



University of Washington Libraries
Interlibrary Loan and Document Delivery Services
Box 352900 - Seattle, WA 98195-2900
(206) 543-1878
interlib@uw.edu
WAW / WAUWAS / RAPID:WAW

4/18/2019 7:21:52 AM

Document Delivery Scan

Seattle

ILLiad TN: 1750053



Loansome Doc:



Customer Reference:

Billing Category:

Needed By: 05/17/2019

Maximum Cost: n/a

NOTICE OF COPYRIGHT

The document above is being supplied to you in accordance with United States Copyright Law (Title 17 US Code). It is intended only for your personal research or instructional use.

The document may not be posted to the web or retransmitted in electronic form.

Distribution or copying in any form requires the prior express written consent of the copyright owner and payment of royalties. Infringement of copyright law may subject the violator to civil fine and/or criminal prosecution.

Special Instructions:

Notes/Alternate Delivery: 4/17/2019 1:28:12 PM (System) RAPID request held locally (Suzzallo Library)

Location: Suzzallo and Allen Libraries
- Stacks

Call #: QH541.5.S3 E58

Work Order Location:

Journal Title: Environmental biology of fishes. Environmental biology of fishes.

Volume: 30

Issue: 1

Month/Year: , 1991

Pages: 225-243

Article Author: Love, Milton

Article Title: The ecology of substrate-associated juveniles of the genus *Sebastes*

ISSN: 0378-1909

OCLC #:

Email: rachela3@uw.edu

EMAIL: RACHELA3@UW.EDU

ILLiad

The ecology of substrate-associated juveniles of the genus *Sebastes*

Milton S. Love,¹ Mark H. Carr² & Lewis J. Haldorson³

¹ Marine Science Institute, University of California, Santa Barbara, CA 93106, U.S.A.

² Department of Biological Sciences, University of California, Santa Barbara, CA 93106, U.S.A.

³ School of Fisheries and Science, University of Alaska, 11120 Glacier Highway, Juneau, AK 99801, U.S.A.

Received 30.10.1989

Accepted 14.2.1990

Key words: Recruitment, Movements, Rockfish, Ontogeny

Synopsis

This paper reviews current knowledge of substrate-associated juvenile *Sebastes*. In general, juvenile rockfish recruit to shallower depths than those occupied by conspecific adults. Habitat use by newly recruited rockfish differs markedly among species. While a few species recruit to shallow-dwelling macrophytes, such as *Zostera*, many others recruit to larger brown algae, such as *Nereocystis* and *Macrocystis*. A few deeper dwelling species recruit to low relief or soft substrata. However, little is known on recruitment of these deeper dwellers. Crustaceans are the major component of the diets of newly recruited *Sebastes*. Species which continue to forage in the water column shift to larger crustaceans (e.g. euphausiids) and fish as they grow. Species which shift to substrate-associated prey soon begin to feed on larger algal-associated gammarid amphipods, shrimps and isopods. Field studies indicate variation in intraspecific growth rates over large geographic distances, among nearby sites and among algal habitats on the same reef, with food availability and water temperature being major factors in the differences. In particular, laboratory studies have shown that temperature is one of the most important factors in growth rates. Many species of juvenile rockfish make ontogenetic movements, often moving into deeper water as they age. Most seasonal movements appear to be related to changes in water temperature and turbulence.

Introduction

A major goal of fish ecologists is to understand the relative contribution of each life history interval of a species to the dynamics and regulation of its abundance. As early as Hjort (1914), variation in survival and transport of larvae has been considered an important determinant of year class strength. Similarly, with the development of stock-recruitment models (Ricker 1954, Cushing 1973), attention has focused on factors responsible for variation in abundance and fecundity of the adult stock. Receiving little attention is the relative importance of the juvenile period in many marine

fishes, including most rockfishes of the genus *Sebastes* that develop a strong association with some form of substrate (e.g. algal, rocky, sand, or mud) after a temporary planktonic larval phase. The transition between environments by the pelagic larvae and substrate-associated juveniles alters the competitors, predators, and use of resources, providing a new suite of potential determinants of cohort strength. Despite its importance, the juvenile period has been neglected for several reasons: (1) theoretical emphasis directing research towards larval and adult periods, (2) historical emphasis on recruitment of subadults or adults to the fishery rather than recruitment of juveniles to a substrate-

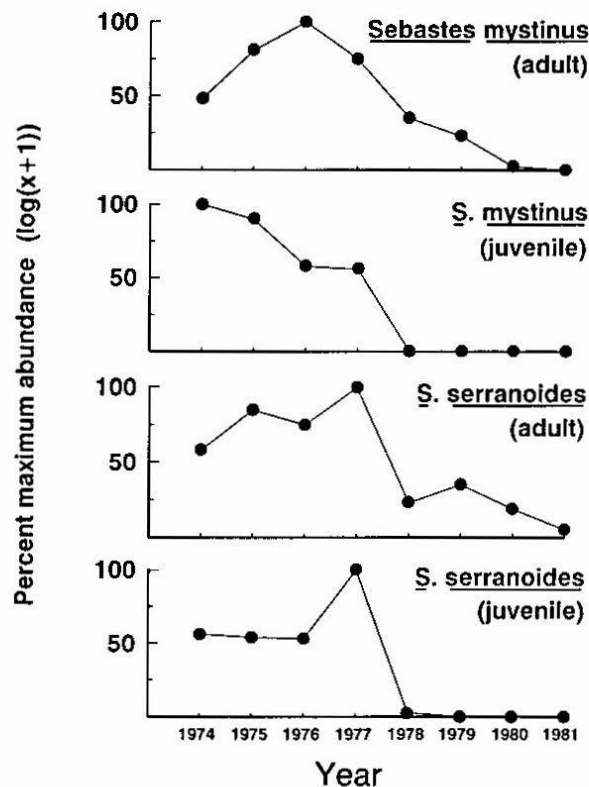


Fig. 1. Patterns of annual abundance of juvenile and adult *Sebastes mystinus* and *S. serranoides* on a shallow, rocky reef in southern California (after Stephens et al. 1984).

associated stock and (3) difficulties using standard techniques (e.g. trawls, scuba) for sampling small juveniles at depth and typically in areas with rough terrain.

In this review, we examine the ecology of substrate-associated juveniles of the genus *Sebastes* for four reasons: (1) Ultimately, the recruitment of substrate-associated juveniles by planktonically dispersed larvae is crucial to the replenishment and maintenance of local populations (Sale 1980, Richards & Lindeman 1987). (2) Both within and between species, the degree of variability in the number of recruits to a fishery (or the adult spawning stock) and the extent to which substrate-associated juveniles are concentrated in benthic habitats are inversely related, suggesting a density-dependent regulation of populations during the early juvenile period (Beverton 1984). (3) Frequently, larval abundance is a poor predictor of subsequent adult year class strength, suggesting that processes oc-

curing during the substrate-associated juvenile period strongly influence adult numbers (Sissenwine 1984). (4) The process of juvenile recruitment has received very little attention by temperate reef fish ecologists.

While we focus on the importance of juveniles that are already associated with the substrate, the initial patterns of distribution and abundance of such juveniles are probably strongly influenced by the availability of potential recruits (i.e., larvae and pelagic juveniles). The spatial and temporal distribution patterns of larvae and pelagic juveniles are considered by Moser & Boehlert (1991). After settlement, the distribution and abundance of recruits will reflect the combined influences of resource availability (food and shelter), mortality (usually due to predation) and the redistribution of fish among habitats. One or more of these factors are likely to be responsible for the habitat associations exhibited by recruits. For logistical reasons, our understanding of the importance of each of these factors is biased toward shallow-dwelling species.

Results

Temporal patterns of recruitment

The duration and timing of peak abundance of recruits of different species onto shallow reefs off central California is related to the timing of parturition (Carr 1983, 1990); this is modulated, however, by factors in the pelagic habitat that influence the transport and survival of larvae and juveniles (Moser & Boehlert 1991). Studies relating these factors are needed to better explain the temporal and spatial dynamics of recruitment to the benthic habitat within years.

Interannual variation in the magnitude of recruitment is a widespread phenomenon among rockfishes. Particularly strong or weak year classes of substrate-associated juveniles have been noted for many species (Carlson & Haight 1976, Moulton 1977, Larson 1980a, Stephens et al. 1984). Mearns et al. (1980) showed that long-term (8-year) patterns of recruitment of *S. saxicola* and *dalli* to soft

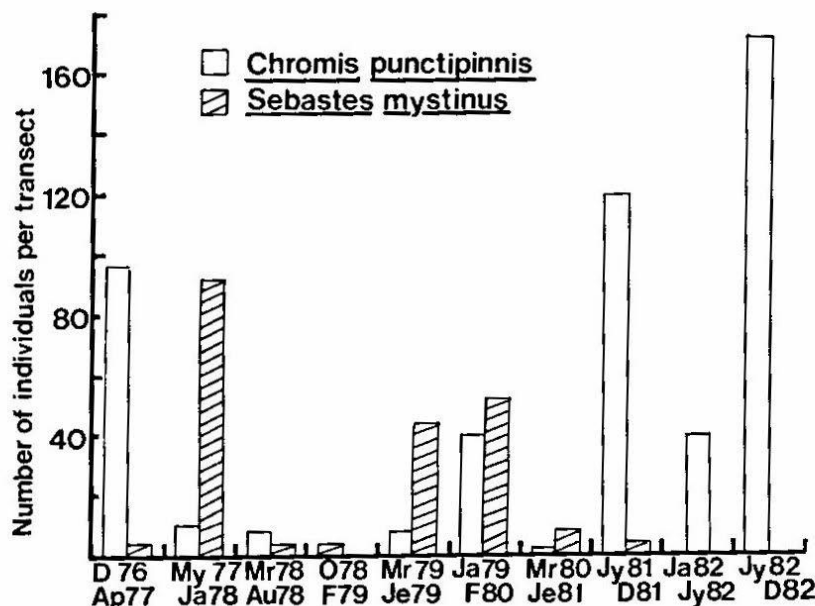


Fig. 2. Density of recruits (young-of-year) of *Sebastes mystinus* and a pomacentrid (*Chromis punctipinnis*) of warmer water affinity on a shallow, rocky reef off Santa Barbara, California (after Ebeling & Hixon 1990).

bottom habitats in southern California are inversely related to one another; they concluded that cooler years favor recruitment of *S. saxicola* into the area whereas warmer years favor recruitment of *S. dalli*. Recruitment strength of *S. mystinus* and *serranoides* to shallow reefs in the Southern California Bight also appears to be temperature-related. Recruitment of these two cooler-water species has declined dramatically in the central (Fig. 1; Stephens et al. 1984) and northern (Fig. 2; Ebeling & Hixon 1990) portions of the Bight during a long-term warming trend. This kind of variability in the relative abundance of recruits among years may have important consequences on temporal dynamics of the structure of substrate-associated rockfish assemblages.

