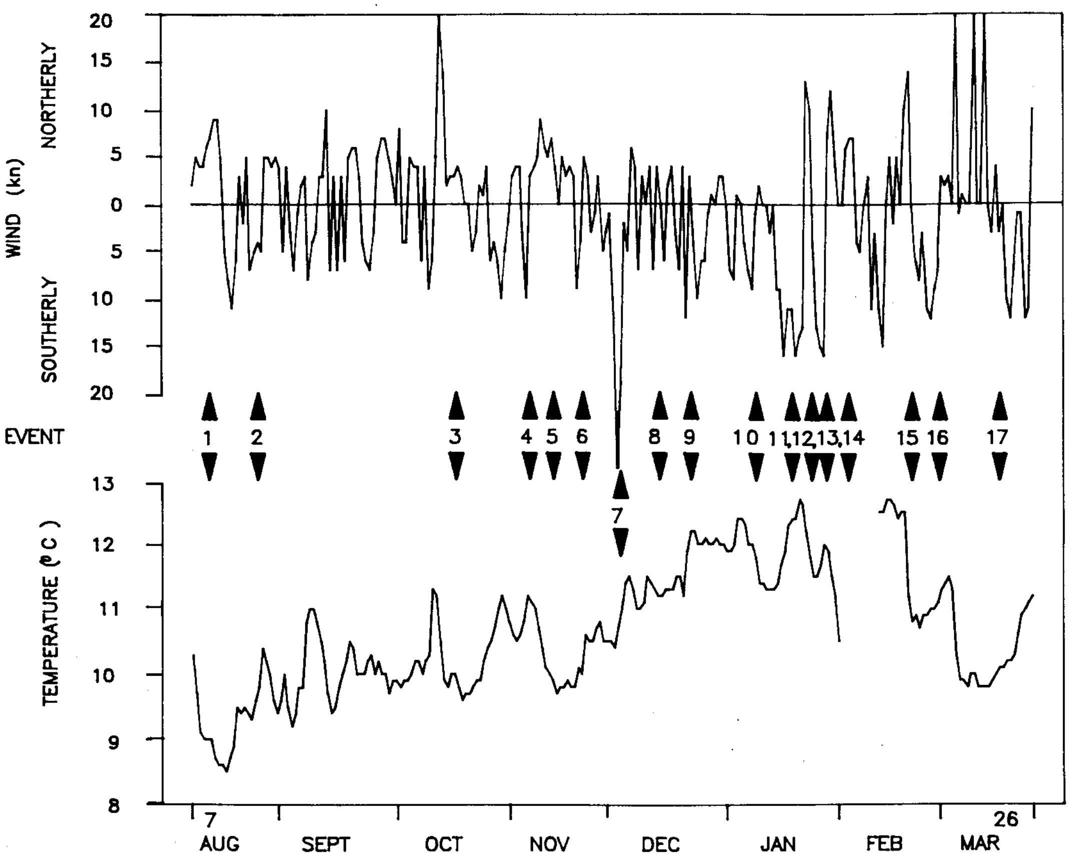

FIGURE 9.—Sea temperatures and wind off Mendocino during the 1980-81 downwelling season. See capture of Figure 4 and text for methods used in obtaining and plotting the data.

EVENT 1—Sea temperature fell to 8.5°C on 16 August after 9 consecutive days of 7-10 K northerlies, producing the last episode of strong upwelling during the 1980 upwelling season.

EVENT 2—Sea temperature rose to 10.4°C on 26 August after southerlies of 5-12 K on 9 of the preceding 11 days. Then began a 6-wk transition to the downwelling season, during which 1-4 day periods of 2-10 K northerlies, with slightly lowered sea temperatures, alternated with 1-4 day periods of southerlies, with slightly elevated temperatures.

EVENT 3—The last bit of upwelling before the season's first major downwelling episode began on 14 October with 7 consecutive days of northerlies—20 K during the first 2, 4-8 K during the next 5.

EVENT 4—Sea temperatures rose to 11.2°C on 7 November after 16 straight days of 2-12 K southerlies or weak (2-5 K) northerlies.

EVENT 5—Sea temperatures fell to 9.7°C during a major cooling that coincided with 8 days of 3-9 K northerlies (with gusts to 20 K) from 8 to 15 November.

EVENT 6—On 21 November the wind shifted to the south, with gusts to 20K, and sea temperatures began rising.

EVENT 7—A 3-day storm (1-3 December) with 20-30 K southerlies (and rain) briefly accelerated the rise in temperature.

EVENT 8—The warming trend was briefly interrupted by several 1-3 day periods of 4-10 K northerlies.

EVENT 9—By 22 December sea temperatures had risen to levels above 12°C that characterized the 1980-81 downwelling season. Although southerlies predominated over the next 3 weeks, on some days reaching 25 K (e.g., on 25 December), there were no further large increases in temperature.

EVENT 10—Sea temperatures anomalously fell during the first 2 weeks of January, even though winds during that period were mostly southerlies of up to 10 K.

EVENT 11—An 8-day storm (15-22 January) with 12-20 K southerlies (and rain) resulted in sea temperatures rising to 12.7°C—the warmest of the year (equaled 3 weeks later).

