Abstract—There is much interannual variation in numbers of first-year *Sebastes* that settle near shore off northern California, and when more abundant, they become prey of an increased variety of predators. Among predators that concentrate on these abundances are the black rockfish (*Sebastes melanops*); the blue rockfish (*Sebastes mystinus*); and the kelp greenling (*Hexagrammos decagrammus*). One might expect *S. melanops* to be involved in these attacks because it is known to be piscivorous, but *S. mystinus* and *H. decagrammus* ordinarily feed on invertebrates. The predation on *Sebastes* juveniles is concentrated during a relatively brief period shortly after they have settled in nearshore habitats. Most of this predation occurs during June and decreases sharply through July and August, and relatively little after that. We argue that the pattern of predation reflects removal of less adapted individuals during the period shortly after settlement.

Manuscript accepted 3 November 2000.
Fish. Bull. 99:292–302 (2001).

Interannual variation in predation on first-year *Sebastes* spp. by three northern California predators

Edmund S. Hobson
Santa Cruz Laboratory
Southwest Fisheries Science Center
110 Shaffer Road
Santa Cruz, California 95060
E-mail address: ted.hobson@noaa.gov

James R. Chess
P. O. Box 96
Piercy, California 95587

Daniel F. Howard
Gulf of the Farallones National Marine Sanctuary
Fort Mason, Bldg. 201
San Francisco, California 94123

First-year *Sebastes* spp. off California vary greatly in number from year to year (Stephens et al., 1984; Love, et al., 1991), as do young-of-the-year of many marine fishes (Hjort, 1926; Cushing, 1973; Ricker, 1954). It has been argued that this variability between years is set during the earliest stages of life history, so that numbers present at settlement can be used to predict ultimate strength (or weakness) of year classes (Bailey and Spring, 1992; Myers and Cadigan, 1993; Ralston and Howard, 1995). But such predictions may need to consider postsettlement mortality, which has been recognized as a density-dependent force that reduces the interannual variation in year-class size evident at settlement (e.g. Sissenwine, 1984).

Early evidence that young-of-the-year (YOY) suffer density-dependent mortality after settlement came from studies of fishes caught by trawlers in temperate seas. Some of these studies identified predation as the main cause of this mortality (e.g. Lockwood, 1980), but most recognized predation as just one of several possibilities (Veer, 1986; Myers and Cadigan, 1993). More recently, investigators using scuba to observe underwater have studied postsettlement juvenile mortality in a variety of tropical and temperate species. Although some have concluded that this mortality is not density dependent (e.g. Victor, 1986; Sale and Ferrell, 1988), others have concluded not only that it is density dependent but also that it acts to regulate populations (Sano, 1997) and is a result of predation (Hixon and Carr, 1997; Steele, 1997). That predation is the major cause of mortality during and after settlement now seems generally accepted, and attempts are being made to identify the mechanisms involved under controlled conditions in laboratories (e.g. Bertram and Leggett, 1994; Witting and Able, 1995).

Although there have been many studies of the relations between predation and recruitment, all have been of short duration and thus limited as examinations of interannual variations. An opportunity to draw on 11 years of data for such a study developed from our work with marine communities off northern California. There, an investigation of trophic relations in fishes overlapped annual assessments of YOY *Sebastes* spp., and during this period (1977 to 1987) certain predators attacked the recently settled *Sebastes* only during years when these were more numerous.

Among predators drawn to YOY abundances were three of the region's most prominent species: the black rockfish (*Sebastes melanops*), the blue rockfish (*Sebastes mystinus*), and the kelp greenling (*Hexagrammos decagrammus*) (Fig. 1). The attacks by *S. melanops* might have been expected because this predator is known to prey regularly on a variety of fishes (Moulton, 1977; Rosenthal et al., 1988), but *S. mystinus* ordinarily feeds mainly on pelagic invertebrates (Gotshall et al., 1965; Hobson and Chess, 1988), and *H. decagrammus,* a benthivore with more varied food habits, feeds mainly on crustacea (particularly crabs), polychaetes, and mollusks (Moulton, 1977; Simenstead et al[1]).

Our objective was to determine when these varied predators attack YOY *Sebastes* spp., how this predation relates to changes in YOY abundance, and to identify implications for management.

Materials and methods

All of our studies on California's north coast involved using scuba to investigate organisms in their natural settings. Under these circumstances, we routinely noted events like settlement of juvenile *Sebastes* even when our attention was directed elsewhere. This feature of our work was important in enabling us to integrate elements of disparate studies in preparing this report.

Study area

The area of study was in 5–15 m of water within 300 m of shore, about 2 km north and south of Albion, in Mendocino County (lat. 39°13′N; long. 123°14′W). Because this coast is fully exposed to north Pacific seas, strong surge and turbulence prevailed most of the time. The ocean floor there consists mainly of irregular rock pavement and boulders (some 5–15 m in diameter) and isolated patches of sand.