Habitat-related distribution of recruitment

Habitat use by newly recruited rockfishes differs markedly among species (Table 1). Recruits of several deep-dwelling species are abundant on soft substrata or low relief rock (e.g., *S. alutus*, *dalli*, *diploproa*, *saxicola*); however, the relative impor-

tance of higher relief substratum to these species is unclear. Recruitment in deep (> 40 m) habitats has been sampled only by trawling techniques, which are ineffective in areas of high relief. Visual observations from submersibles and remote video have demonstrated high densities of juvenile rockfish in high-relief habitats (Carlson & Straty 1981, Percy et al. 1990). In general, little is known of the habitat requirements of species dwelling below scuba depths.

Recruitment of several species is positively related to the occurrence of macrophytes (Table 1). Several rockfish species (e.g. *S. inermis*, *melanops*, *oblongus*, *caurinus*, *schlegeli*) recruit to seagrass beds (*Zostera* sp.) in shallow, soft bottom embayments. Usually, these habitats are occupied temporarily (weeks or months) as larger individuals gradually move to deeper habitats. Forests of large kelps (*Nereocystis luetkeana*, *Macrocystis integrifolia* and *M. pyrifera*) are common in shallow (< 30 m) depths and are usually restricted to hard substrata. These tall-growing algae extend through the entire water column and often form dense canopies at the surface. Large numbers of recruits of shallow- and deep-dwelling species (*S. atrovirens*,

Table 1. Characteristic habitat type to which *Sebastes* recruit. Under substrate type, soft refers to mud, sand and gravel substrata; hard refers to bedrock, cobble and larger rock structure. Under soft, *S. inermis*, *melanops*, *oblongus*, *paucispinis* and *schlegeli* associate with seagrass on soft substrates and algal structure on hard substrates. *S. miniatus* and *pinniger* are found on the rock-sand interface. ND = no data.

Species of <i>Sebastes</i>	Substrate type			Relief		Source
	Soft	Hard	Macrophyte	Low (< 1 m)	High (> 1 m)	
<i>aleutianus</i>	X					1
<i>alutus</i>		X		X	1	
<i>atrovirens</i>			X			2, 3, 4, 5, 6, 7, 8, 9
<i>auriculatus</i>		X			X	10, 11, 12
<i>aurora</i>	ND					
<i>brevispinis</i>	ND					
<i>carnatus</i>		X	X		X	6, 7, 8, 9, 13, 14, 15
<i>caurinus</i>		X	X	X	X	2, 3, 6, 7, 8, 9, 12, 16, 17, 18
<i>chlorostictus</i>	ND					
<i>chrysomelas</i>		X	X		X	3, 13, 14, 15
<i>ciliatus</i>	ND					
<i>constellatus</i>	ND					
<i>crameri</i>	X			X		19
<i>dalli</i>	X	X		X		11, 20, 21
<i>diploproa</i>	X			X		21, 22
<i>elongatus</i>	ND					
<i>emphaeus</i>		X			X	23
<i>ensifer</i>	ND					
<i>entomelas</i>	X		X	X		2, 6, 8
<i>fasciatus</i>	ND					
<i>flavidus</i>		X	X		X	2, 3, 6, 7, 8, 9, 23, 24
<i>goodei</i>	ND					
<i>hopkinsi</i>	ND					
<i>inermis</i>	X		X	X	X	25, 26
<i>jordani</i>	X			X		21
<i>levis</i>	ND					
<i>macdonaldi</i>	ND					
<i>maliger</i>	ND					
<i>marinus</i>	ND					
<i>marmoratus</i>		X		X	X	27
<i>melanops</i>	X	X	X	X	X	2, 6, 7, 8, 9, 12, 24, 28, 29
<i>melanostomus</i>	ND					
<i>mentella</i>	ND					
<i>miniatus</i>	X	X		X		6, 7, 8, 9, 11
<i>mystinus</i>		X	X		X	2, 3, 6, 7, 8, 9, 10, 30, 31, 32
<i>nebulosus</i>	ND					
<i>nigrocinctus</i>	ND					
<i>oblongus</i>	X	X	X	X	X	25
<i>ovalis</i>		X	X		X	2
<i>pachycephalus</i>	X		X			33
<i>paucispinis</i>	X	X	X	X	X	6, 7, 8, 10, 30, 34
<i>pinniger</i>	X	X		X		2, 12
<i>proriger</i>	ND					
<i>rastrelliger</i>		X				30
<i>rosaceus</i>	ND					
<i>rosenblatti</i>	ND					

Table 1. (Continued).

Species of <i>Sebastes</i>	Substrate type			Relief		Source
	Soft	Hard	Macrophyte	Low (< 1 m)	High (> 1 m)	
<i>ruberrimus</i>	ND					
<i>rufus</i>	ND					
<i>saxicola</i>	X		X			20, 21
<i>schlegeli</i>	X	X	X			35
<i>semicinctus</i>	ND					
<i>serranoides</i>		X	X		X	2, 3, 6, 7, 8, 9, 10, 11, 30, 36
<i>serriceps</i>		X			X	30
<i>taczanowski</i>	ND					
<i>thompsoni</i>	ND					
<i>umbrosus</i>		X			X	37
<i>vulpes</i>	ND					
<i>zacentrus</i>	ND					

1 = Carlson & Haight (1976)	20 = Mearns et al. (1980)
2 = Miller & Geibel (1973)	21 = Sherwood & Mearns (1981)
3 = Burge & Schultz (1973)	22 = Boehlert (1977)
4 = Coyer (1979)	23 = Moulton (1977)
5 = Carlson & Straty (1981)	24 = E. Hobson (personal communication)
6 = Carr (1983)	25 = Harada (1962)
7 = Carr (in press)	26 = Kanamoto (1977)
8 = Anderson (1983)	27 = Tsukahara (1962)
9 = Singer (1985)	28 = Leaman (1976)
10 = Carlisle et al. (1964)	29 = Bayer (1981)
11 = Turner et al. (1969)	30 = Feder et al. (1974)
12 = Gascon & Miller (1981)	31 = Hallacher & Roberts (1985)
13 = Larson (1980a)	32 = Bodkin (1988)
14 = Hoelzer (1987)	33 = Siokawa & Tsukahara (1961)
15 = Hoelzer (1988)	34 = Moser (1967)
16 = Patten (1973)	35 = Sakai et al. (1985)
17 = Haldorson & Richards (1987)	36 = Hobson & Chess (1976)
18 = Matthews (personal communication)	37 = Chen (1971)
19 = Richardson & Laroche (1979)	

carnatus, *chrysomelas*, *caurinus*, *entomelas*, *flavidus*, *jordani*, *melanops*, *mystinus*, *paucispinis* and *serranoides*) associate to varying degrees with one or more of these algae. Experimental removals of kelp canopies (Miller & Geibel 1973, Carr 1983) or entire forests (Leaman 1976, Carr 1983, 1990, Bodkin 1988) have caused marked responses in the local abundance or distribution of recruits. Many species (e.g. *S. caurinus*, *inermis*, *oblongus*, *paucispinis*, *rastrelliger*, *schlegeli*) also recruit to lower growing algae (e.g. *Sargassum* spp., *Pterygophora californica*).

Some species exhibit ontogenetic shifts among algal habitats. Planktonic *S. inermis* larvae and juveniles initially recruit to shallow *Zostera* beds in embayments around Japan (Fig. 3). With increased size [ca. 60 mm total length (TL)], they shift to deeper *Sargassum* covered reefs (Harada 1962). Similarly, in the Strait of Georgia, initial recruits of *S. caurinus* are most abundant in the canopy of *Nereocystis luetkeana* forests. With increased size, young-of-the-year are more abundant in adjacent, lower growth algae (*Zostera* and *Agarum*) (Haldorson & Richards 1987). Along central Califor-

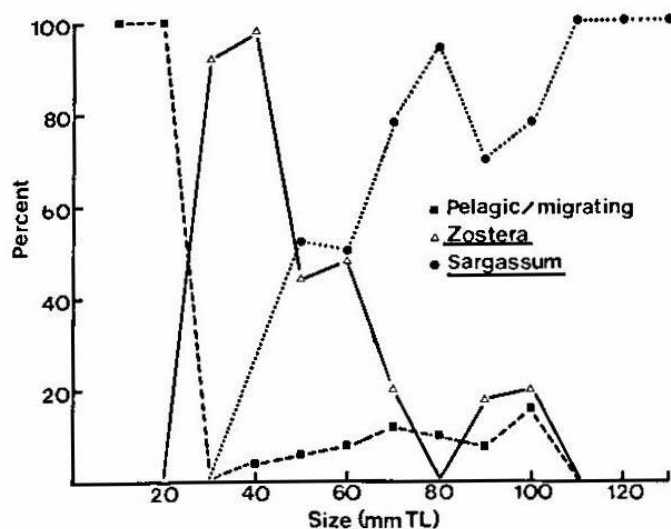


Fig. 3. Size-related habitat use by young-of-year *Sebastes inermis*, expressed as the percentage (of all fish) in three different habitats. Data were digitized from Figure 19 in Harada (1962).

nia, several shallow-dwelling benthic species (*S. atrovirens*, *carnatus* and *caurinus*) initially recruit to the upper portions of *Macrocystis pyrifera* plants. With increased size, recruits move down plants and disperse among benthic habitats including drift algae (Carr 1983, 1990). In southern California, recently settled *S. serranoides* form aggregations at mid-depth along the shoreward margin of *M. pyrifera* beds. Older juveniles aggregate near the bottom along the outer edge of the kelp bed and disperse over adjacent *Dictyopterus* beds at night (Hobson & Chess 1976).