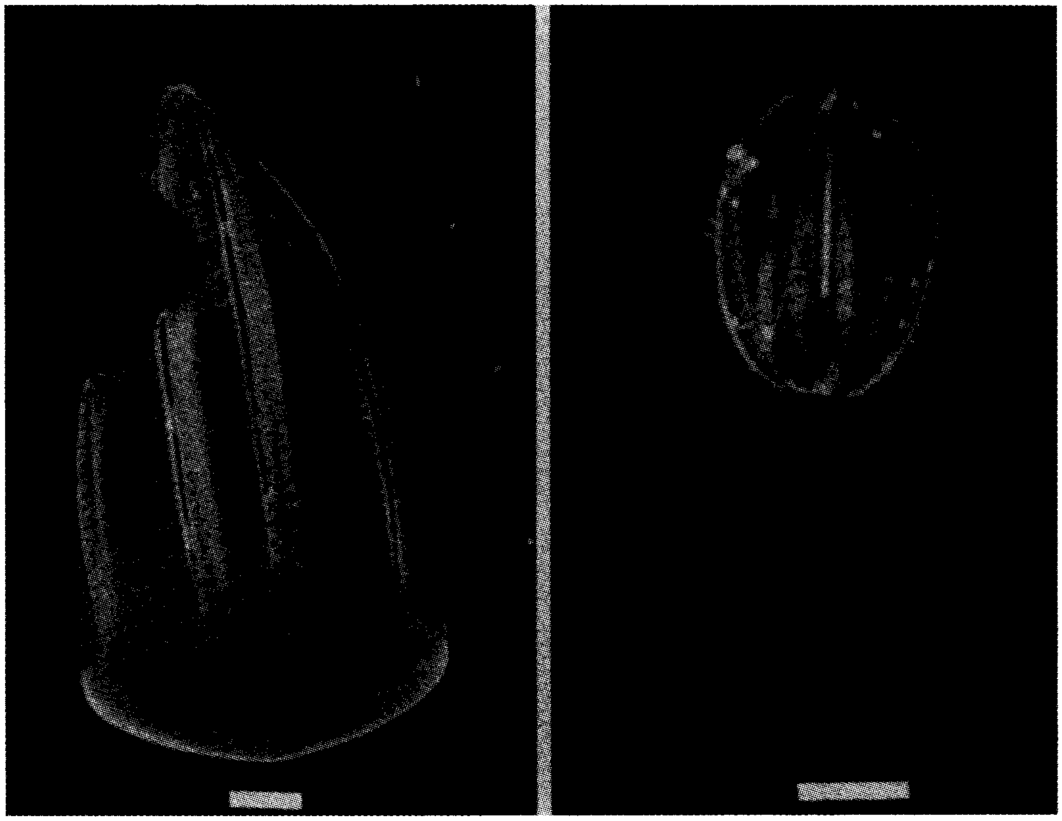

FIGURE 10.—Ctenophores off Mendocino. *Beroe forskali* (left), missing piece probably taken by planktivore, and *Pleurobrachia bachei* (right). Scale indicator = 1 cm.

EVENT 12—The process abruptly reversed with a shift to northerlies that gusted to 30 K for 2 days, and sea temperature fell to 11.5°C on 25 January.

EVENT 13—In another abrupt reversal, 3 days (27–29 January) of 15–25 K southerlies (with rain) resulted in sea temperature rising to 12°C.

EVENT 14—Reversing again, northerlies of 12–20 K on 30–31 January drove sea temperatures down to 10.5°C, at which point (1 February) the thermograph malfunctioned. Southerlies predominated while the thermograph was inoperative, and when it was reinstalled on 11 February, rising sea temperature 2 days later (13 February) equaled the season high of 12.5°C. But when northerlies returned the next day the downwelling season began its decline.

EVENT 15—Two days of 20–25 K northerlies (19–20 February) resulted in the season's largest 24-h change in sea temperatures.

EVENT 16—Sea temperature rose to 11.5°C on 3 March following 8 consecutive days of 8–15 K southerlies (with rain), or weak northerlies (to 6 K). An abrupt shift followed, as 2 days of 15–25 K northerlies (4–5 March) resulted in the season's second largest 24-h change in sea temperature—the first time since November that sea temperature had fallen below 10°C.

EVENT 17—After a week of light variable winds, during which sea temperatures remained essentially unchanged at about 9.8°C, southerlies increased to 15–20 K (on 15 March) and sea temperatures began rising to begin the final downwelling episode of the 1980–81 downwelling season (which was followed by the abrupt reversal that marked the beginning of the 1981 upwelling season, see Figure 4).

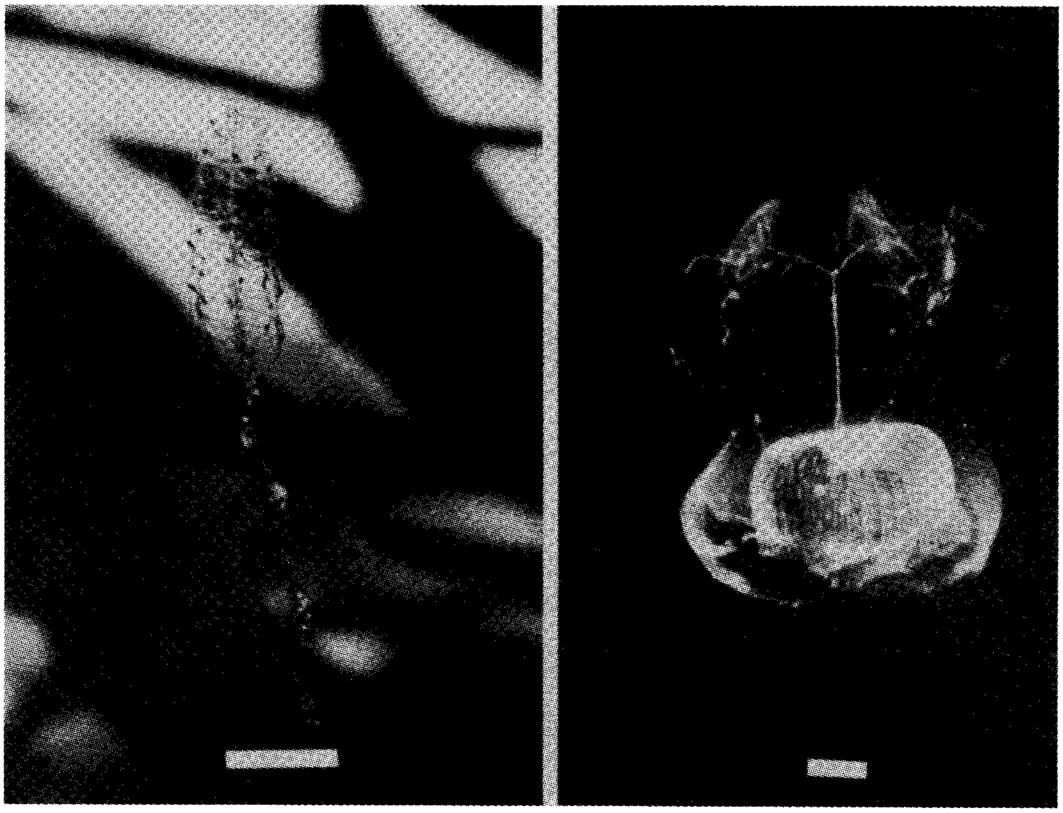

FIGURE 11.—Siphonophores off Mendocino. The physonect *Stephanomia bijuga* (left), and the calycophore *Praya dubia* (right). Scale indicator = 1 cm.

tions, but because fall and winter were so different, we consider them separately. We did not observe upwelling conditions during this period.