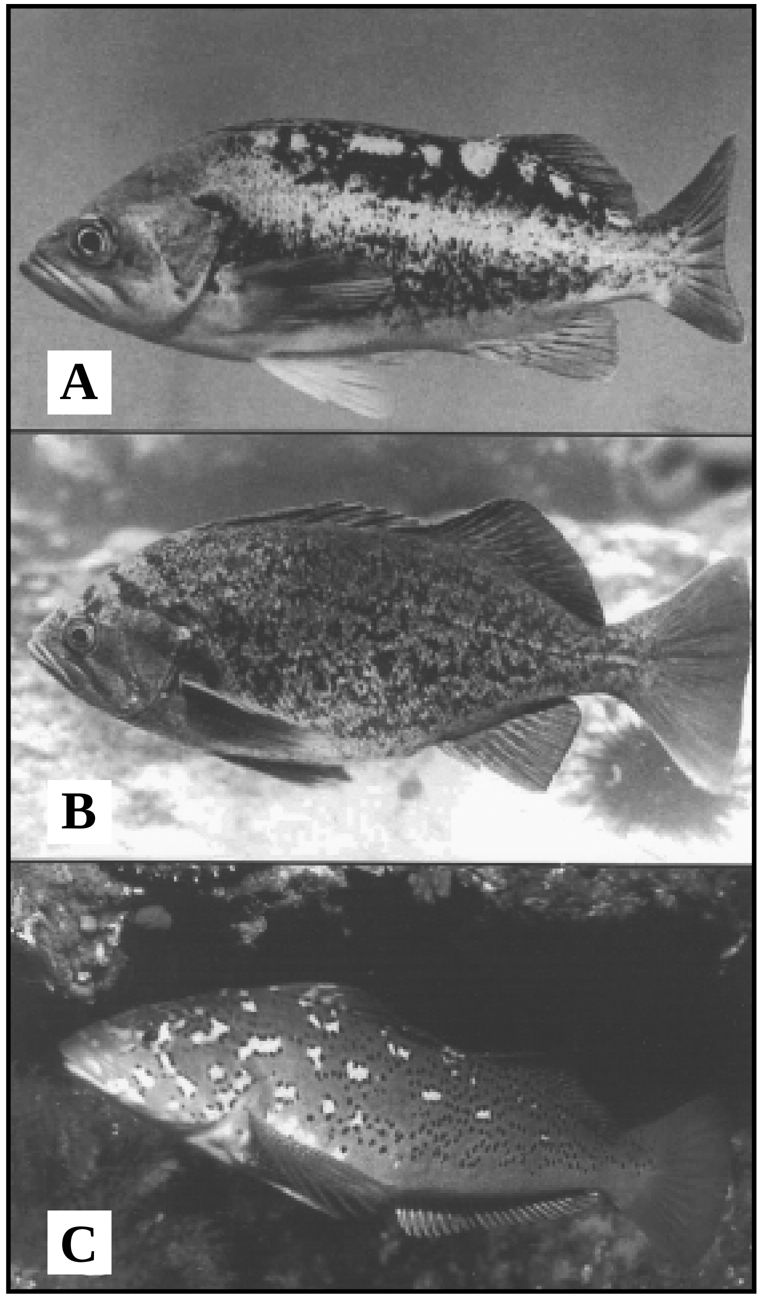

Figure 1

(**A**) Black rockfish, *Sebastes melanops.* (**B**) Blue rockfish, *Sebastes mystinus.* (**C**) Kelp greenling, *Hexagrammos decagrammus.* The black rockfish, with a larger mouth and a body form more conducive to speed, is morphologically better adapted than the other two species for running down and capturing elusive prey above the sea bed. The more oval shape of the blue rockfish suggests less need for speed in capturing its regular prey, whereas its smaller mouth and shorter snout (which increases an ability to simultaneously train both eyes on small targets close ahead) are more typical of planktivores than piscivores. Both rockfishes have a lower jaw that extends beyond the upper, which is consistent with attacking prey that are above the seabed, whereas the kelp greenling has an upper jaw that extends beyond the lower, for attacking prey that are on the seabed. Also, the kelp greenling's elongate body functions better swimming among, rather than above, the rocks.

[1] Simenstead, C. A., B. S. Miller, C. F. Nyblade, K. Thornburg, and L. J. Bledsoe. 1980. Food web relationships of northern Puget Sound and Straight of Juan De Fuca. Report to Marine Ecosystem Analysis (MESA), Puget Sound Project. U.S. Environmental Protection Agency, Washington, D.C. 20460, 335 p.

There are substantial seasonal changes in the habitat, particularly those associated with variable coastal upwelling (Bakun, 1973; Hobson and Chess, 1988). From late spring through fall, beds of bull kelp, *Nereocystis leutkeana*, form canopies at the sea's surface in many places, but most are swept away by storm seas during the subsequent winter. We began our study there in 1975, and the area, along with its flora and fauna, had become familiar to us by the time data presented in this report had been collected.

Measures of juvenile abundance

We had noted interannual variation in numbers of first-year *Sebastes* spp. as an incidental adjunct to more than 15 years of study in California's nearshore habitats, but were prompted to begin annual assessments of their abundance only after exceptionally large numbers settled along the north coast during 1977. At the outset, time available for this work was limited by other projects; therefore through 1982 our effort was directed mainly at developing means for identifying species. Features now used to distinguish *Sebastes* juveniles were at that time largely unknown, and of the three dominant forms settling in Mendocino habitats, only *S. mystinus* could be recognized at the outset. The other two juveniles—*S. flavidus* and *S. melanops*—remained indistinguishable until diagnostic features were determined by Laroche and Richardson (1980).

Despite the uncertain identities involved, one of us (ESH) estimated the relative abundance of YOY *Sebastes* present each year from 1978 to 1982 as a percentage of large total abundance in 1977. These estimates were made during the course of other projects and without consideration of publication, but nevertheless were recorded in field notes. Each annual estimate during these years represented a consensus based on repeated assessments (about weekly) between June and October, and although they lacked precision, they represented the only measures of YOY abundance for years that produced much of the data on predation. Some readers will dismiss these estimates as overly subjective, but others will appreciate the opportunity of considering all available evidence.

The annual assessments of YOY abundance became a major activity in 1983. By then, virtually all YOY *Sebastes* spp. seen underwater at the study sites could be identified, and we had developed standard procedures to assess their abundance. From that year on, YOY were counted during midday (1000 to 1400 h) at four sites within the study area. We attempted to make counts at least once each week but found that our ability to do so was determined largely by weather conditions The first counts each year were made shortly after the initial settlement of YOY, which occurred some time during late spring or early summer. The counts then continued through October, when it became evident that YOY of one major species—*S. flavidus*—were leaving the area.

During each assessment one to three of us swam at constant speeds close to the seabed, making frequent changes in direction. We counted the YOY *Sebastes* within 3 m of varied tract lines that traversed all major habitats represented at the sites. Because the highly variable turbidity and turbulence characteristic of this area strongly influenced our ability to see the fish, counts were made only when horizontal visibility exceeded 4 m and turbulence was not excessive. This limitation precluded a fixed schedule because counts were aborted more often than completed.