Forests of *Macrocystis* spp. exhibit dramatic temporal variation in their occurrence and abundance (Dayton 1985). Consequently, temporal as well as spatial variability of rockfish recruitment may be a function of algal availability. Because the presence of *Macrocystis* may affect the recruitment of some rockfish species, the species composition of local assemblages of rockfish recruits may also be strongly influenced by the occurrence of *Macrocystis* (or other algae) (Carr 1983, 1990).

Depth-related distribution of recruitment

In general, rockfish recruit to shallower depths than the depth range occupied by conspecific adults (Boehlert 1977). Of the 48 species for which data

are available, juveniles of 40 of these recruit to water shallower than adult depth, or at least in the shallowest part of the adult range. Exceptions to this pattern include species whose adults inhabit very shallow (2–20 m) water (*S. atrovirens*, *chrysomelas*, *rastrelliger* and *serriceps*) and two deep-dwelling species (*S. semicinctus* and *rosaceus*; Love et al. 1990). The discrepancy between recruitment and adult depth varies geographically, particularly for species whose geographical range includes a broad temperature range. For instance, juvenile *S. caurinus* recruit to depths as shallow as 5 m throughout the species' range. Adults, north of central California, typically inhabit these depths, whereas adults off southern California are rarely found at depths less than 60 m. Similarly, juvenile *S. mystinus* and *serranoides* recruit to shallow reefs throughout their ranges. Adults inhabit these same reefs off central California, but rarely occur at depths shallower than 30 m off southern California.

Although juveniles usually recruit to shallower depths than adults occupy, there is also a relationship between depth of recruitment and the depth range adults occupy. The juveniles of deeper dwelling species recruit at deeper depths. This is most apparent in the deepest dwelling species, such as *S. crameri* and *melanostomus*, but is obscured among species of intermediate (30–150 m) depths. Juveniles of water-column aggregating or benthopelagic species (*S. entomelas*, *flavidus*, *jordani*, *paucispinis* and *pinniger*) recruit in large numbers on shallow reefs with recruits of shallow-dwelling species. Nonetheless, juveniles of the more demersal species living at intermediate depths (e.g. *S. chlorostictus*, *constellatus*, *rosaceus*) recruit to these depths and, therefore, to greater depths than the water-column aggregating species living at intermediate depths.

Mortality

There is no evidence that disease or starvation contribute greatly and directly to the natural mortality of juvenile rockfishes. Although starvation and disease may increase the vulnerability of juvenile rockfishes to predation, experimental tests of

this hypothesis have not been conducted. Young-of-the-year rockfish are heavily preyed upon by a variety of piscivorous fish, including older rockfish (Merkel 1957, Love & Westphal 1981, Hallacher & Roberts 1985), and birds (Ainley et al. 1981, Ainley & Boekelheide 1990). The relative importance of predation in determining spatial and temporal patterns of rockfish recruitment and juvenile abundance has not been addressed. The local effect of predation will probably be determined by the abundance and species composition of predators, and the vulnerability of juveniles to different predators and in different habitats. The vulnerability of juveniles to various predators will probably differ among species (particularly between demersal and water column aggregating species) based on differences in (1) size at recruitment, (2) growth rate, (3) morphology (e.g., color) and (4) predator-avoidance behavior (including habitat use). The role of any of these factors in vulnerability of juvenile rockfishes has not been studied.

Though algal structure on shallow reefs has been suggested to provide shelter from predation (Harada 1962, Leaman 1976, Carr 1983, 1990), experiments needed to test this hypothesis for rockfish have not been done. Speculation regarding the importance of algal structure as a refuge from predation for juvenile rockfish relies on evidence from other systems (Ebeling & Laur 1985, Holbrook & Schmitt 1988 a, b). Differences in mortality of juvenile rockfish at sites with and without algal structure or between shallow and deeper reefs have not been demonstrated. Existing evidence suggests that the abundance of potential predators (i.e. piscivorous fishes) can be greater on algae-rich reefs than reefs lacking algal structure (Bodkin 1988, DeMartini & Roberts 1990, Holbrook et al. 1990). Consequently, depending on the effectiveness of algae as a refuge for juvenile rockfishes from these potential predators, it remains unclear whether algae-rich reefs provide greater refuge from predation than reefs lacking algae.

Food habits

Food habit studies of substrate-associated juvenile

rockfish indicate that crustaceans are an extremely important component of their diet and that individual fish demonstrate marked size-related shifts in diet composition during their first year, particularly those species that shift from planktonic prey to substrate-associated prey. These ontogenetic shifts are reinforced by size-related shifts among habitats. Generally, recruits initially feed predominantly on planktonic crustaceans, particularly copepods. For species that continue to forage from the water column as they grow, diets shift to larger crustaceans (e.g. euphausiids) and fish. For instance, the relative importance of copepods and euphausiids in the diet of 1- and 2-year-old *S. alutus* recruits (56 and 35% weight of contents, respectively) reverses for 3- and 5-year-old juveniles (36 and 50%, respectively) (Carlson & Haight 1976). The shift from predominantly calanoid and cyclopoid copepods (mean = 60% volume of contents) in small (30–54 mm TL) *S. serranoides* to gammarid amphipods (44%) and mysids (13%) in larger (> 54 mm TL) individuals coincides with shifts from diurnal to nocturnal foraging in the water column (Hobson & Chess 1976). Young-of-the-year *S. paucispinis* grow rapidly and begin foraging on the other young-of-the-year fishes during their first year (Phillips 1964, Feder et al. 1974). Similarly, *S. melanops* feed predominantly on zooplankton and begin to forage on clupeid larvae during their first year (Leaman 1976). In kelp forests, these water column foragers appear to remove large amounts of plankton, including barnacle larvae destined for intertidal habitats (Gaines & Roughgarden 1987). Consequently, young-of-the-year rockfish may strongly influence availability of larvae to intertidal (Gaines & Roughgarden 1987) and subtidal communities, possibly influencing the distribution and relative abundance of their component species.

Recruits that shift to substrate-associated prey exhibit greater changes in prey composition. Recently settled *S. carnatus* and *caurinus* forage predominantly on planktonic crustaceans but soon shift to larger, algal-associated gammarid amphipods, caridean and mysid shrimp and isopods (Singer 1985). These diet shifts coincide with the migration of recruits from the *Macrocystis* canopy

(< 45 mm TL) to the bottom (> 45 mm TL). Very similar size- and habitat-related dietary shifts are described for *S. caurinus*, which recruit to *Nereocystis* canopy and eventually move to lower-growth algal habitats (Haldorson & Richards 1987). Recently settled *S. atrovirens* also begin feeding on algal-associated gammarid amphipods soon after settlement (Singer 1985). Harada (1962) and Kanamoto (1977) reviewed several studies on the food habits of substrate-associated juvenile *S. inermis*. Upon settlement, the smallest recruits (25–67 mm standard length) feed on planktonic copepods (Kitamori et al. 1959, Fuse 1962). Small *Zostera*-associated crustaceans quickly begin to dominate the diet, including amphipods, isopods, mysids and caprellids (Fuse 1962, Hatanaka & Iizuka 1962). Later, within the first year, the diet of larger juveniles is composed of larger items, including small shrimp, amphipods and fish (Fuse 1962, Kikuchi 1966). However, Fuse (1962) argues that the later diet shifts reflect temporal changes in the availability of these prey groups rather than changes in prey preferences. Factors contributing to spatial and temporal patterns of prey composition (prey availability and morphological and habitat-related foraging efficiency) are discussed below.

Growth

Growth of young-of-the-year rockfish in the field has been estimated by one of three methods: (1) integrated over the year based on mean size at age 1, (2) size at age based on daily growth increments of otoliths and (3) modal analysis based on change in the size frequency of a cohort over time. Whereas growth rates among species range widely (0.12–0.72), considering the different ageing techniques employed, number of species sampled, variation in size of individuals sampled and wide range of environmental conditions under which estimates have been made, the similarity in growth rates is striking (Table 2a). In 21 field studies of growth, 11 of 17 species yielded daily growth rates between 0.2 and 0.3 mm. The mean daily growth rate (± 1 SD) of the 21 studies is 0.29 (± 0.15) mm. With the notable exception of *S. paucispinis* and the difference in

growth between water column and demersal species described below, this value may be a reasonable estimate for substrate-associated juvenile rockfishes in general. As the number of growth studies increases, encompassing a greater variety of environmental conditions, greater resolution in patterns of growth based on habitat and life history may develop.

Estimates of growth rate in the field indicate that water-column aggregating species grow significantly faster than demersal species: mean daily growth rate (± 1 SE) is 0.17 (± 0.012) and 0.28 (± 0.024) mm per day for the demersal and water-column aggregating species, respectively, included in Table 2a (t-test: $p = 0.0047$ for log transformed rates). This difference may reflect differences in morphology. Water column species are generally more elongate than demersal species. Thus the different rates of increase in length may not reflect different rates of increase in biomass. Information on both weight and length at age would help clarify this issue.

Field studies have demonstrated variation in intraspecific growth rate over large geographic distances (Chen 1971), among nearby sites (Miller & Geibel 1973) and among algal habitats on the same reef (Haldorson & Richards 1987). Three factors – food availability and foraging and assimilation efficiency – are particularly important to growth and may contribute to variation in growth at each of these spatial scales.