The major foods during six days of fall downwelling, based on the ranking indices (Table 4), were pelagic hydrozoans, specifically siphonophores, but vegetation comprised a larger part of the total diet volume. Virtually all plant materials taken at these times, however, were sori of *N. leutkeana*. As was true during the upwelling season, there tended to be more vegetation in the diet when there were fewer of the larger gelatinous zooplankters in the water column. For example, during the sampling session of 18 October 1978 (Table 1), when the surface plankton-collections took 400 siphonophores and ctenophores, only 1 of the 9 fish collected had consumed plant material (one sorus of *N. leutkeana*). On the other hand, during the sampling session of 16 October 1979 (Table 1), when the surface plankton-collection took only 30 siphonophores and ctenophores, 10 of 13 fish collected had consumed vegetation ($\bar{x}$ diet volume = 80%, virtually all of it sori of *N. leutkeana*; number taken = 1–21, $\bar{x}$ = 9.0), and two others were empty.

Our assessment of the diet and concurrent composition of the plankton during winter downwelling is limited to four days of sampling (Table 5). Data from these collections are combined for consistency

FIGURE 12.—Pelagic gastropods off Mendocino. The heteropod *Caranaria japonica* (upper), and the pteropod *Corolla spectabilis* (lower). Scale indicator = 1 cm. Often in areas where blue rockfish are feeding many of the *C. spectabilis* present have lost the bulbous central part of their body (pseudoconch and viscera).

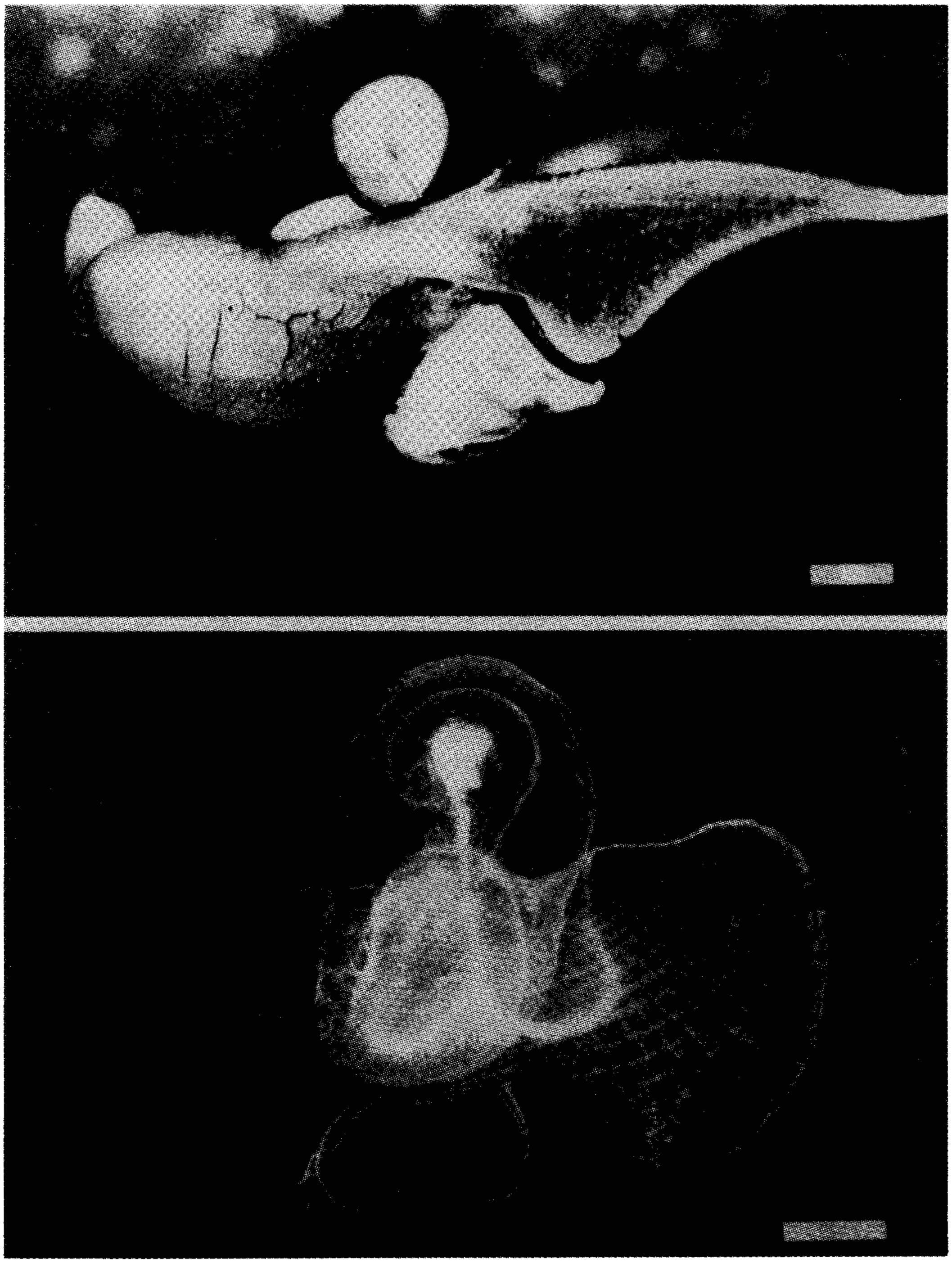

TABLE 4.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of fall. $n = 6$.