Assessments were made at widespread sites along the coast of northern California, from Mendocino southward to Marin; however, only data from Mendocino were used in this report because that is where the predators were sampled. Similarly, although juveniles counted in the environment were identified to species, our report refers to all as *Sebastes* spp. because they were compared with juveniles recovered from gut contents, which too often were damaged beyond recognition as species.

The study of trophic relations in *S. mystinus* included YOY, and although food habits of these lack relevance here, sizes of individuals sampled from June through October provide a measure of sizes available to predators during the first five months after settlement. This information has broad implications, because growth in *S. mystinus* is similar to growth in the vast majority of *Sebastes* YOY that settle in this habitat (except *S. paucispinnus*, which was not included).

Food habits of predators

The predators were sampled with scuba and hand-held spears throughout the 11 years of overlap between the two investigations. Only specimens with identifiable gut contents were used in this report. They were collected during midday (1000 and 1400 h), and all months were represented (Fig. 2). Specimens representing each species ranged upward in size from the smallest found with a YOY *Sebastes* among its gut contents. This eliminated from consideration the many specimens that were too small to include YOY among their prey. Each specimen was observed in its natural setting before capture, and many were collected as part of comprehensive assessments of the biota. Both of these circumstances contributed to interpretations of the gut contents.

Following capture, specimens were measured (standard length), and their digestive tracts were removed and preserved in 10% formalin. During later examination in the laboratory, the gut contents were removed and studied under magnification. Food items were identified to species when feasible, and the record of each prey taxon included number, size, stage of digestion, and percent contributed to the total diet. Much of this information is of limited interest here, but the last variable listed (labeled "percentage of diet" in the figures) was used to show the relative importance of each prey category as food. This measure was obtained by grouping elements of the various prey categories as they lay spread out in a petri dish, and then visually estimating the percentage that each category represented of the entire sample. Generally, values presented are means calculated from individual diets in specified groups of predators.

Juveniles of the highly distinctive *Sebastes jordani* were exceptions to the generalization that YOY *Sebastes* recov-

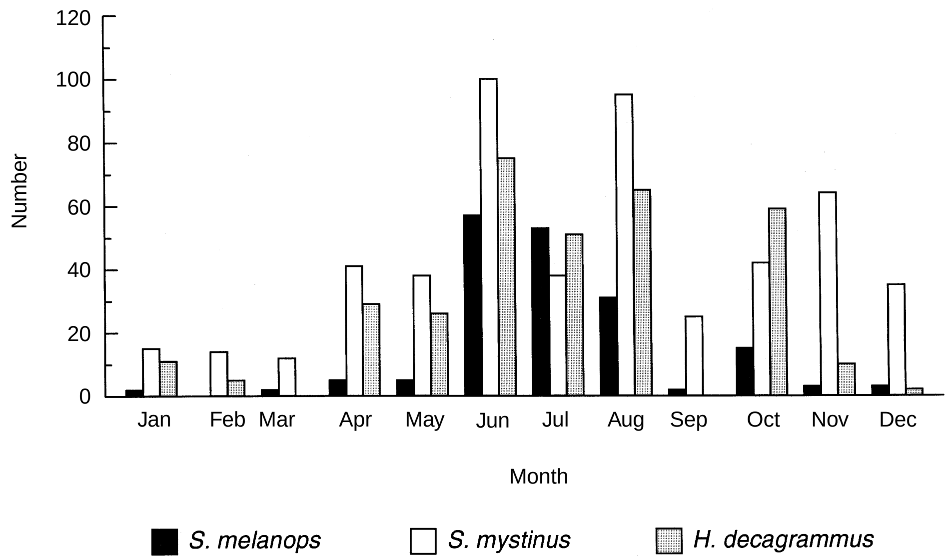

Figure 2

Monthly sampling of predators used in study of predation on YOY *Sebastes* spp. near shore off Mendocino.

ered from gut contents often had been damaged beyond recognition as species. Owing to their distinctive morphology, *S. jordani* juveniles were identifiable even when extensively damaged, but they are excluded from our report because they were in the study area for reasons other than those accounting for the presence of the other *Sebastes* species (Hobson and Howard, 1989).

Results

YOY *Sebastes*

The number of YOY *Sebastes* varied greatly from year to year (Fig. 3). Their initial appearance near shore tended to be earlier in the season during years of greater abundance; thus the earliest first sighting was during April of the year that YOY were most numerous (1987), and the latest first sighting was during June of the year that YOY were least numerous (1983). Upon arrival, these fish were <4.0 cm SL, often numerous, and still showed the silvery hues characteristic of their pelagic stage. Our record of first arrivals was limited. Ordinarily, visits to the Mendocino study sites at this time of year were separated by at least a week, sometimes up to a month (during extended periods of inclement weather), and our efforts were concentrated close to the seabed. Observations in the surface canopy of bull kelp came mostly during brief surveys following more extensive observations at greater depths. Once alerted to their presence, however, we intensified our search (even during the same day) and often found a few individuals or small groups among the rocks below. Most of these were 4.0 to 4.5 cm SL and showed darker hues more appropriate to reef settings.

Numbers of juveniles increased rapidly over the weeks that followed (except during years of low abundance, e.g. 1983) to reach maximum levels between mid June and early July. Throughout this time, and over subsequent months, the juveniles aggregated at varying distances from the seabed or kelp—some in mixed species aggregations. Their distance from these structures was influenced by the water's transparency, however, and this affected our ability to measure abundance. When visibility was reduced, as during phytoplankton blooms of late spring and early summer, the juveniles stayed closer to shelter—many often out of sight among the rocks. It was often difficult to assess their abundance under these conditions, even when visibility was sufficient to perform the counts. In contrast, when visibility was extended, as when oceanic waters flowed shoreward with relaxation of upwelling during the fall, the juveniles ranged farther from shelter and were readily counted. Thus, although the greatest numbers were recorded during a period of exceptionally clear water during July 1987, counts were at times higher during September or October than during June or July (Table 1), even though we assumed that there were fewer individuals present. This circumstance did not affect interannual comparisons because the pattern was basically the same each year, but it effectively precluded comparisons between months or seasons.