Few field studies of rockfish food and growth have incorporated information on prey availability. Within a given depth stratum, variation in growth rates among and within reefs are more likely related to differences in prey availability and habitat-related foraging rates than temperature-related growth differences. Young-of-the-year *S. mystinus* grew faster under a pier where food was supplemented by the discharge of fish carcasses than on a nearby natural reef (Miller & Geibel 1973). Haldorson & Richards (1987) have estimated that the growth rate (length and weight) of young-of-the-year *S. caurinus* inhabiting a *Zostera* bed is 10% faster than those inhabiting a nearby *Agarum*-dominated site. This difference in growth rate may be the result of greater prey availability in

the fine-structured eelgrass than in the broad blades of *Agarum* (or lower vulnerability to predators and, therefore, higher foraging rates of fish inhabiting eelgrass). To our knowledge, no comparative data exist for prey availability between reefs within and among depth strata. Though the supply of planktonic food is likely to vary among reefs of varying exposure to currents, the effect of this variation on differences in juvenile growth

rates among reefs is unknown. Similarly, the effect of algal structure on the transport (i.e. delivery) of planktonic food across reefs is not clear. Though crustacean abundance and species composition are known to vary among algal species (Holbrook & Schmitt 1988 a, b), the effects of variation in species composition and abundance of algae on prey availability and growth performance of juvenile rockfish have yet to be addressed. Consequently, the

Table 2. Growth rates of young-of-year *Sebastes* from laboratory and field studies; modified from Boehlert & Yoklavich (1983).

Species of <i>Sebastes</i>	Temperature (°C)	Size (mm)	Growth (mm · day ⁻¹)	Source
A. Field studies				
<i>alutus</i>		62	0.17 ¹	Carlson & Haight (1976)
<i>caurinus</i>		32–48	0.15 ²	Halderson & Richards (1987)
		73	0.20 ¹	Patten (1973)
<i>diploproa</i>		9–43	0.19 ²	Boehlert (1981)
<i>fasciatus</i> (?)		6–50	0.40 ³	Kelly & Barker (1961)
<i>flavidus</i>		45–80	0.20 ³	Laroche & Richardson (1980)
		ca. 50	0.46 ²	Woodbury (personal communication)
<i>inermis</i>		12–70	0.27 ³	Harada (1962)
<i>jordani</i>		ca. 50	0.59 ²	Woodbury (personal communication)
<i>melanops</i>		48–60	0.20 ³	Laroche & Richardson (1980)
		100	0.27 ¹	Leaman (1976)
		70	0.30 ¹	Bayer (1981)
<i>melanostomus</i>		15–31	0.30 ²	Moser & Ahlstrom (1978)
<i>mystinus</i>		85	0.23 ¹	Miller & Geibel (1973)
<i>oblongus</i>		24–76	0.43 ³	Harada (1962)
<i>p. pachycephalus</i>		68	0.19 ¹	Shiokawa (1962)
<i>paucispinis</i>		ca. 50	0.72 ²	Woodbury (personal communication)
<i>saxicola</i>		65–70	0.22 ³	Love (unpublished)
<i>semicinctus</i>		38–63	0.20 ³	Love (unpublished)
<i>serranoides</i>		62–108	0.30 ³	Love (unpublished)
<i>umbrosus</i>		42.5	0.12 ¹	Chen (1971)
			mean = 0.29	
B. Laboratory studies				
<i>dalli</i>	15	5–22	0.37	Moser & Butler (1981)
<i>diploproa</i>	10	30–60	0.15	Boehlert (1981)
	15	30–60	0.21	Boehlert (1981)
	20	30–60	0.10	Boehlert (1981)
<i>melanops</i>	7	35–99	0.09	Boehlert & Yoklavich (1983)
	12	39–109	0.30	Boehlert & Yoklavich (1983)
	18	38–111	0.31	Boehlert & Yoklavich (1983)
<i>p. pachycephalus</i>	15	7–13	0.30	Shiokawa & Tsukahara (1961)
<i>schlegeli</i>	17	7–50	0.60	Kusakari (1978)
<i>thompsoni</i>	17–22	52–63	0.23	Ikehara & Nagahara (1978)
			mean = 0.27	

¹ Mean size at 1 year of age.

² Daily growth increments of otoliths.

³ Modal (i.e. size frequency) analysis.

role of prey availability in determining patterns of juvenile recruitment and growth is poorly understood.

The foraging efficiency (rate of food harvested relative to energy expended) of juvenile rockfish is related to their feeding morphology and habitat characteristics. The kinds of prey juvenile rockfish utilize are related to their feeding morphology (Singer 1985). Habitat characteristics influence both the availability of prey types and the ability of the fish to utilize them. Local increases in algal abundance may enhance food abundance but also reduce the efficiency at which prey are detected, attacked and successfully captured (Ryer 1988). The effect of predators on the amount of time juvenile fish spend foraging and the habitat in which foraging occurs may vary among reefs which differ in the relative abundance of predators and refugia. Greater predator abundance may force fish to feed in refuge habitats of lower food availability or quality (Holbrook & Schmitt 1988a, 1988b, Werner & Hall 1988). Similarly, lower refuge availability may increase vigilance and reduce time spent foraging (Schmitt & Holbrook 1985). Such indirect effects of predators and shelter availability have not been examined for rockfishes.

The effect of temperature on growth is probably important to variation in growth over large distances and between reefs situated in different water depths. Temperature-dependent assimilation efficiency has been suggested to contribute to the recruitment of juvenile rockfish to warmer, shallow habitats. Growth studies conducted in the laboratory have demonstrated that smaller *S. diploproa* grow faster than larger individuals at temperatures above 10°C and exhibit their maximum growth rate at a higher temperature than larger individuals (Fig. 4; Boehlert 1981). Below 10°C, growth rates were higher for larger fish than smaller fish. This same pattern was demonstrated for young-of-the-year *S. melanops* (Fig. 4; Boehlert & Yoklavich 1983). As temperature increases, evacuation rate increases, and it is likely that food energy can be processed more efficiently. These size-related growth differences suggest that small, young recruits achieve their highest growth rates in

the warmer water of shallow habitats, whereas larger, older juveniles achieve highest growth rates in deeper, cooler water. This pattern not only suggests why small fish might recruit to shallow reefs, but also suggests that size and temperature-related growth optima contribute to the progressively deeper movement of some rockfish with age or size. However, such an ontogenetic migration may also be related to depth differences in the prey types used by different sized fishes. There is too little information on the depth distribution of prey types to compare the relative importance of these two mechanisms.

The mean daily growth rate for laboratory raised fish (0.27, 1 SE = 0.045) is very similar to that estimated in the field (0.29 mm, Table 2b), suggesting that laboratory studies of growth-related processes are probably applicable to natural populations. Further, the highest growth rates observed in the laboratory, exhibited by fish fed to satiation, are comparable to average rates estimated in the field. Young-of-the-year on shallow rock reefs feed during the day (Hobson & Chess 1976, Leaman 1976, Singer 1985), fill their stomachs rapidly and take at least 9 to 12 hours for a full stomach of prey to be half digested (Singer 1982). Together these laboratory and field results suggest that young-of-the-year rockfish in the field may not be food limited.

Redistribution

Movement patterns of juveniles of substrate-associated rockfish can be categorized as one of four types: (1) ontogenetic – movement that is age or size related, presumably in response to changing resource requirements and vulnerability to predation; (2) relocation – movement of similarly sized fish between habitats (e.g. in search of prey); (3) seasonal – movement in response to seasonal change in environmental factors (e.g. temperature, turbulence or food availability); (4) diel – movement, usually small scale, repeated daily and associated with changes in ambient light conditions (i.e. diurnal, crepuscular and nocturnal).

Ontogenetic movements

Ontogenetic movements of juvenile rockfishes occur within and among reefs and across depths. Within a reef, some young-of-the-year rockfish exhibit size-related shifts between algal habitats. For example, planktonic *S. inermis* larvae and juveniles initially recruit to shallow *Zostera* beds in embayments around Japan (Fig. 3). With increased size (ca. 60 mm TL), they shift to deeper *Sargassum* covered reefs (Harada 1962). Similarly, in the Strait of Georgia, initial recruits of *S. caurinus* are most abundant in the canopy of *Nereocystis luetkeana* forests. With increased size, young-of-the-year fish are more abundant in adjacent, lower growing algae (*Zostera* and *Agarum*) (Haldorson & Richards 1987). Along central California, several shallow-dwelling, reef-associated species (*S. atrovirens*, *carnatus* and *caurinus*) initially recruit to the upper portions of *Macrocystis pyrifera* plants. With increased size, recruits move down the plants and disperse among benthic habitats including drift algae (Carr 1983, 1990). In southern California, recently settled *S. serranoides* form aggregations at mid-depth along the shoreward margin of *M. pyrifera* beds. Older juveniles aggregate near the bottom along the outer edge of the kelp beds and disperse over adjacent beds of the low, brown alga *Dictyopterus* at night (Hobson & Chess 1976).

Examples of size-related movements between habitats at similar depth are rare. At sites characterized by broken, uneven substrate, Carlson & Haight (1976) collected large numbers of 1- and 2-year-old *S. alutus* and very few larger, older individuals. In contrast, on sand bottoms at similar depths, large numbers of 3- to 6-year-old fish and very few younger fish were collected.