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	In plankton: Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	**PELAGIC HYDROZOA (10455.98)**	**2–15**	**46**	**18.04**	**12.5**	**1–25**	**83**	**1747.12**	**26.5**
	Hydromedusae								
	Eutonina indicans	18	1	0.03	<0.1	18–25	33	1516.81	14.7
	Others	15	4	0.02	<0.1	<1–20	33	26.10	0.2
	Syphonophora								
	Muggiaea atlantica	6–15	10	0.34	0.7	5–12	67	15.83	2.0
	Stephanomia bijuga	10	17	1.33	0.8	10	17	2.39	0.3
	Others	2–15	31	16.32	10.9	1–8	4	185.99	9.3
	Chondrophora								
	Velella velella[2]	—	0	0.00	0.0	NA[2]	NA	NA	NR
2	**PLANTS (4123.00)**	**NR[3]**	**54**	**2.06**	**37.1**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	51	1.94	35.6	NR	NR	NR	NR
	Porphyra sp.	NR	2	NR	0.2	NR	NR	NR	NR
	Smithora naidum	NR	6	0.06	<0.1	NR	NR	NR	NR
	Others	NR	6	0.06	1.3	NR	NR	NR	NR
3	**CTENOPHORA (1742.66)**	**3–15**	**33**	**5.74**	**9.2**	**<1–10**	**0.67**	**295.79**	**5.4**
	Pleurobrachia bachei	3–15	31	5.73	9.2	<1–10	50	288.59	5.2
	Others	12	1	0.01	<0.1	3	17	7.20	0.2
4	**PELAGIC GASTROPODA (554.00)**	**2–160**	**25**	**3.20**	**6.8**	**<1–45**	**100**	**187.82**	**8.4**
	Heteropoda								
	Caranaria japonica	12–160	15	0.33	2.1	30–45	17	1.21	0.7
	Pteropoda								
	Corolla spectabilis	5–22	16	2.69	4.7	2–20	50	72.90	7.5
	Limacina helicina	2	1	0.18	<0.1	1–3	17	109.80	0.2
	Others	—	0	0.00	0.0	<1–3	17	3.91	<0.1
5	**SCYPHOZOA (89.96)**	**10–35**	**18**	**0.51**	**9.8**	**NA**	**NA**	**NA**	**NA**
	Fragments	10–35	18	0.51	9.8	NA	NA	NA	NA
6	**THALIACEA (31.97)**	**5–29**	**16**	**0.54**	**3.7**	**2–5**	**17**	**3.01**	**NR**
	Undetermined species	5–29	16	0.54	3.7	2–5	17	3.01	NR
7	**EUPHAUSIACEA (22.93)**	**4–10**	**21**	**0.78**	**1.4**	**<1–9**	**67**	**162.90**	**2.2**
	Larvae	4	1	0.01	<0.1	4	50	129.01	1.2
	Thysanoessa spp.	4–10	19	0.74	1.4	5–9	33	33.89	1.0
	Others	8	1	0.03	<0.1	—	0	0.00	0.0

with the other tables and figures, but the combinations obscure the great variation in feeding conditions at this time of year. For example, taxa of the major food categories listed in Table 5 were numerous in the diet and plankton only during the two sampling sessions in February and March of 1979. Of the 14 fish collected at those times, all but one was well fed ($\bar{x}$ no. prey = 26.7), with the exception being a pregnant female whose gut was empty. Thaliaceans dominated on these occasions, both in the diet and in the plankton, and hyperiid amphipods, *Vibilia* spp. (which are parasites of thaliaceans (Laval 1980)), were similarly abundant. In contrast, the collecting session of January 1980 indicated there were more zooplankters in the water column, but that they were exceptionally small. The plankton collection took 1,488 zooplankters (compared with 109 and 715 in the two 1979 collections), but only 2% were of species that occurred as large as 2 mm (compared with 86% in 1979). That these small zooplankters were unsuitable as prey of adult *S. mystinus* is implicit in the fact that of 16 fish collected, only 3 contained food—all of it the alga *Porphyra* sp. (The other 13 represented 76% of all fish with empty guts in the winter collections.) Significantly, of the taxa identified as food of adult *S. mystinus* during the winter (Table 5), only one, the calanoid *Calanus pacificus*, was represented in the January 1980 plankton collection. Conditions were intermediate during the sampling session of January 1981, when some of the listed food taxa occurred in both diet and plankton (though in reduced numbers) and five of eight fish sampled contained food.

TABLE 4.—*Continued.*

		In diet				In plankton			
Rank	Food organism Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
8	CALANOIDA (14.32)	**2–7**	**22**	**0.93**	**0.7**	**<1–7**	**100**	**9528.11**	**28.3**
	Nauplii	—	0	0.00	0.0	<1–1	33	68.99	<0.1
	Acartia spp.	—	0	0.00	0.0	<1–1	83	1751.42	4.3
	Calanus pacificus	3	6	0.13	<0.1	<1–4	83	4609.21	15.8
	Eucalanus californicus	4–7	15	0.67	0.7	2–7	100	255.39	1.2
	Rhincalanus nasutus	4	4	0.06	<0.1	—	0	0.00	0.0
	Others[4]	2–3	3	0.07	<0.1	<1–3	100	2843.10	7.0
9	HYPERIIDEA (8.28)	**1–8**	**24**	**1.15**	**0.4**	**1–7**	**83**	**292.19**	**0.4**
	Hyperoche medusarum	2	3	0.16	0.1	1–7	50	273.01	0.2
	Vibilia spp.	—	0	0.00	0.0	—	0	0.00	0.0
	Others	1–8	21	0.99	0.3	1–3	33	19.18	0.2
10	POLYCHAETA (3.20)	**4–40**	**16**	**0.40**	**0.5**	<1–7	83	118.21	1.7
	Larvae	—	0	0.00	0.0	<1–4	33	103.81	1.5
	Postlarvae	4–40	16	0.40	0.5	3–7	50	14.40	0.2
OTHER CATEGORIES									
	Molluscan larvae	—	0	0.00	0.0	<<1–<1	50	189.59	0.7
	Cladocera	—	0	0.00	0.0	<1–1	33	142.20	0.8
	Cyclopoida	NR	1	0.01	NR	<1–1	67	648.00	4.0
	Cirripedean larvae	—	0	0.00	0.0	<<1–<1	67	128.70	0.2
	Reptantian larvae	—	0	0.00	0.0	<1–6	83	52.20	0.3
	Natantian larvae	—	0	0.00	0.0	1–5	33	237.60	NR
	Bryozoan larvae	—	0	0.00	0.0	<1	33	244.49	0.2
	Larvacea	2	3	0.12	0.1	<1–4	67	844.20	2.8
	Chaetognatha	10–11	3	0.06	0.2	5–20	83	225.59	5.0
	Eggs, undetermined	—	0	0.00	0.0	<1	17	1535.99	4.3
	Eggs, fish	3	1	0.01	<0.1	<1–2	33	40.19	4.4
	Fishes	6–24	4	0.04	0.2	4–20	33	5.40	0.7
UNIDENTIFIABLE MATERIAL[5]		—	—	—	17.4	—	—	—	—

No. fish examined: 73
218–350, $\bar{x}$ = 290.3 mm SL
No. empty = 7
$\bar{x}$ no. prey: individuals = 32.4
taxa = 3.6

No. plankton collections: 6
$\bar{x}$ no. zooplankters: 9663.0

[1]Value is estimated mean number per 100 m^3 of water, based on water filtered (54.8 m^3) during the 5-min collection.
[2]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[3]NR = not recorded. The enumeration was either omitted or unfeasible.
[4]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[5]Digested beyond recognition.