Sizes of YOY available to predators during the five months after settlement can be approximated from data of the YOY *S. mystinus* sampled from June through October for study of gut contents. The 82 from June were 3.7 to 5.8

Table 1

Number of YOY *Sebastes* counted during months after settlement (n=number of 1-min counts).

Year	May			June			July			August			September			October		
	date	*n*	no./min.	date	*n*	no./min.	date	*n*	no./min.	date	*n*	no./min.	date	*n*	no./min.	date	*n*	no./min.
1983		—			—		7 Jul	150	1.1		—		6 Sept	85	3.8		—	
1984		—		5 Jun	50	1.3		—		8 Aug	214	5.8		—			—	
										23 Aug	100	15.9						
1985	31 May	25	89.5	19 Jun	52	424.6	9 Jul	59	304.2	30 Aug	50	192.6		—			—	
							23 Jul	18	74.8									
1986		—		4 Jun	59	8.2	8 Jul	51	3.8	7 Aug	49	32.6	29 Sep	29	46.4	23 Oct	29	30.4
				24 Jun	37	47.9				26 Aug	53	16.4						
1987		—		30 Jun	32	81.2	14 Jul	42	220.9	12 Aug	32	210.8	1 Sep	51	606.7	19 Oct	10	133.2
							21 Jul	10	93.9	20 Aug	15	118.9	22 Oct	10	235.0			
							22 Jul	18	517.6									

cm, $\bar{x}$=5.2 cm SL; the 42 from July were 4.5 to 6.3 cm, $\bar{x}$= 5.4 cm SL; the 73 from August were 4.9 to 6.7 cm, $\bar{x}$= 5.6 cm SL; the 28 from September were 4.6 to 7.1 cm, $\bar{x}$= 6.2 cm SL; and the 46 from October were 5.8 to 8.0 cm, $\bar{x}$= 7.0 cm SL. Inferences based on these data can be extended to YOY of most *Sebastes* spp. in this setting because they grow at rates similar to *S. mystinus*. Another source for sizes of YOY *Sebastes* came from predator gut contents. There, individuals as small as 4.0 cm SL continued to be present throughout the three months of intensive predation, whereas individuals smaller than this were present only through June (Table 2).

It was evident that the YOY *Sebastes* remained where they had settled for at least five months. Over 90% of those counted at all sites from Mendocino to Marin were either *Sebastes mystinus* or *S. flavidus*. (The third species alluded to above, *S. melanops*, dominated shoreward of the census area and followed the same pattern of annual abundance.) Fidelity to specific locations was noted through the end of October, when representatives of *S. flavidus* left the area, presumably for deeper water.

Although this chronicle of YOY occurrence ends each year with counts made through October, during some years assessments continued through the winter and following spring. Results of these extended counts confirmed findings of others that juveniles of these species remain where they settle for at least a year (Love et al., 1991). That YOY *S. flavidus* left our study area for deeper water about five months after settlement may be related to Mendocino being toward the southern limit of its distribution. To the north, in Puget Sound (Moulton, 1977) and southeastern Alaska (Carlson and Barr, 1977), schools of juvenile *S. flavidus* have been observed at the same shallow sites for one to several years.

Predators and general features of predation

When diets of the predators during all months of all years are combined, the results (Fig. 4) generally are consistent with diets attributed to them in previous reports (e.g. Gotshall, et al., 1965; Rosenthal et al., 1988; Simenstad et al.[1]), except that *S. melanops* appeared even more piscivorous than the other *Sebastes* species. The extent that *S. melanops* was found to consume fishes, however, can be attributed to 79% of the specimens examined having been collected from June through August (compared with 45% of *S. mystinus* and 57% of *H. decagrammus*). In fact, all three species consumed more fishes during the summer than during other seasons, and most of the increase came from eating YOY *Sebastes* (Fig. 5). It is significant that all but 6 of 537 YOY *Sebastes* recovered from gut contents of the three predator species came from specimens collected during these three months. Most were consumed during June, and sharply decreasing numbers were taken through July and August (Table 3).

Interannual variation in predation on YOY *Sebastes*

There was much interannual variation in predation on YOY *Sebastes*, and it can be related to interannual varia-

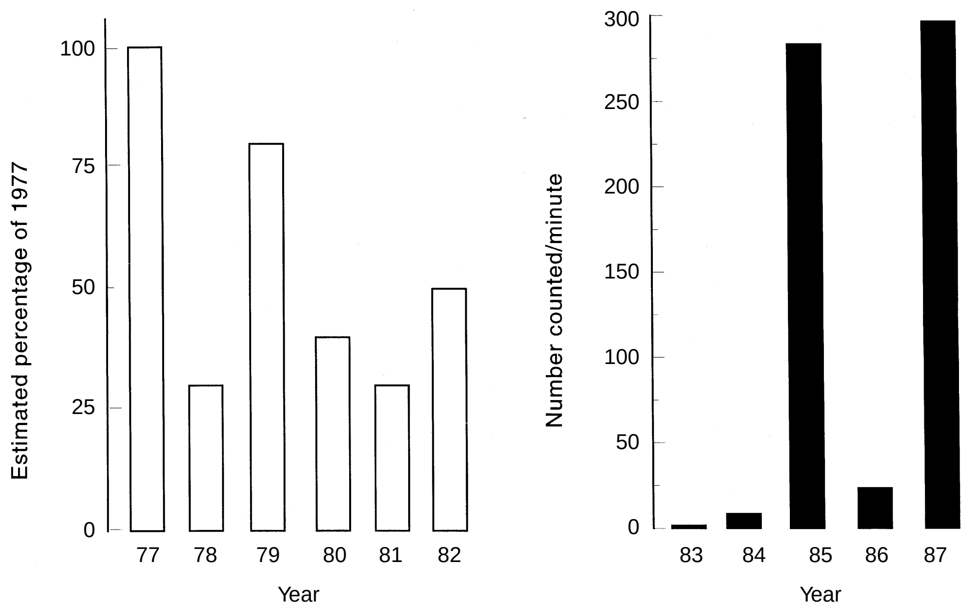

Figure 3

Annual measures of YOY *Sebastes* spp. near shore off Mendocino, 1977 to 1987. Measures representing 1977 to 1982 represent estimated proportions of the abundance observed during 1977. Measures representing 1983 to 1987 represent visual counts in the environment. The two panels, estimates and counts, are equated in the same way that the estimates of 1978–82 are related to those of 1977, i.e. by extracting from the 1985 field notes a consensus that abundance that year was approximately that of 1977. Each annual measure is the average of all individual samples from that year.