Size-related movements across depths are very common among rockfish since most species recruit to habitat shallower than the adult habitat. A well-documented example is the recruitment of *S. melanops* to shallow kelp habitats (Leaman 1976, Anderson 1983, Carr 1983, 1990, Singer 1985) and the eventual migration to deeper, offshore reefs characteristic of adult habitat. Much of the movement of juveniles into deeper water probably is attribut-

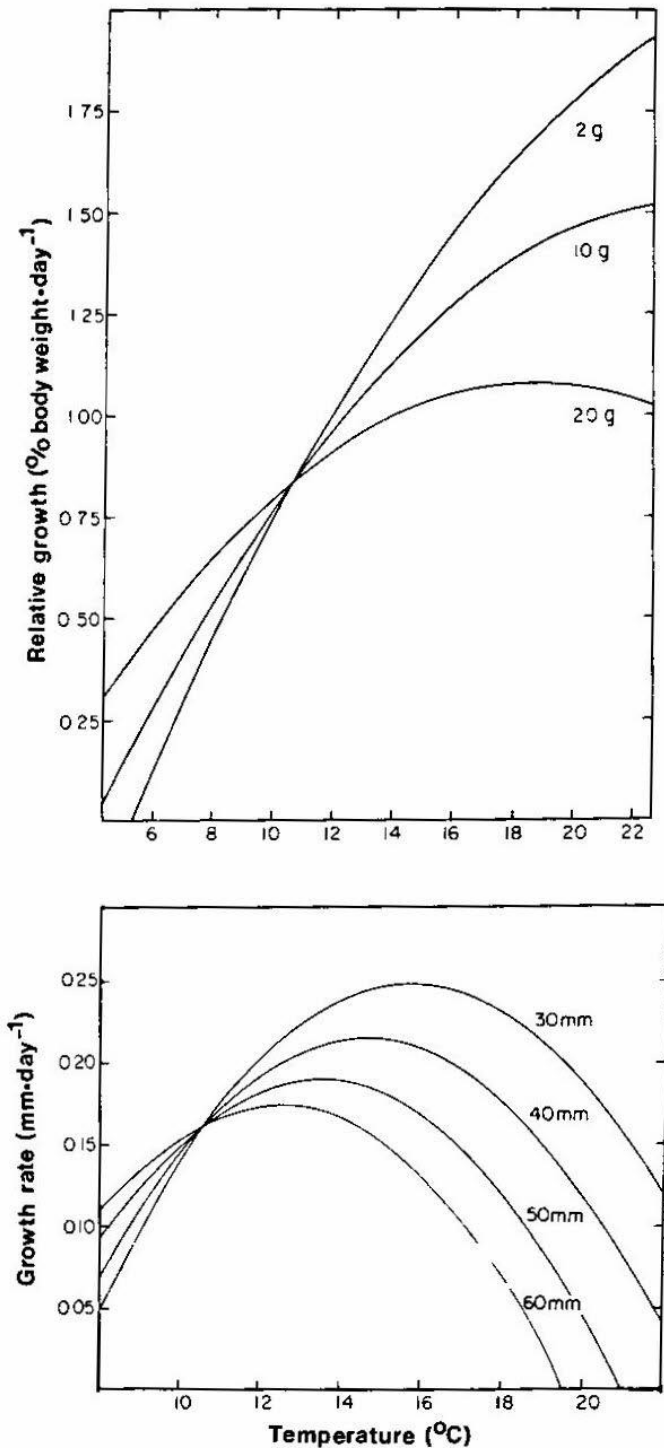


Fig. 4. Upper: Growth as a function of temperature for *Sebastes diploproa*. Separate functions are depicted for fishes of different size. These functions were generated using multiple regression models derived from growth experiments under a 16L : 8D light periodicity and unrestricted ration in the laboratory (after Boehlert 1981). Lower: Instantaneous relative growth of juvenile *S. melanops* as a function of temperature at unrestricted ration. Separate functions are depicted for fish of different weights and were generated using multiple regression models derived from growth experiments (after Boehlert & Yoklavich 1983).

able to ontogenetic changes in temperature preference, rather than lack of suitable prey or habitat. The proximate basis for this preference may be related to the size- and temperature-related growth efficiency described earlier (growth section). This mechanism is suggested by the length frequency of four rockfish species (*S. caurinus*, *mystinus*, *paucispinis* and *serranoides*) in shallow water along the Channel Islands off southern California (Love et al. 1985). Shallow water temperature increases along this chain of islands from west to east. To the east, larger juveniles and adults only occur in deep water, and apparently only young juveniles inhabit the warmer, shallow water. To the west, where the thermocline is less pronounced, both young juveniles and adults were abundant in the cool, shallow waters. In contrast, fishes of similar size and with similar food habits as adult rockfish (*Paralabrax clathratus*, *Scorpaena guttata*, *Ophiodon elongatus*) are abundant in the warm, eastern, shallow waters, suggesting that prey are not limiting adult rockfish abundance there. Quantitative information on prey availability in the shallow, warm and cool water areas would help substantiate this hypothesis.

Juveniles may travel substantial distances during ontogenetic movements to adult habitats. Juvenile *S. auriculatus* tagged in San Francisco Bay have been taken in the open ocean as much as 50 km away (W. Lenarz personal communication). Juvenile *S. flavidus* tagged in Puget Sound migrate to the open coast as much as 360 km (Mathews & Barker 1983). The timing and duration of such movements vary widely among species. While juveniles of some species, such as *S. flavidus* in Puget Sound, occupy one habitat until they migrate to deeper reefs (Moulton 1977), others such as *S. paucispinis* make a series of moves to successively deeper reefs, over perhaps 5 years (Love personal observation).

Relocation

Although juveniles of many rockfish species undergo large-scale ontogenetic movements, others (particularly shallow-dwelling species) exhibit very

little post-settlement movement. Using both mechanical tags and parasite markers, Love (1980) has demonstrated that juvenile *S. serranoides* rarely, if ever, move off shallow (4–20 m) reefs in the Santa Barbara Channel, even when other suitable habitats are within 2 km. Similarly, Hartman (1987) has observed off-reef movement in only 14% of the 435 juvenile *S. serranoides* tagged and recaptured off southern California. Other species also exhibit little tendency to emigrate from the reef to which they initially recruited. *Sebastes mystinus* tagged in kelp forests and breakwaters off central California moved little or not at all after 6 months (Miller & Geibel 1973). Young-of-the-year *S. melanops* recruited to a *Macrocystis* forest and remained there through the winter (Leaman 1976). Similarly, Moulton (1977) observed a school of juvenile *S. flavidus* in the same area for at least one year, and in southeast Alaska, Carlson & Barr (1977) observed a school of juvenile *S. flavidus* for several years at the same shallow site. Juveniles of the usually motile redfish complex remained near a dock at Eastport, Maine, for at least 2 years (Kelly & Barker 1961).

The extent to which juveniles of the deep-dwelling populations relocate is unknown. However, there is a general trend toward greater mobility with depth (Miller & Geibel 1973, Love 1980, 1981, Atkinson 1984, Hartman 1987). Juvenile *S. serranoides* tagged at oil platforms (bottom depth about 50 m water depth) exhibited inter-platform movement of about 0.8 km, which is far greater than the restricted movement of shallower dwelling *S. serranoides* (Love 1980). Similarly, juvenile *S. serranoides* tagged on natural reefs deeper (10–50 m water depth) than those sampled by Love (1980) exhibited movement similar to that observed among platforms (Hartman 1987). Deeper dwelling juvenile *S. mystinus* also exhibited greater movement than their shallow counterparts (Miller & Geibel 1973). Some evidence indicates that food is less abundant and more patchily distributed in offshore waters than on shallow reefs (Ahlstrom 1959, 1961, Longhurst 1967, Marlow & Miller 1975). In response, deeper dwelling species (e.g. *S. alutus*, *goodei*, *melanostomus* and *paucispinis*) may spend more time and cover a greater area searching

for food. On a smaller scale, deeper-living *S. carnatus* have larger home ranges than shallower-living *S. chrysomelas*, reflecting a significant decline in food with depth (Larson 1980b).

Seasonal movements

Seasonal movements of juvenile rockfish appear to be related to changes in temperature and turbulence. The most extensive seasonal movements have been documented for juvenile redfish (*S. fasciatus* and *mentella*) in the Gulf of St. Lawrence (Atkinson 1984). During the summer, juveniles are found throughout the Gulf, primarily at 181–260 m. In autumn, juveniles begin to migrate southeast, traveling over deeper water (to 340 m), then wintering in 181–220 m off southeast Newfoundland. In the Northeast Pacific, juvenile *S. alutus* make seasonal depth migrations (Westrheim 1970). On the west coast of Vancouver Island, older juveniles spend summer and fall at about 160–200 m, then travel down to 200–240 m in winter and spring. Both of these examples appear to be avoidance responses to influxes of cold water. Much of the western Gulf of St. Lawrence freezes over in winter, and similarly, water temperature is higher off Vancouver Island during these migrations to deep water (B. Leaman personal communication).

With the onset of fall and winter storms, juveniles recruited to shallow reefs appear to move to deeper reefs. The abundance of many species (*S. entomelas*, *flavidus*, *jordani*, *melanops*, *miniatus*, *mystinus*, *ovalis*, *paucispinis*, *pinniger* and *serranoides*) that recruit to shallow kelp forests off Monterey, California, declines with the first heavy winter storms (Miller & Geibel 1973, Carr 1983, 1990). This was true for both young-of-the-year and older juveniles (Miller & Geibel 1973). Miller & Geibel (1973) have hypothesized that juveniles of these species hide in crevices on the same reefs during turbulent conditions and thus were difficult to survey. Having found few or no individuals of the deeper dwelling and water-column aggregating species during winter samples, Carr (1983) has suggested that these individuals move to deeper, less turbulent reefs. Turbulent conditions may initiate

migration of juveniles of the deeper-dwelling species (i.e. *S. entomelas*, *flavidus*, *jordani*, *melanops*, *miniatus*, *ovalis*, *paucispinis*, *pinniger*) toward adult depths. Individuals of these species do not return as 1-year-olds. Simultaneously, juveniles of the shallow-dwelling species (i.e. *S. mystinus* and *serranoides*), which are abundant as 1-year-olds on shallow reefs, may either move along shore until they find reduced turbulence in sheltered areas or move to slightly deeper reefs. Juvenile *S. caurinus*, *flavidus* and *melanops* in Puget Sound overwinter along the same section of shoreline as in summer, but in slightly deeper water (Moulton 1977). Leaman (1976) has observed a similar depth shift for juvenile *S. melanops*. These examples argue further for a depth shift, rather than horizontal movement for the majority of shallow species. Similar winter reductions or disappearances from inshore waters have been noted for juveniles of other species (Burge & Schultz 1973, Gascon & Miller 1981). In contrast to the winter reductions in density observed on reefs exposed to strong turbulence, juveniles that recruit to reefs in more protected waters remain there throughout the year. At three sites within the more protected Southern California Bight (Naples Reef, Santa Cruz Island and King Harbor), no seasonal diminishment in the number of young-of-the-year *S. mystinus* or *serranoides* has occurred (A. Ebeling personal communication, J. Stephens personal communication).