DISCUSSION

It is clear that wind-driven movement of the surface water profoundly influences feeding by *Sebastes mystinus* off northern California. Water set in motion by the wind can be tens of meters deep (Bakun 1973; Barber and Smith 1981), and so carries most of the foods of nearshore planktivores. The movement is seaward (with upwelling) under northerly winds and shoreward (with downwelling) under southerly winds. Thus, with winds along the Mendocino coast being northerly or southerly about 80% of the time (based on records of the NOAA weather station there), adult *S. mystinus* in that area alternate between periods when planktonic foods are being carried into their habitat and periods when these foods are being carried away.

This perception of alternations between upwelling and downwelling is simplified, perhaps overly so, to emphasize features we consider essential to the feeding of *S. mystinus*, and also because details of what clearly is a complex oceanographic system remain unclear. In particular, we stress the importance of shoreward surface transport in carrying prey to *S. mystinus* in nearshore habitats. The major prey of adult *S. mystinus*—thaliaceans, pelagic hydrozoans, and other relatively large, gelatinous zooplankters—tend to be concentrated in areas of oceanic convergence, and dispersed in areas of oceanic divergence (e.g., Bakun and Parrish 1980). Thus, when offshore surface waters converge on the coast, the planktonic foods of *S. mystinus* become concentrated near shore.

TABLE 5.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of winter. $n = 4$.

	Food organism	In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	**THALIACEA (29034.03)**	**7–20**	**71**	**12.90**	**31.7**	**5–45**	**50**	**9.90**	**34.8**
	Undetermined species	7–20	71	12.90	31.7	5–45	50	9.90	34.8
2	**HYPERIIDEA (3278.81)**	**1–5**	**62**	**23.40**	**2.2**	**1–6**	**75**	**2.25**	**0.8**
	Hyperoche medusarum	—	0	0.00	0.0	4	25	0.45	NR[3]
	Vibilia spp.	1–5	57	23.06	2.1	5–6	25	0.90	0.8
	Others	6	5	0.34	0.1	1	25	0.90	NR
3	**EUPHAUSIACEA (1567.61)**	**6–12**	**43**	**11.76**	**3.1**	**10**	**75**	**2.25**	**12.5**
	Larvae	—	0	0.00	0.0	—	0	0.00	0.0
	Thysanoessa spp.	6–12	38	11.67	3.1	10	75	2.25	12.5
	Others	6	5	0.09	<0.1	—	0	0.00	0.0
4	**SCYPHOZOA (1054.20)**	**NR**	**38**	**1.43**	**19.4**	**NR**	**NR**	**NR**	**NR**
	Fragments[2]	NR	38	1.43	19.4	NR	NR	NR	NR
5	**PELAGIC GASTROPODA (726.34)**	**6–30**	**48**	**2.91**	**5.2**	**1–20**	**25**	**8.10**	**0.8**
	Heteropoda								
	Caranaria japonica	15–30	10	0.24	0.5	—	0	0.00	0.0
	Pteropoda								
	Corolla spectabilis	6–20	48	2.67	4.7	20	25	0.45	0.8
	Limacina helicina	—	0	0.00	0.0	1–2	25	7.65	NR
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	**PELAGIC HYDROZOA (437.91)**	**3–13**	**43**	**1.52**	**6.7**	**1–6**	**75**	**14.85**	**1.3**
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	—	0	0.00	0.0
	Others	10–22	40	0.33	3.5	1–4	50	12.60	0.5
	Syphonophora								
	Muggiaea atlantica	8–13	38	0.86	2.1	6	50	1.35	0.8
	Stephanomia bijuga	—	0	0.00	0.0	—	0	0.00	0.0
	Others	3–20	19	0.33	1.1	3	25	0.90	NR
	Chondrophora								
	Velella velella	—	0	0.00	0.0	NA[4]	NA	NA	NA
7	**PLANTS (380.00)**	**NR**	**38**	**NR**	**10.0**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	5	0.10	0.1	NR	NR	NR	NR
	Porphyra sp.	NR	19	NR	5.2	NR	NR	NR	NR
	Smithora naidum	—	0	0.00	0.0	NR	NR	NR	NR
	Others	NR	19	NR	4.7	NR	NR	NR	NR

Shoreward transport can be either wind-driven (Ekman transport), or result simply from relaxation of the forces that drive upwelling. But in either case our observations indicate that shoreward flowing surface waters override the colder waters near shore, a process we refer to as downwelling. Usually the term downwelling is limited to conditions that result from shoreward Ekman transport (e.g., Gross 1977), but we have found that relaxation of upwelling has essentially the same effect on the nearshore ecosystem, the difference being simply in degree of effect.

Some studies have concluded that warming of the nearshore surface waters during relaxation of upwelling results from alongshore advection (e.g., Send et al. 1987), but even though zooplankters entering our study area during downwelling generally moved southward along the coast, the characteristic presence of such forms as thaliaceans, ctenophores, and pteropods indicate that the advection is from offshore. So despite the complexities of circulation and mixing that occur in the coastal waters off northern California (e.g., Winant et al. 1987), the net result affecting the trophic relations of *S. mystinus* are alternations between seaward and shoreward transport.