Table 2

Standard length (SL, in cm) of YOY *Sebastes* spp. recovered from gut contents (*n*=number for which size was recorded[1]).

	June		July		August	
Sebastes species	*n*	SL range	*n*	SL range	*n*	SL range
S. melanops	93	3.0–5.5	29	4.0–6.4	24[2]	4.0–8.0
S. mystinus	18	3.5–5.5	4	4.0–5.4	0	0–0
H. decagrammus	45	2.9–5.5	11	4.0–5.5	3	4.4–5.0

[1] Not all YOY recovered from gut-contents were measured. When samples included >2 individuals of one species, or indistinguishable as species, only the largest and smallest were measured. These samples were analyzed to characterize food habits and the intent of the analysis was simply to determine range of sizes consumed. Also, records of *S. paucispinus* are excluded because this species grows much faster than the others, and several individuals of the subject species were excluded because it was evident they were in their second year.

[2] Two distinct groups are included here (t=9.129, 4 df, P<0.001). Nineteen ranged from 4.0 to 6.0 cm SL, whereas the other five ranged from 7.0 to 8.0 cm SL.

Table 3

Number of YOY *Sebastes* spp. consumed by each of the three predator species during June, July, August, and during all other months, 1977–87 (values in parentheses=number predators examined that had gut contents).

Sebastes species	June	July	August	All other
S. melanops	313 (57)	44 (53)	40 (31)	1 (37)
S. mystinus	32 (100)	5 (37)	0 (95)	1 (286)
H. decagrammus	81 (75)	12 (51)	4 (65)	4 (142)

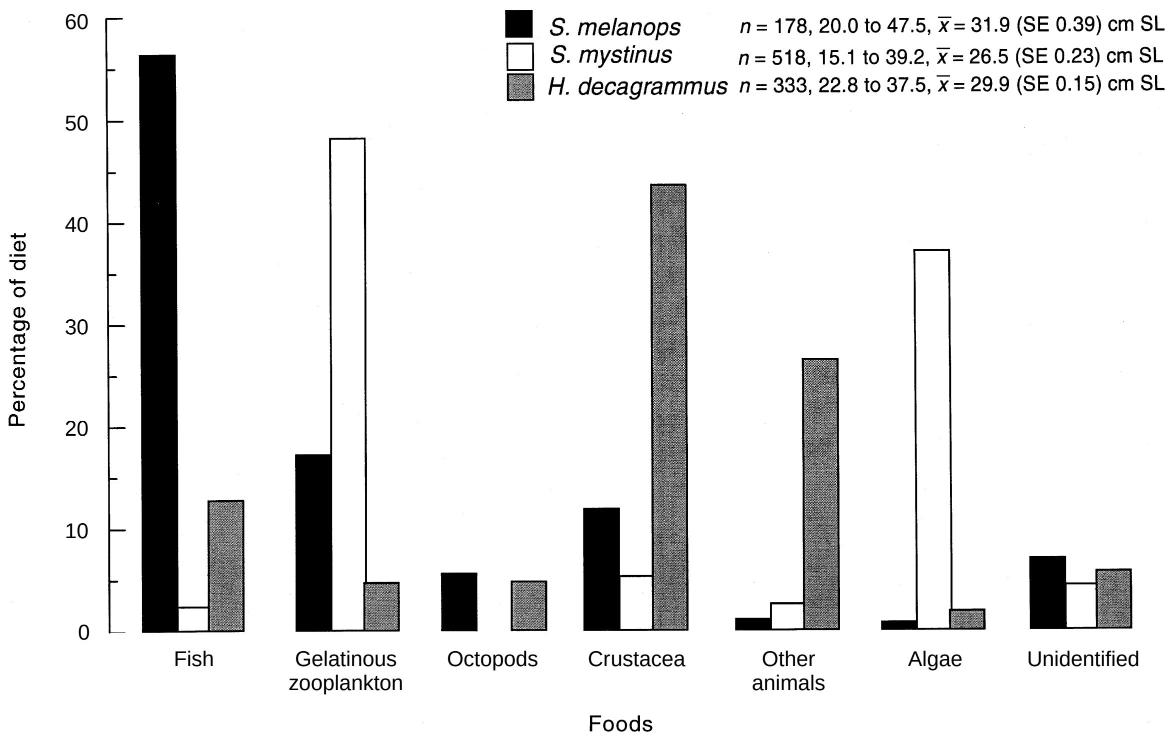

Figure 4

Foods consumed by the three predator species (*Sebastes melanops, S. mystinus,* and *S. decagrammus*) 1977–87 (*n*= individuals with identifiable food in gut).

tion in YOY abundance (Fig. 6). Evidence of predation was strongest during years when YOY were most numerous in the habitat (1977, 1979, 1985, and 1987), and there was virtually no evidence of predation during the years when YOY were least numerous in the habitat (1983, 1984, and 1986). Furthermore, it was only during the years that YOY were more numerous that we found them among the prey of *S. mystinus*—1985 being the year we found the most.

We saw no indication that distributions of adult *S. melanops, S. mystinus,* or *H. decagrammus* were influenced by the presence of YOY *Sebastes.* Even when YOY were most numerous, attackers seemed limited to residents of the immediate area. This finding should have been expected because each year's relative abundance was in effect coast wide.