Diel movements

Information on the diel movements of juvenile rockfish is restricted to species that recruit to shallow rocky reefs. On shallow reefs, both horizontal and vertical movements associated with daily changes in light intensity have been described. One prevalent pattern – young-of-the-year fish aggregating in the water column during the day and settling on the bottom at night – has been observed for young-of-the-year *S. serranoides* (Hobson & Chess 1976, Carr 1983), *flavidus*, *mystinus* and *melanops* (Carr 1983). During the morning crepuscular period, individuals gradually rise from the bottom and aggregate just above the reef. They remain and

feed (Hobson & Chess 1976, Singer 1985) in the water column throughout the day. During the evening crepuscular period, individuals descend to the bottom, and at night they lie in contact with the reef surface, often taking shelter among rocks and algae (Hobson & Chess 1976, Carr 1983). Similarly, young-of-the-year *S. entomelas*, which occur in the open water column outside of a kelp forest during the day, have been observed in contact with the sand bottom at night (Anderson 1983).

Horizontal shifts in distribution also occur. Young-of-the-year *S. pinniger* aggregate during the day in areas of low-relief rock and mixed rock and sand, characteristic of sand channels and the reef-sand interface. During the evening crepuscular period, they accumulate along the outer edge of the reef and move out over open sand bottom, where they remain through the night. The process is reversed at dawn (Carr 1983). Young-of-the-year *S. serranoides* off central California also occur outside of the forest on the sand bottom at night, rather than restricting their nocturnal distribution to the reef surface (Carr 1983).

Diel movements and patterns of activity change during juvenile ontogeny. At Santa Catalina Island, small (<55 mm TL) young-of-the-year *S. serranoides* are active diurnally and remain on the reef throughout the balance of the diel period. Larger juveniles aggregate at the outer edge of the bed during the day and move off the reef to forage in the water column at night (Hobson & Chess 1976). Young-of-the-year *S. melanops* (30–100 mm TL) restrict their vertical migrations to the kelp forest. However, older juveniles (101–200 mm TL) are more abundant outside of the bed during the day and move into the forest at night (Leaman 1976). Other species also shift from foraging diurnally as small juveniles to foraging predominantly at night as larger juveniles [e.g. *S. caurinus*, *flavidus*, *maliger* (Moulton 1977) and *S. inermis* (Harada 1962)].

Two reasons have been proposed for the nocturnal descent of small, young-of-the-year fish. Hobson & Chess (1976), Leaman (1976) and Moulton (1977) have all argued that settlement on the bottom among rock and algal structures provides cover from nocturnal predators. Alternatively,

Carr (1983) has suggested that settlement on the reef may be a means of conserving energy. Since small juveniles do not appear to feed at night (see growth section), they would gain little by remaining in the water column and otherwise expend more energy maintaining position over a reef in the face of surge and currents. The two explanations are not mutually exclusive and both may contribute to the observed diel migration.

Discussion

Several mechanisms have been emphasized as determinants of recruitment success and population size for temperate fishes (Beverton 1984, Sissenwine 1984) and coral reef fish assemblages (Doherty & Williams 1988, Warner & Hughes 1989). We briefly address some of these mechanisms here, primarily to discuss evidence for their relevance to rockfishes, shortcomings in our understanding of their importance to rockfish recruitment, and to suggest avenues of future research.

The current emphasis on recruitment to the population (and community) of reef fishes stems from recent evidence that local densities can be limited by the magnitude of recruitment (Mapstone & Fowler 1988, Ebeling & Hixon 1990). We have described evidence for spatial (vertical and horizontal) and temporal (seasonal and interannual) variation in availability (abundance) of potential recruits to particular locations. Further examples are discussed in Moser & Boehlert (1991). Long-term temporal declines of local recruitment and population density have been described for shallow-reef rockfishes (Stephens et al. 1984, 1986, Ebeling & Hixon 1990). These local failures of recruitment have occurred simultaneously at sites separated by tens of kilometers and corresponded with a large-scale oceanographic anomaly (El Niño). These patterns, and the interannual variation in recruitment associated with estimates of offshore transport (Parrish et al. 1981), indicate that potential recruits are not always available to a local population. Examples of the potential importance of nearshore currents and offshore advection of larvae on the dynamics and spatial distribution of

other nearshore temperate species are increasing in number (Ebert & Russell 1988, Roughgarden et al. 1988). Although temperature and offshore water transport indices may prove valuable predictors of recruitment strength, determining the mechanism (s) responsible for these relationships will require the decoupling of the effects of local temperature-dependent spawning success, availability, survival and post-settlement survivorship of larvae on recruitment. These studies will require far more collaboration among nearshore oceanographers and fish ecologists than has been pursued in the past.

During years of high abundance of potential recruits, resources critical to early post-settlement survival may limit the density of recruits. Resources thought to be potentially limiting to substrate-associated rockfishes include food and shelter or territory availability (Larson 1980a). While some authors have suggested that local density or rockfish recruits were below levels at which food (Singer 1985) and habitat (Carr 1983, 1990) were limiting, no experimental manipulations of resources or fish densities have been conducted to clearly test these conclusions. Also, these conclusions may have been derived at times when recruitment was below the higher magnitudes occasionally (or commonly) experienced by these species.

While food limitation will most likely be manifested in differences in growth rate, age at maturity, or fecundity, size-dependent vulnerability to predation may also cause density effects due to predation. Tests of food limitation for tropical reef fishes have provided mixed results. Shulman (1984) did not detect an effect of food availability on recruitment or early survival of several Caribbean reef fishes. However, Jones (1986) supplemented food availability to a tropical planktivorous pomacentrid at natural densities in the field and demonstrated increased growth rates. Manipulative field experiments of intra and interspecific density effects on foraging success and growth of substrate-associated juveniles have been successful for tropical species (Jones 1987a, 1987b) and would greatly enhance our understanding of resource limitation in rockfishes.

The importance of shelter availability to the

recruitment and post-recruitment survival of substrate-associated juvenile rockfishes has not been studied. In contrast, shelter availability has been shown to influence recruitment of several coral reef fishes (Shulman 1984, 1985) and some temperate demersal species (Behrems 1987, Steiner et al. 1982). Shelter availability is probably very important at and soon after settlement since the highest rates of mortality for several juvenile coral reef fishes have been shown to occur within the first 2 weeks after settlement (Sale & Ferrell 1988). Similarly, the ability of recruits to invade and/or persist in adult territories is thought to be related to shelter availability (Sale et al. 1980, Doherty 1983, Behrems 1987). Algae (particularly kelps) are thought to be an important source of shelter for the juveniles of several rockfishes (see references in habitat-related distribution of recruitment section). Experimental manipulations of algal presence has demonstrated significant effects on the distribution and abundance of recruitment of other temperate reef fishes (Jones 1984, Carr 1989). Replicated experimental manipulations of algal habitats would greatly enhance our understanding of the effects of algae on recruitment, growth and survivorship of juvenile rockfishes.

Long-term patterns of local recruitment levels, necessary for establishing reasonable ranges of fish density for experimental work, are unknown for most (if not all) rockfish species. Knowledge of recruitment densities and experimental assessment of the effects of resource availability and fish densities on growth and survivorship are fundamental to achieving an understanding of the importance of resource limitation and density dependent processes.

The role of predators in influencing post-settlement densities has yet to be determined for any rockfishes. Evidence for high mortality of settlers (and recruits) due to predation has been presented here (Burge & Schultz 1973, Hallacher & Roberts 1985). Since much of this predation is from older rockfishes, cannibalism may prove to be an important means of density regulation. However, the impact of predation on patterns of rockfish recruitment has not been demonstrated. In contrast, predator exclusion (Behrems 1987) and/or prey

(juvenile fish) manipulations (Shulman 1985) have been conducted with varying success. Because of the difficulties inherent with predator manipulations, the role of predation is certainly the least understood and underemphasized aspect of reef fish ecology. Studies of the relative contribution of predation on local densities of recruits and numbers surviving to maturation are crucial avenues of future research.

Acknowledgements

We thank W. Lenarz and members of the Rockfish Research Program at the National Marine Fisheries Service (NOAA) Laboratory at Tiburon, California, for unpublished data and suggestions. T. Anderson, J. Bence, A. Ebeling, L. Hallacher, S. Holbrook, T. Hughes, B. Leaman, W. Lenarz and an anonymous reviewer provided several helpful suggestions for the manuscript. We particularly appreciate the many excellent comments of L. Williams and the great patience of T. Shaw, who re-typed much of this manuscript. M. Carr received support from the Sport Fishing Institute EPRI Fellowship Program.