These water movements follow a strong seasonal pattern that is evident in upwelling indices for lat. 39°N (which crosses Mendocino) produced by the Pacific Fisheries Environmental Group of the Southwest Fisheries Center, NMFS, NOAA. In addition to the seasonal trend, short-term episodes of seaward and shoreward transport produce day-to-day, even hour-to-hour, changes in the foods available to

TABLE 5.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	% occur.	x̄ no.	x̄ % vol.	In plankton: Size (mm)	% occur.	x̄ no.[1]	x̄ % vol.
8	**CTENOPHORA (4.73)**	**11–20**	**10**	**0.43**	**1.1**	—	**0**	**0.00**	**0.0**
	Plerobrachia bachei	11	5	0.09	0.1	—	0	0.00	0.0
	Others	20	5	0.34	1.0	—	0	0.00	0.0
9	**MYSIDACEA (4.47)**	**6–20**	**14**	**0.29**	**1.2**	**3–8**	**50**	**1.80**	**0.5**
	Acanthomysis sculpta	6	5	0.19	1.0	—	0	0.00	0.0
	Others	18–20	10	0.10	0.2	3–8	50	1.80	0.5
10	**CALANOIDA (1.18)**	**2–5**	**14**	**0.28**	**0.3**	**1–5**	**100**	**684.00**	**25.6**
	Nauplii	—	0	0.00	0.0	—	0	0.00	0.0
	Acartia spp.	—	0	0.00	0.0	<1–1	25	229.50	7.5
	Calanus pacificus	2–3	14	0.14	0.1	1–3	100	110.70	3.8
	Eucalanus californicus	5	10	0.14	0.2	3–5	50	12.60	0.8
	Rhincalanus nasutus	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	1–2	100	331.20	13.5
OTHER CATEGORIES									
	Molluscan larvae	—	0	0.00	0.0	<<1–<1	50	38.70	2.5
	Cyclopoida	—	0	0.00	0.0	1	75	61.20	1.5
	Cirripedean larvae	—	0	0.00	0.0	1–2	75	24.75	0.5
	Reptantian larvae	4	<1	0.05	<0.1	<1–3	100	240.30	9.3
	Larvacea	—	0	0.00	0.0	3–6	50	6.30	1.3
	Chaetognatha	—	0	0.00	0.0	5–35	75	14.85	5.0
	Fishes	8–10	<1	0.10	NR	3–7	75	7.65	2.8
UNIDENTIFIABLE MATERIAL[5]		—	—	—	19.1	—	—	—	—

No. fish examined: 38
200–345, x̄ = 265.3 mm SL
No. empty: 17
x̄ no. prey: individuals = 45.2
taxa = 4.8

No. plankton collections: 4
x̄ no. zooplankters: 634.3

[1]Value is estimated mean number per 100 m^3 of water, based on water filtered (54.8 m^3) during the 5-min collection.
[2]Adult *S. mystinus* often were seen feeding on large individuals of *Cyanea capillata*, which were avoided by us during plankton collections because they would have made collections unmanageable.
[3]NR = not recorded. The enumeration was either omitted or unfeasible.
[4]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[5]Digested beyond recognition.

planktivorous fishes. The following discussion considers how the diet of *S. mystinus*, summarized in Figure 13, is influenced by these alternations in surface transport during distinct upwelling and downwelling seasons.

The Upwelling Season

The spring-summer upwelling season produces optimal feeding conditions for *S. mystinus*. During this period the combined effects of increased nutrients (from strong upwelling) and increased daylight (from longer days, higher sun-angle, and less storm-produced sediments in suspension) result in growth of diatom populations that constitute the food-base of the zooplankton community.

Seaward Ekman transport in response to the season's persistent northerly winds carries the upwelled nutrients and increasing number of diatoms offshore, where the response of zooplankters can be spectacular. Consider, for example, thaliaceans, which are a major prey of adult *S. mystinus*. Recent study has shown that populations of *Salpa fusiformis* (a common thaliacean in the California Current) normally are food-limited, but can grow rapidly when diatoms are abundant (Silver 1975). In response to a diatom bloom, *Thalia democratica* (another salp common in the California Current), can increase in size by up to 10%/hour and in numbers up to 2.5 times/day, the highest rate recorded for a metazoan animal (Heron 1972a, b).

Zooplankters thus increased in size and number are then carried to *S. mystinus* near shore by the shoreward flow that develops with relaxation of upwelling, or, more forcefully, with shoreward Ekman transport under southerly winds. It remains uncertain, however, whether the numbers of zooplankters entering the Mendocino nearshore habitats are in fact related to the productivity of local upwelling. Wickett (1967) concluded that zooplankton abun-

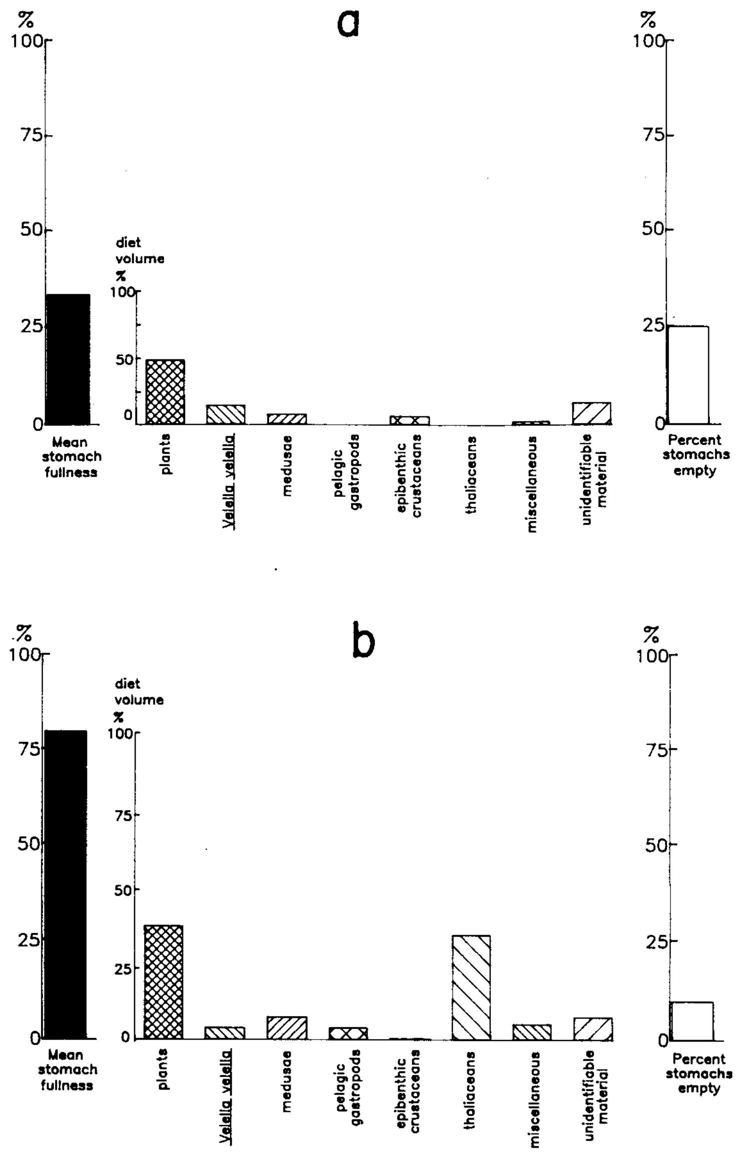

FIGURE 13.—Seasonal variations in the diet of *Sebastes mystinus*:
a. Diet during upwelling episodes of the upwelling season. $n = 51$.
b. Diet during downwelling episodes of the upwelling season. $n = 85$.