Discussion

Much predation is opportunistic; thus predators often are drawn to concentrations of organisms that would not otherwise be their prey. Consider, for example, that when the squid *Loligo opalescens* deposits great masses of eggs on sediment off central California, various fishes, marine mammals, and birds converge from surrounding habitats to forage on what is for them an unusual food (Morejohn et al., 1978). Similarly, when the herring *Clupea pallasi* deposits eggs in great abundance on the seabed in San Francisco Bay, these become food for the brown rockfish, *Sebastes auriculatus,* which otherwise feeds mainly on decapod crustacea and fishes (Ryan, 1986). Another example is an incident during 1962 in the Gulf of California, where a 1-m moray eel (Muraenidae) was observed thrashing at the water's surface in a vigorous attempt to feed from a dense swarm of larval fishes, each no more than 1 cm long (Hobson, 1968). Certainly this predator was behaving in a manner that was contrary to its usual mode of feeding. So perhaps it should have been expected that YOY *Sebastes* in exceptionally large numbers would draw attacks from predators not otherwise prone to show them interest.

But the level of predation on YOY *Sebastes* off Mendocino involved more than relative abundance of prey. The attacks were concentrated during June, declined sharply through July and August, then remained at low levels during the rest of the year. This pattern did not follow the number of YOY present. These YOY gained abundance through most of June to attain maximum numbers late that month or during July, and then remained abundant after predation had subsided to low levels at the end of August. Often our counts of YOY were higher during September or October than during June or July, and although to a considerable extent this higher court was related to increased visibility in clear water, it nevertheless argues

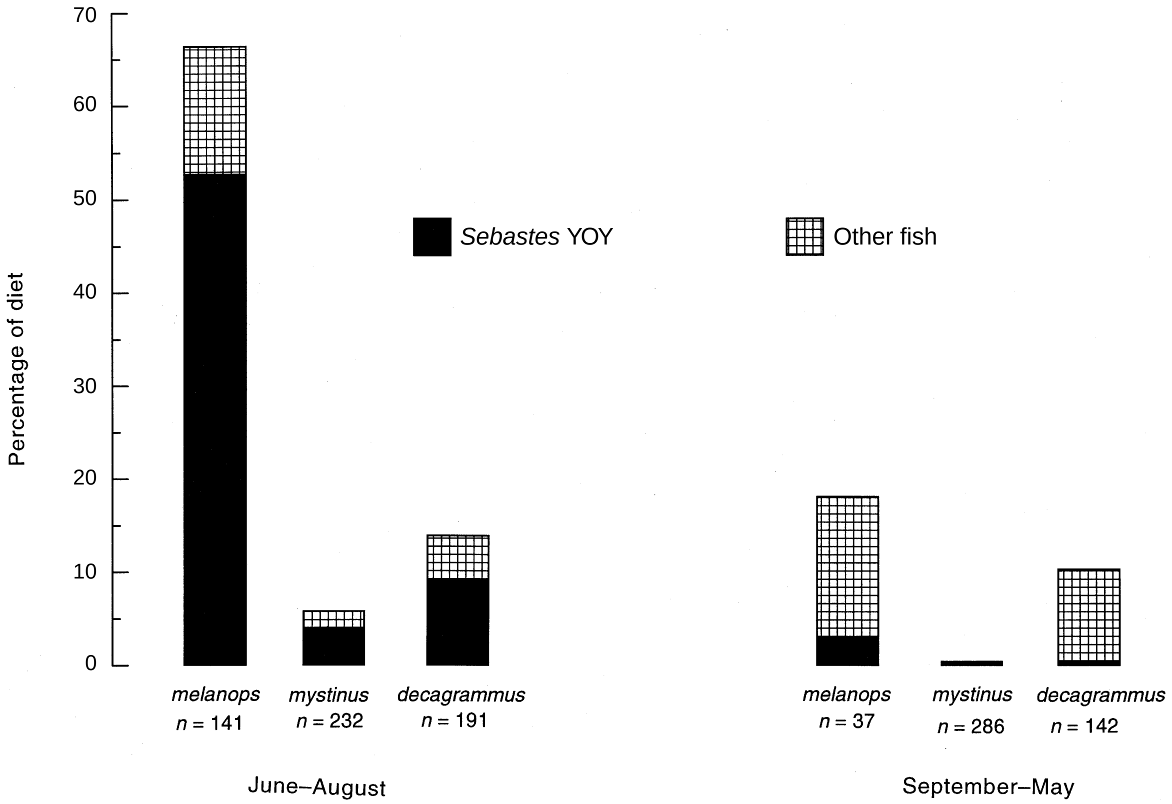

Figure 5

Fish in diet of the three predators (*Sebastes melanops, S. mystinus*, and *S. decagrammus*) June through August compared with September through May. YOY *Sebastes* spp. are distinguished from other fish. n=individuals with identifiable food in gut.

against attributing the precipitous decline in predation through late August simply to shortages of prey.

It has been widely reported that mortality among YOY of a variety of fishes is greatest during and immediately after settlement (e.g. Doherty and Sale, 1985; Victor, 1986; Shulman and Ogden, 1987), but there has been virtually no attempt to explain this finding, other than to implicate predation. We propose that the intense predation of early summer, and its subsequent sharp decline, mirrored a pattern of vulnerability among the YOY. Abilities critical for survival are quickness in responding to attacks, speed in attaining shelter, and the ability to use shelter that is available. And increasingly important with time is the ability to acclimate to novel situations—the capacity to learn. These abilities are based on inherent characteristics that can be expected to vary widely among individuals, with the more deficient being more vulnerable to predators. It follows that individuals most deficient are likely to be among those consumed during or shortly after settlement, whereas individuals progressively less deficient would be consumed in diminishing numbers over the following months.

Certainly other factors contributed to the decline in predation during the summer. That YOY decreased in number and increased in size must have influenced the intensity of predation. There is evidence that by summer's end most YOY had grown too large for predation by *S. mystinus* and *H. decagrammus*. The largest YOY *Sebastes* among the gut contents of either species were 5.5 cm SL (Table 2), and by September most in the environment were larger than this (based on growth evident in the representative *S. mystinus* sampled for study of food habits).