References cited

- Ahlstrom, E.H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Bull. 60: 107-146.
- Ahlstrom, E.H. 1961. Distribution and relative abundance of rockfish (*Sebastes* spp.) larvae off California and Baja California. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 150: 169-176.
- Ainley, D.G., D.W. Anderson & P.R. Kelly. 1981. Feeding ecology of marine cormorants in southwestern North America. Condor 83: 120-131.
- Ainley, D.G. & R.J. Boekelheide. 1990. Seabirds of the Farallon Islands: ecology, structure and dynamics of an upwelling system community. Stanford University Press, Palo Alto. 463 pp.
- Anderson, T.W. 1983. Identification and development of near-shore juvenile rockfishes (genus *Sebastes*) in central California kelp forests. M. Sc. Thesis, California State University, Fresno. 216 pp.
- Atkinson, D.B. 1984. Distribution and abundance of beaked redfish in the Gulf of St. Lawrence, 1976-1981. J. Northw. Atl. Sci. 5: 182-193.
- Bayer, R. 1981. Shallow-water intertidal ichthyofauna of the Yaquina Estuary, Oregon. Northwest Sci. 55: 182-193.
- Behrens, K.C. 1987. The influence of shelter availability on recruitment and early juvenile survivorship of *Lythrypnus dalli* Gilbert (Pisces: Gobiidae). J. Exp. Mar. Biol. Ecol. 107: 45-59.
- Beverton, R.J.H. 1984. Dynamics of single species. pp. 13-58. In: R.M. May (ed.) Exploitation of Marine Communities, Springer-Verlag, Berlin.
- Bodkin, J.L. 1988. Effects of kelp removal on associated fish assemblages in central California. J. Exp. Mar. Biol. Ecol. 117: 227-238.
- Boehlert, G.W. 1977. Timing of the surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off southern California. U.S. Fish. Bull. 75: 887-890.
- Boehlert, G.W. 1981. The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field. U.S. Fish. Bull. 79: 789-794.
- Boehlert, G.W. & M.M. Yoklavich. 1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. Env. Biol. Fish. 8: 17-28.
- Burge, R.T. & S.A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dept. Fish & Game, Mar. Resour. Tech. Rpt. 19. 433 pp.
- Carlisle, J.G., Jr., C.H. Turner & E.E. Ebert. 1964. Artificial habitat in the marine environment. Calif. Fish & Game, Fish Bull. 124. 93 pp.
- Carlson, H.R. & 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. M.F.R. paper 1242. Mar. Fish. Rev. 39: 23-24.
- Carlson, H.R. & R.E. Haight. 1976. Juvenile live of Pacific ocean perch, *Sebastes alutus*, in coastal fiords of southeastern Alaska: their environment, growth, food habits, and schooling behavior. Trans. Amer. Fish. Soc. 105: 191-201.
- Carlson, H.R. & R.R. Straty. 1981. Habitat and nursery grounds of Pacific rockfish, *Sebastes* spp., in rocky coastal areas of southeastern Alaska. Mar. Fish. Rev. 43: 13-19.
- Carr, M.H. 1983. Spatial and temporal patterns of recruitment of young-of-the-year rockfishes (genus *Sebastes*) into a central California kelp forest. M.Sc. Thesis, San Francisco State University, San Francisco. 102 pp.
- Carr, M.H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. J. Exp. Mar. Biol. Ecol. 126: 59-76.
- Carr, M.H. 1990. The effect of habitat structure on recruitment of a guild of temperate zone rockfishes. J. Exp. Mar. Biol. Ecol. (in press).
- Chen, L.C. 1971. Systematics, variation, distribution, and biology of rockfishes of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr. Univ. Calif. 18. 115 pp.

- Coyer, J.A. 1979. The invertebrate assemblage associated with *Macrocystis pyrifera* and its utilization as a food source by kelp forest fishes. Ph.D. Dissertation, University of Southern California, Los Angeles. 364 pp.
- Cushing, D.H. 1973. The dependence of recruitment on parent stock. *J. Fish. Res. Board Can.* 30: 1965-1976.
- Dayton, P.K. 1985. Ecology of kelp communities. *Ann. Rev. Ecol. Syst.* 16: 215-245.
- DeMartini, E.E. & D.A. Roberts. 1990. The effects of giant kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. *Bull. Mar. Sci.* (in press).
- Doherty, P.J. 1983. Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64: 176-190.
- Doherty, P.J. & D. McB. Williams. 1988. The replenishment of coral reef fish populations. *Oceanogr. Mar. Ann. Rev.* 26: 487-551.
- Ebeling, A.W. & M.A. Hixon. 1990. Tropical and temperate reef fishes: comparison of community structures. *In: P.F. Sale (ed.) The Ecology of Coral Reef Fishes*, Academic Press, New York (in press).
- Ebeling, A.W. & D.R. Laur. 1985. The influence of plant cover on surfperch abundance at an offshore temperate reef. *Env. Biol. Fish.* 12: 169-179.
- Ebert, T.A. & M.P. Russell. 1988. Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. *Limnol. Oceanogr.* 33: 286-294.
- Feder, H.M., C.H. Turner & C. Limbaugh. 1974. Observations of fishes associated with kelp beds in southern California. *Calif. Dept. Fish & Game, Fish Bull.* 160. 144 pp.
- Fuse, S. 1962. Animal communities in the *Zostera* belts. *Physiol. Ecol.* 11: 10-18.
- Gaines, S.D. & J. Roughgarden. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science* 235: 479-481.
- Gascon, D. & R.A. Miller. 1981. Colonization by nearshore fish on small artificial reefs in Barkley Sound, British Columbia. *Can. J. Zool.* 59: 1635-1646.
- Haldorson, L. & L. Richards. 1987. Post-larval copper rockfish in the Strait of Georgia: habitat use, feeding, and growth in the first year. pp. 129-142. *In: Proc. Int. Rockfish Symp.*, October, 1986, Anchorage, Alaska Sea Grant Rept. No. 87-2.
- Hallacher, L.E. & D.A. Roberts. 1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California. *Env. Biol. Fish.* 12: 91-110.
- Harada, E. 1962. A contribution to the biology of the black rockfish, *Sebastes inermis* (Cuvier et Valenciennes). *Publ. Seto Mar. Biol. Lab.* 5: 307-361.
- Hartman, A.R. 1987. Movement of scorpionfishes (Scorpaenidae: *Sebastes* and *Scorpaena*) in the Southern California Bight. *Calif. Fish & Game* 73: 68-79.
- Hatanaka, H.M. & K. Iizuka. 1962. Studies on the fish community in the *Zostera* area. III. Efficiency of production of *Sebastes inermis*. *Bull. Jap. Soc. Sci. Fish.* 28: 305-313.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in light of biological research. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer* 20: 1-228.
- Hobson, E.S. & J.R. Chess. 1976. Trophic interactions among zooplankters near shore at Santa Catalina Island, California, U.S. *Fish. Bull.* 74: 567-598.
- Hoelzer, G.A. 1987. The effect of early experience on aggression in two territorial scorpaenid fishes. *Env. Biol. Fish.* 19: 183-194.
- Hoelzer, G.A. 1988. Juvenile movement patterns in a territorial scorpaenid fish before and during settlement. *Mar. Ecol. Prog. Ser.* 45: 193-195.
- Holbrook, S.J., M.H. Carr, R.J. Schmitt & J.A. Coyer. 1990. The effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bull. Mar. Sci.* (in press).
- Holbrook, S.J. & R.J. Schmitt. 1988a. The combined effects of predation risk and food reward on patch selection. *Ecology* 69: 125-134.
- Holbrook, S.J. & R.J. Schmitt. 1988b. Effects of predation risk on foraging behavior: mechanisms altering patch choice. *J. Exp. Mar. Biol. Ecol.* 121: 151-163.
- Ikehara, K. & M. Nagahara. 1978. Fundamental studies for establishing rockfish culture techniques. IV. On the favorable contents of protein and lipid in compound food for a young rockfish, *Sebastes thompsoni* (Jordan et Hubbs). *Bull. Jap. Sea Reg. Fish. Res. Lab.* 29: 103-110.
- Jones, G.P. 1984. Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch & Schneider (Pisces: Labridae). I. Factors influencing recruitment. *J. Exp. Mar. Biol. Ecol.* 75: 257-276.
- Jones, G.P. 1986. Food availability affects growth in a coral reef fish. *Oecologia* 70: 136-139.
- Jones, G.P. 1987a. Some interactions between residents and recruits in two coral reef fishes. *J. Exp. Mar. Biol. Ecol.* 114: 169-182.
- Jones, G.P. 1987b. Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* 68: 1534-1547.
- Kanamoto, Z. 1977. On the ecology of hexagrammid in fish. III. Niches of *Agrammus agrammus* (Temminck et Schlegel) and *Hexagrammos otakii* (Jordan et Starks) and the mode of life of some reef fish. *Jap. J. Ecol.* 27: 215-226.
- Kelly, G.F. & A.M. Barker. 1961. Vertical distribution of young redfish in the Gulf of Maine. *Int. Comm. Northwest Atl. Fish. Spec. Publ.* 3: 220-233.
- Kikuchi, T. 1966. An ecological study on animal communities of the *Zostera marina* belt in Tomioka Bay, Amakusa, Kyushu. *Amakusa Mar. Biol. Lab. Kyushu Univ.* 1. 47 pp.
- Kitamori, R., K. Nagata & S. Kobayashi. 1959. The ecological study on Moba (zone of *Zostera marina* L.). (II). Seasonal changes. *Bull. Naikai Reg. Res. Lab.* 11: 7-16.
- Kusakari, M. 1978. Annual Report of the Hokkaido Institute of Mariculture. pp. 117-139.
- Laroche, W.A. & S.L. Richardson. 1980. Development and occurrence of larvae and juveniles of the rockfish *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. *U.S. Fish. Bull.* 77: 901-924.