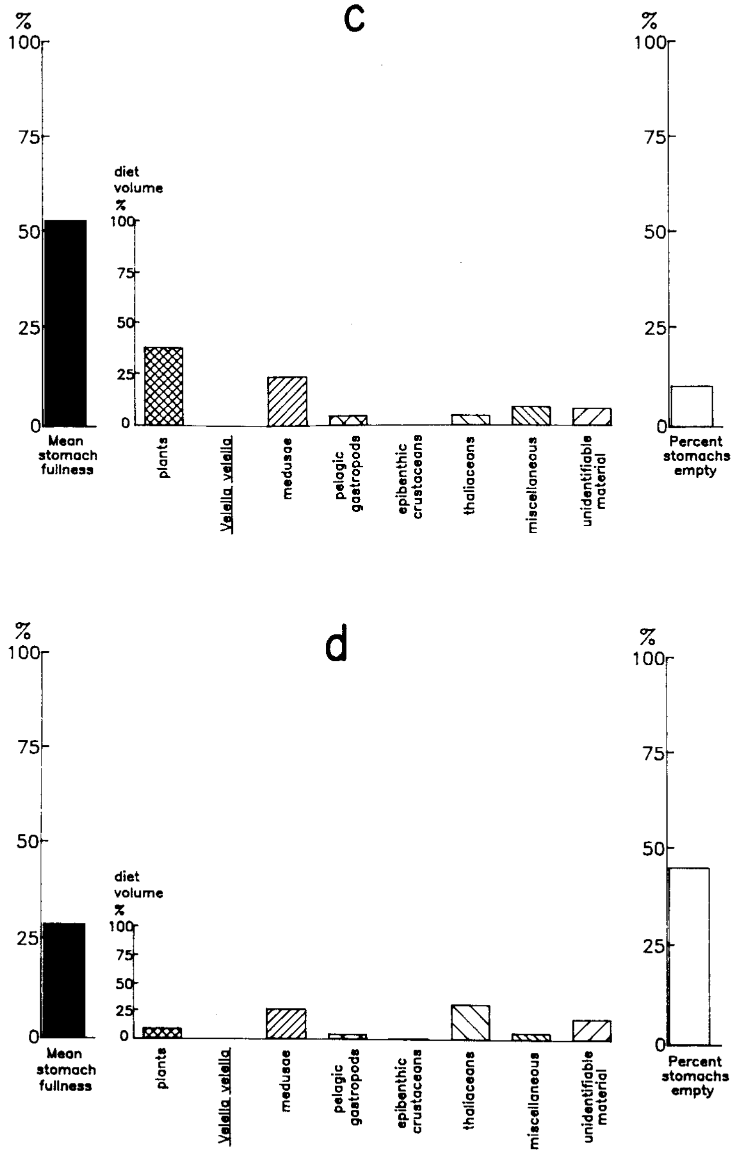

FIGURE 13.—*Continued*—Seasonal variations in the diet of *Sebastes mystinus*:
c. Diet during fall of the downwelling season. $n = 73$.
d. Diet during winter of the downwelling season. $n = 38$.

dances off California depend on nutrients from the Gulf of Alaska, and Chelton et al. (1982) concluded not only that phytoplankton off California depend on nutrients from higher latitudes but also that wind-forced coastal upwelling is relatively unimportant in supplying these nutrients. Despite this uncertainty, growth in thaliaceans is so rapid that it would seem at least many of those off the Mendocino coast could result from local upwelling. Regardless of what determines the growth of thaliaceans in this region, their appearance in large numbers next to the beach is evidence that shoreward transport has developed. These animals are readily detected by in situ observations, and also by their occurrences in samples of both plankton and gut contents (Table 3).

Intermittent shoreward transport during the upwelling season seems especially strong off northern California. This is evident in the upwelling indices of Bakun (1973), and also in that fewer thaliaceans get inshore at this time of year, both to the north, off Oregon (Hubbard and Pearcy 1971), and to the south, off central and southern California (Blackburn 1975). Thus, it is clear that the major foods of *S. mystinus* along the Mendocino coast are most available during downwelling episodes of the upwelling season.

Despite the increased productivity of the upwelling season, *S. mystinus* experiences relatively poor feeding conditions during that season's upwelling episodes. Not only are fewer prey taken during upwelling than during downwelling, a higher proportion of the fish have empty stomachs (Fig. 13). This is because the shoreward flow that transports zooplankters from offshore during downwelling is replaced by the seaward flow that is part of the upwelling condition.

There is, however, one relatively large gelatinous zooplankter from offshore that is most available as prey during upwelling. This is the chondrophore *Velella velella*, a pelagic hydrozoan known as "by-the-wind-sailor". It is, in fact, entirely because of this animal that the food category "Pelagic Hydrozoa" ranked second as food during upwelling episodes (Table 2). Because *V. velella* floats on the water's surface and is equipped with a sail-like structure (Fig. 8), its movements are determined more by wind than by current. The species includes two forms distinguished by whether their sails are oriented to the left of or to the right of the main body axis. This orientation determines their direction in sailing before the wind—left-handed individuals sail to the left of the wind direction and right-handed individuals sail to the right (Bieri 1959). Although it has been reported that the right-handed form predominates off California (Morris et al. 1980), all those we examined from off Mendocino were left-handed, and so would have been driven shoreward by the northerly winds that generated upwelling.