Other considerations, however, argue against the importance of prey-size in shaping the observed pattern of predation. *Sebastes melanops*, which is morphologically better suited than either *S. mystinus* or *H. decagrammus* to prey on fishes (Fig. 1), was able to feed on YOY *Sebastes* of up to at least 8.0 cm SL (Table 2), yet ate very few of them after August. Also, the great variation in size among predators, as well as in growth among YOY would be expected to dampen the effects of prey-size on population-level feeding intensity. Another consideration is the continued presence of YOY as small as 4.0 cm SL (Table 2) during the late-summer switch to other prey.

Although probably a combination of factors contributed to the decline in predation during the summer, we continue to consider that the concentrated attacks immediately after settlement are mostly likely elicited by the presence of inherently less-adaptive individuals. This is classic nat-

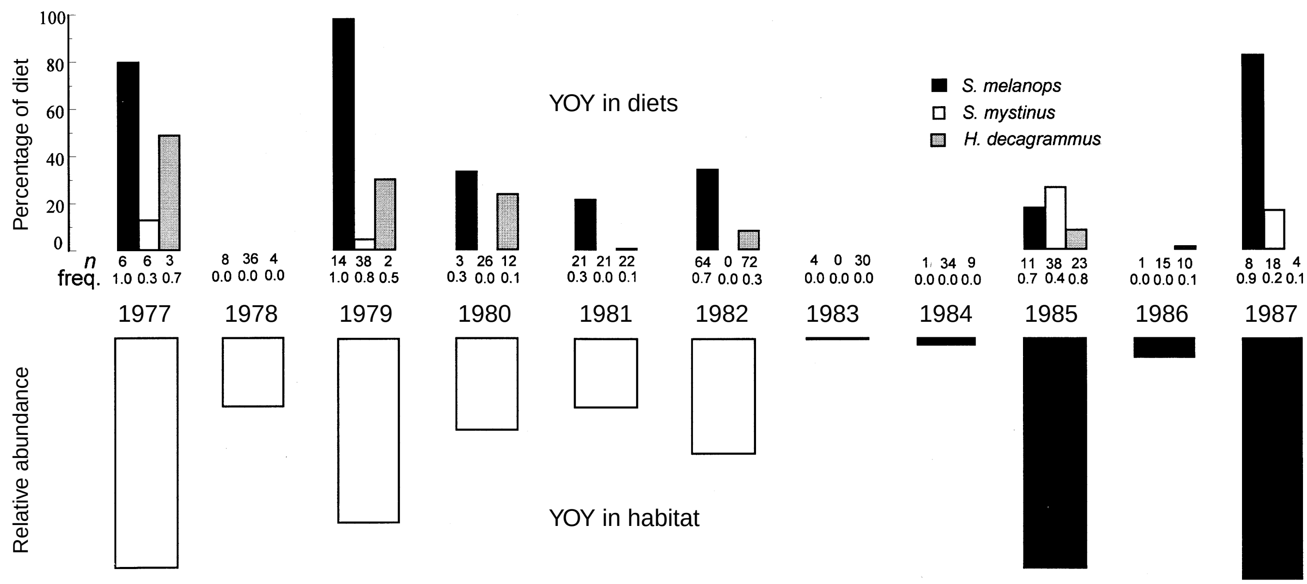

Figure 6

Inter-annual variation in occurrence of YOY *Sebastes* spp. in predator diets in relation to abundance of YOY in the habitats, June through August. Measures of YOY abundance in habitat are based on information presented in Figure 3. *n* = Individuals examined that had identifiable food in gut.

ural selection. That predators studied in our study had essentially resumed their regular diets by the end of summer indicated to us that YOY vulnerable to their attacks had by that time become scarce.

There are other predators that follow similar temporal patterns in feeding on YOY *Sebastes* off northern California. Pacific hake, *Merluccius productus*, for example, have been reported attacking YOY *S. jordani* so close to shore that many are driven onto the beach—but only during June and early July of years when these prey were particularly abundant (Hobson and Howard, 1989). Similarly, king salmon, *Oncorhynchus tshawytscha*, regularly switch to YOY *Sebastes* from other prey during late May and June, then switch back before the end of July (Adams et al.[2]). Other examples include *Sebastes* spp. studied by Hallacher and Roberts (1985) in kelp forests off Carmel, CA. In a chronicle that followed activities of these fishes over one year (with limited data from July and August of two other years), it was determined that *S. atrovirens, S. carnatus, S. chrysomelas,* and *S. melanops* fed primarily on YOY *Sebastes* during the "upwelling season" (April to August), but all except *S. carnatus* switched to invertebrates during the "non-upwelling season" (September to March). Hallacher and Roberts attributed this pattern to seasonal differences in YOY abundance.

The decline in attacks during the summer does not lead to essentially an end to predation on YOY, however. At least one resident piscivore, the ling cod, *Ophiodon elongatus*, remains a regular threat (Miller and Geibel, 1973). In fact, Adams and Howard (1996), studying in part the same series of assessments used in our study, considered predation the major cause of natural mortality in YOY *S. mystinus* from late summer through early spring. Their estimates were higher during years that YOY were more abundant, indicating persistent density-dependent predation, but were much lower than most other published rates of natural mortality for juvenile fishes, probably because they missed the intense predation of late spring and early summer. And although Hallacher and Roberts (1985) reported that most *Sebastes* spp. off Carmel switched to predation on invertebrates from September to March, they noted that *S. carnatus* continued to prey on YOY *Sebastes* during that period.

There is evidence that density-related predation continues to dampen interannual variation in year-class size through entry into the fishery, which for most *Sebastes* spp. is at about age 3–4 years (Ralston and Howard, 1995). Arguments for the importance of postsettlement mortality in establishing ultimate year-class size have emphasized the extended effect of this mortality (e.g. Sissenwine, 1984) but do not recognize the extent that mortality from predation is concentrated during a relatively brief period immediately after settlement. We suggest that management needs would be most effectively met by measuring year-class size soon after this period of intense predation.

---

2 Adams, P. B., W. M. Samiere, and C. J. Ryan. 1986. Unpubl. manuscript. Prey selection and diet of marine chinook salmon, *Oncorhynchus tshawytscha*, 17 p. Natl. Mar. Fish. Ser., NOAA, Tiburon CA 94920.

Although a measure based on recruits entering the fishery would more accurately define the resource, there have been no effective methods developed to determine abundance at that point. And even if available, the lateness of such a measure would limit its effectiveness. An assessment made at the end of the first summer based on direct visual counts by underwater observers, as described above, is an effective compromise. The YOY are readily counted, much of the postsettlement mortality is included, and there is time to use the results in planning management strategy.

Acknowledgments

We thank Mickey Eldridge and Bruce McFarlane for constructive criticism of the manuscript.

Literature cited

Adams, P. B., and D. F. Howard.
1996. Natural mortality of blue rockfish, *Sebastes mystinus*, during their first year in nearshore benthic habitats. Fish. Bull. 94:156–162.

Bakun, A.
1973. Coastal upwelling indices, west coast od North America, 1946–71. U. S. Dep. Commer., NOAA Tech Rep. NMFS SSRF-671, 103 p.

Bailey, K. M., and S. M. Spring.
1992. Comparison of larval, age-0 juvenile and age-2 recruit abundance indices of walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska. ICES J. Mar. Sci. 49:297–304.

Bertram, D. F., and W. C. Leggett.
1994. Predation risk during the early life history periods of fishes: separating the effects of size and age. Mar. Ecol. Prog. Ser. 109:105–114.

Carlson, H. R., and L. Barr.
1977. Seasonal changes in spatial distribution and activity of two species of Pacific rockfishes, *Sebastes flavidus* and *S. ciliatus*, in Lynn Canal, southeastern Alaska. Mar. Fish. Rev. 39:23–24.

Cushing, D. H.
1973. Recruitment and parent stock in fishes. Univ. Washington, Seattle, WA, 197 p.

Doherty, P. J., and P. F. Sale.
1985. Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs 4:225–234.

Gotshall, D. W., J. G. Smith, and A. Holbert.
1965. Food of the blue rockfish, *Sebastodes mystinus*. Calif. Fish Game 51:147–162.

Hallacher, L. E., and D. A. Roberts.
1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California. Environ. Biol. Fish. 12:91–110.

Hixon, M. A., and M. H. Carr.
1997. Synergistic predation, density dependence, and population regulation in marine fish. Science (Wash. D.C.) 277: 946–949.

Hjort, J.
1926. Fluctuations in the year classes of important food fishes. J. Cons. Int. Explor. Mer 1:5–38.

Hobson, E. S.
1968. Predatory behavior of some shore fishes in the Gulf of California. U. S. Fish Wildl. Serv. Res. Rep. 73, 92 p.

Hobson, E. S., and J. R. Chess.
1988. Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California. Fish. Bull. 86:715–743.

Hobson, E. S., and D. F. Howard.
1989. Mass stranding of juvenile shortbelly rockfish and Pacific hake along the coast of northern California. Calif. Fish Game 75:169–183.

Laroche, W. A., and S. J. Richardson.
1980. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. Fish. Bull. 77:901–923.

Lockwood, S. J.
1980. Density-dependent mortality in 0-group plaice (*Pleuronectes platessa* L.) populations. J. Cons. Int. Explor. Mer 39: 148–153.

Love, M. S., M. H. Carr, and L. J. Haldorson.
1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. Environ. Biol. Fish. 30:225–243.

Miller, D. J. and J. J. Geibel.
1973. Summary of blue rockfish and lingcod life histories: a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

Moorejohn, G. V., J. T. Harvey, and L. T. Krasnow.
1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. *In* Biological, oceanographic and acoustic aspects of the market squid, *Loligo opalescens* Berry (C. W. Recksiek and H. W. Frey, eds.), p. 67–98. Calif. Dep. Fish Game Fish Bull. 169.

Moulton, L. L.
1977. An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. Ph.D. diss., Univ.Washington, Seattle. WA, 181 p.

Myers, R. A., and N. G. Cadigan.
1993. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. 50:1576–1587.

Ralston. S., and D. F. Howard.
1995. On the development of year-class variability in two northern California rockfishes. Fish. Bull. 93:710–720.

Ricker, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

Rosenthal, R. J., V. Moran-O'Connell, and M. C. Murphy.
1988. Feeding ecology of ten species of rockfishes (Scorpaenidae) from Gulf of Alaska. Calif. Fish Game 74:16–37.

Ryan, C.
1986. Feeding habits of brown rockfish, *Sebastes auriculatus*, associated with a dock in San Francisco Bay, California. M. A. thesis, San Francisco State Univ., San Francisco, CA, 88 p.

Sale, P. F., and D. J. Ferrell.
1988. Early survivorship of juvenile coral reef fishes. Coral Reef 7:117–124.

Sano, M.
1997. Temporal variation in density dependence: recruitment and postrecruitment demography of a temperate zone sand goby. J. Exp. Mar. Biol. Ecol. 214:67–84.

Shulman, M. J., and J. C. Ogden.
1987. What controls tropical reef populations: recruitment

or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser. 39: 233–242.

Sissenwine, M. P.
1984. Why do fish populations vary? *In* Exploitation of marine communities (R. M. May, ed.), p. 59–94. Springer-Verlag, Berlin.

Steele, M. A.
1997. Population regulation by post-settlement mortality in two temperate reef fishes. Oecologia 112:64–74.

Stephens, J. S., Jr., P. A. Morris, K. Zerba, and M. Love.
1984. Factors affecting fish diversity on a temperate reef: the fish assemblage at Palos Verdes Point, 1974–1981. Environ. Biol. Fish. 11:259–275.

Veer, H. W. Van der.
1986. Immigration, settlement and density-dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 29:223–236.

Victor, B. C.
1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. 56: 145–160.

Witting, D. A., and K. W. Able.
1995. Predation by sevenspine bay shrimp *Crangon septemspinosa* on winter flounder *Pleuronectes americanus* during settlement: laboratory observations. Mar. Ecol. Prog. Ser. 123:23–31.