In the absence of favored open-water zooplankters, *S. mystinus* increased consumption of nearshore hyperbenthic zooplankton, e.g., mysidaceans and gammarideans (Table 2). But fewer of these organisms were taken than might be expected, based on their great abundance during much of the upwelling season. *Acanthomysis sculpta*, the mysid most often taken as prey, typically aggregates in large swarms within 2 m of the seafloor. To prey on them, adult *S. mystinus* must leave the upper levels of the water column in a departure from their usual feeding mode that may reduce feeding effectiveness. In addition, most hyperbenthic zooplankters probably are too small to be ready prey of these fish. Although 5–7 mm mysids (Table 2) should be large enough, most other taxa are less than 2 mm. Organisms as small as 1 mm occur in the diet, including some thought to be strictly benthonic, e.g., smaller of the gammaridean *Jassa* sp. (which also occurred in plankton collections; Table 2). But such forms may be ingested (and taken by plankton nets) while attached to drifting plant fragments. Although *S. mystinus* has a smaller mouth than most of its congeners, presumably as an adaptation to planktivory (Hallacher and Roberts 1985), the adults appear unable to consume the larvae of neritic species, e.g., cirripedeans, that, with maximum dimensions of 1 mm or less, often are the most numerous of the zooplankton (Table 2). These larvae are major prey of juvenile *S. mystinus* (unpubl. data; Gaines and Roughgarden 1987), which further suggests it is their small size that precludes them as prey of the adult.

Foods most often consumed in the absence of preferred zooplankters, however, were plant materials. In fact, during upwelling episodes more plants were consumed than anything else (Table 2), and even during downwelling plants were the second-ranked food category (Table 3). Although these rankings are inflated by undigested plant tissues, certain algal materials appear to be important foods. The availability of plant foods to supplement prey shortages was strongly seasonal, however. Thus, the sharply reduced availability of plants during winter and early spring undoubtedly contributed to the prevalence of empty stomachs among fish collected at those times.

Although a wide variety of plants were ingested, *S. mystinus* seemed able to utilize only certain algal tissues. These included zoospores of *Nereocystis leutkeana* and the two epiphytes, *Porphyra nereocystis* and *Smithora naidum*. Probably this is because as members of a carnivorous family they have only limited abilities to digest plant material.

The zoospores of *N. leutkeana* are especially vulnerable to *S. mystinus* when the sori have dropped from the plants' fronds, because at this time the sori have lost their epidermis (an adaptation of the mature sori that facilitates release of the zoospores (David C. Walker[2])). Zoospores may be appropriate food for this largely carnivorous fish because they are, as their name implies, animal-like: they have cell membranes but not the cellulosic cell walls (Wilson 1952) that preclude plants as food for many fishes (e.g., Lobel 1981). The other algae apparently utilized—*Porphyra nereocystis* and *Smithora naidum*—may be appropriate forage for a fish with limited herbivorous abilities because they are monostromatic plants only 25–60 μ thick (Abbott and Hollenberg 1976). So while Gotshall et al. (1965) reported that algae in the guts of *S. mystinus* generally are undigested, some forms appear to be important foods.

It is possible that plant materials are among items of little or no food value that are ingested during food shortages simply because at such times the adult *S. mystinus* become less discriminating in their choice of drifting objects. On the other hand, it is also possible that these fish have unusual herbivorous abilities as a result of adaptations to a diet rich in thaliaceans, which are among the few animals with cellulosic tissues (Berrill 1961). This second possibility is weakened, however, by the fact that the cellulosic tunics of the thaliaceans appear to pass through the gut undigested (Gotshall et al. 1965; our observations).

The Downwelling Season

As the downwelling season developed in the fall, *S. mystinus* experienced progressively poorer feeding conditions. Offshore water flowing into the nearshore habitats at these times tended to be poor in phytoplankton (hence its transparency and blueness, in contrast to the turbid greenness of a few months before), and so generally lacked the herbivorous thaliaceans that were major prey during periods of peak feeding. Relatively large gelatinous zooplankters continued on occasion to be numerous in the shoreward flow, but the species at this time tended to be carnivores rather than herbivores, and *S. mystinus* did not feed on some of them. For example, while siphonophores made "Pelagic Hydrozoa" the top-ranked food category (Table 4), the most numerous pelagic hydrozoan in the water column, *Eutonina indicans*, went virtually untaken. (The small medusae visible throughout Figure 1, especially against the dark kelp, are of this species.) On the other hand, another relatively large, gelatinous zooplankter, the ctenophore *Pleurobrachia bachei* (Fig. 10), was prominent both as prey and in the plankton. Probably the presence of *P. bachei* accounted for the gut-content occurrences of the hyperiid *Hyperoche medusarum*, which is a parasite of this ctenophore (Brusca 1970).

As was true during late spring and summer, certain plant materials became major foods during the fall when favored zooplankters were in short supply. But unlike late spring and summer, when many different plant forms were taken, virtually the only plant materials consumed in the fall were the sori of *N. leutkeana*. This reflected a decreasing abundance of other plants in the environment at the time. Nevertheless, while sporophytes of *N. leutkeana* were fewer in fall than in summer, those present were larger, more mature, and produced more sori.

Although winter produced the poorest feeding conditions of the year, with by far the highest incidence of empty stomachs among the fish examined (Figure 13; also noted by Gotshall et al. 1965), occasionally the waters flowing into the nearshore habitats were rich in offshore zooplankters, including thaliaceans, and at these times the fish fed well. Our sampling of the highly varied winter conditions was not frequent enough to recognize a pattern, but they differed from fall conditions. In general, the distinctive fall and winter conditions off Mendocino matched the "oceanic" and "Davidson Current" oceanographic seasons defined by Skogsberg (1936) and Bolin and Abbott (1962) for Monterey Bay.

Ekman Transport and the Distribution of *Sebastes mystinus*

Ekman transport may be important to the distribution of *S. mystinus*. This is implicit in our finding that alternations between seaward and shoreward surface transport produce feeding opportunities for

[2]David C. Walker, Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 1W5, Canada, pers. commun. 10 May 1977.

which the species is particularly well adapted. Along the west coast of North America, these alternations are best developed off northern and central California (Bakun 1973; Bakun et al. 1974; Mason and Bakun 1985). And not only is *S. mystinus* most numerous off this same section of the coast, it is perhaps the dominant fish in the nearshore habitat there (Hallacher and Roberts 1985; Bodkin 1984; our observations). Although the species is reported from northern Baja California, Mexico, to the Bering Sea (Miller and Lea 1972), its numbers are sharply reduced northward from northern California (Alverson et al. 1964; Frey 1971; Hart 1973) and southward from central California (Hubbs 1948; Limbaugh 1955; Quast 1968). Although undoubtedly other factors are involved, we suggest that occurrences of *S. mystinus* in these northern and southern regions are limited by less favorable feeding conditions.

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