- Larson, R.J. 1980a. Competition, habitat selection, and the bathymetric segregation of two rockfish species. *Ecol. Monogr.* 50: 221-239.
- Larson, R.J. 1980b. Territorial behavior of the black and yellow rockfish and gopher rockfish (Scorpaenidae, *Sebastes*). *Mar. Biol.* 58: 111-122.
- Leaman, B.M. 1976. The association between the black rockfish (*Sebastes melanops* Girard) and beds of the giant kelp (*Macrocystis integrifolia* Bory) in Barkley Sound, British Columbia. M. Sc. Thesis, University of British Columbia, Vancouver. 109 pp.
- Longhurst, A.R. 1967. Vertical distribution of zooplankton in relation to the eastern Pacific oxygen minimum. *Deep-Sea Res.* 14: 51-63.
- Love, M.S. 1980. Isolation of olive rockfish, *Sebastes serranoides*, populations off southern California. *U.S. Fish. Bull.* 77: 975-983.
- Love, M.S. 1981. Evidence of movements of some deepwater rockfishes (Scorpaenidae: genus *Sebastes*) off southern California. *Calif. Fish & Game* 67: 246-249.
- Love, M.S., P. Morris, M. McCrae & R. Collins. 1990. Life history aspects of 19 rockfish species (Scorpaenidae: *Sebastes*) from the Southern California Bight. NOAA Tech. Rept. 87. 38 pp.
- Love, M.S. & W. Westphal. 1981. Growth, reproduction and food habits of olive rockfish, *Sebastes serranoides*, off central California. *U.S. Fish. Bull.* 79: 533-545.
- Love, M.S., W. Westphal & R.A. Collins. 1985. Distributional patterns of fishes captured aboard commercial passenger fishing vessels along the northern Channel Islands, California. *U.S. Fish. Bull.* 83: 243-252.
- Mapstone, B.D. & A.J. Fowler. 1988. Recruitment and the structure of assemblages of fish on coral reefs. *Trends Ecol. Evol.* 3: 72-77.
- Marlow, G.G. & C.B. Miller. 1975. Pattern of vertical distribution and migration of zooplankton at ocean station. *P. Limnol. Oceanogr.* 20: 824-844.
- Mathews, S.B. & M.W. Barker. 1983. Movements of rockfish (*Sebastes*) tagged in northern Puget Sound, Washington. *U.S. Fish. Bull.* 82: 916-922.
- Mearns, A.J., M.J. Allen, M.D. Moore & M.J. Sherwood. 1980. Distribution, abundance, and recruitment of soft-bottom rockfishes (Scorpaenidae: *Sebastes*) on the southern California mainland shelf. *CalCOFI Rep.* 21: 180-190.
- Merkel, T.J. 1957. Food habits of the king salmon, *Oncorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. *Calif. Fish & Game* 43: 249-270.
- Miller, D.J. & 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. Dept. Fish & Game, Fish Bull.* 158: 137 pp.
- Moser, H.G. 1967. Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off southern California. *Copeia* 1967: 773-797.
- Moser, H.G. & E.H. Ahlstrom. 1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. *J. Fish. Res. Board Can.* 35: 981-996.
- Moser, H.G. & G.W. Boehlert. 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. *Env. Biol. Fish.* 30: 203-224.
- Moser, H.G. & J.L. Butler. 1981. Description of reared larvae and early juveniles of the calico rockfish, *Sebastes dalli*. *CalCOFI Rpt.* 22: 88-95.
- Moulton, L.L. 1977. An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. Ph.D. Dissertation, University of Washington, Seattle. 181 pp.
- Parrish, R.H., C.S. Nelson & A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.* 1: 175-203.
- Patten, B.G. 1973. Biological information on copper rockfish in Puget Sound, Washington. *Trans. Amer. Fish. Soc.* 102: 412-416.
- Pearcy, W.G., D.L. Stein, M.A. Hixon, B.K. Pikitch, W.H. Barss & R.M. Starr. 1990. Submersible observations of deep-reef fishes of Hecata Bank, Oregon. *U.S. Fish. Bull.* (in press).
- Phillips, J.B. 1964. Life history studies on ten species of rockfishes (genus *Sebastes*). *Calif. Dept. Fish & Game, Fish Bull.* 126. 70 pp.
- Richards, W.J. & K.C. Lindeman. 1987. Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis. *Bull. Mar. Sci.* 41: 392-410.
- Richardson, S.L. & W.A. Laroche. 1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger* and *Sebastes helvomaculatus* (family Scorpaenidae) off Oregon. *U.S. Fish. Bull.* 77: 1-46.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 11: 559-623.
- Roughgarden, J., S.D. Gaines & H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460-1466.
- Ryer, C.H. 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. *Mar. Ecol. Prog. Ser.* 48: 37-45.
- Sakai, K., H. Nagashima & K. Kiso. 1985. Growth and movement of artificially reared young rockfish, *Sebastes schlegeli*, after release in Matushima Bay. *Bull. Tohoku Reg. Fish. Res. Lab.* 47: 21-32.
- Sale, P.F. 1980. The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol. Ann. Rev.* 18: 367-421.
- Sale, P.F. & D.J. Ferrell. 1988. Early survivorship of juvenile coral reef fishes. *Coral Reef* 7: 117-124.
- Sale, P.F., P.J. Doherty & W.A. Douglas. 1980. Juvenile recruitment strategies and coexistence of territorial pomacentrids. *Bull. Mar. Sci.* 30: 147-158.
- Schmitt, R.J. & S.J. Holbrook. 1985. Patch selection by juvenile black surfperch (Embiotocidae) under variable risk: interactive influence of food quality and structural complexity. *J. Exp. Mar. Biol. Ecol.* 85: 269-285.
- Sherwood, M.J. & A.J. Mearns. 1981. Fate of post larval bot-

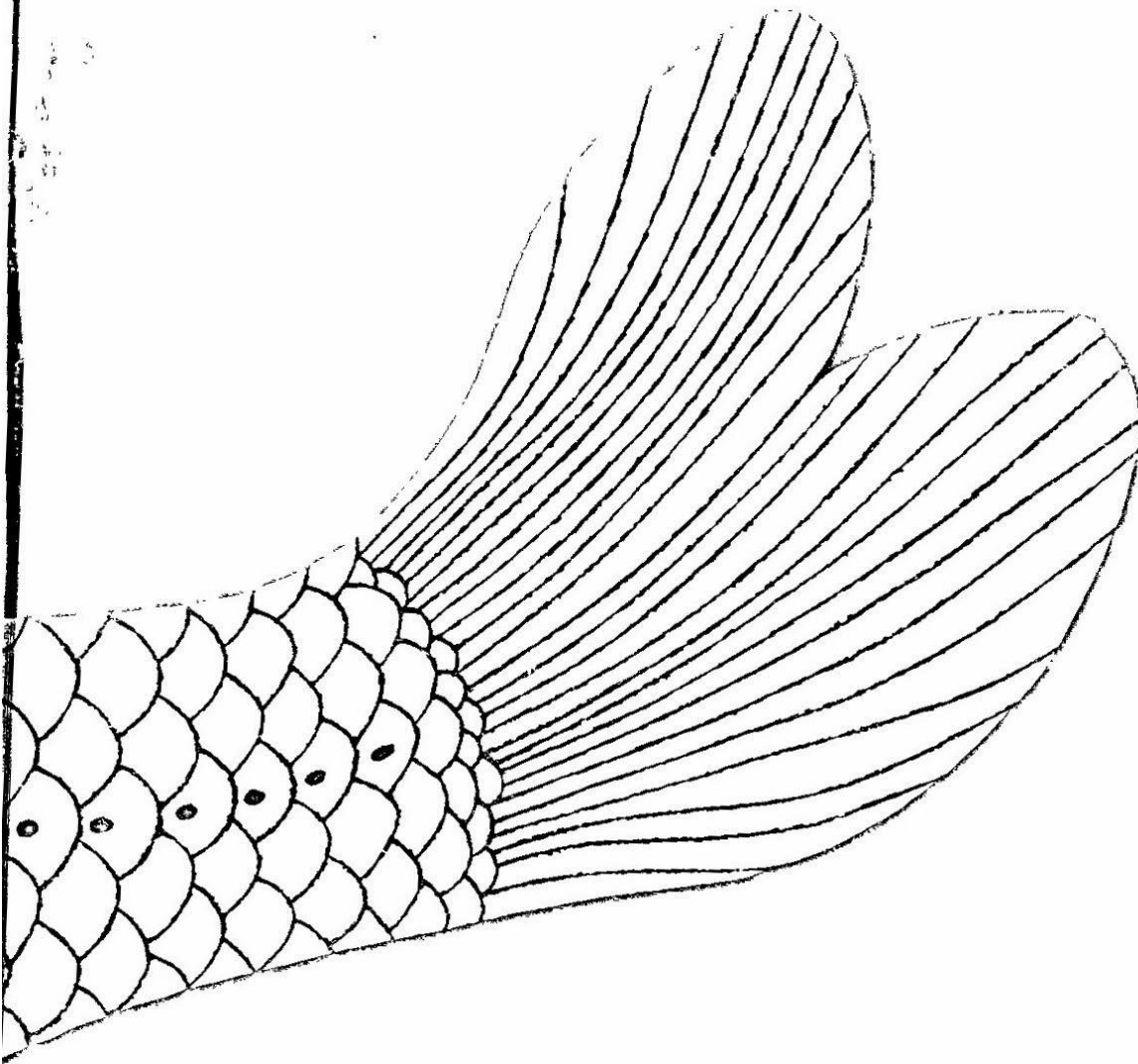
- tom fishes in a highly urbanized coastal zone. Rapport P.-V. Reun. Cons. Int. Explor. Mer 178: 104–111.
- Shiokawa, T. 1962. Studies on habits of coastal fishes in the Amakusa Islands. Part II: Growth and maturity of the purple rockfish, *Sebastes pachycephalus pachycephalus* Temminck et Schlegel. Rec. Oceanogr. W. Japan Spec. 6: 103–111.
- Shulman, M.J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. J. Exp. Mar. Biol. Ecol. 74: 85–109.
- Shulman, M.J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66: 1056–1066.
- Singer, M.M. 1982. Food habit and activity patterns of juvenile rockfishes (*Sebastes*) in a central California kelp forest. M.A. Thesis, California State University, San Jose. 75 pp.
- Singer, M.M. 1985. Food habits of juvenile rockfishes (*Sebastes*) in a central California kelp forest. U.S. Fish. Bull. 83: 531–541.
- Siokawa, T. & H. Tsukahara. 1961. Studies on habits of coastal fishes in the Amakusa Islands. Part I: Early life history of the purple rockfish, *Sebastes pachycephalus pachycephalus* Temminck et Schlegel. Rec. Oceanogr. W. Japan Spec. 5: 123–127.
- Sissenwine, M.P. 1984. Why do fish populations vary? pp. 59–94. In: R.M. May (ed.) Exploitation of Marine Communities, Springer-Verlag, Berlin.
- Steiner, W.W., J.L. Luczlovich & B.L. Olla. 1982. Activity, shelter usage, growth and recruitment of juvenile red hake *Urophycis chuss*. Mar. Ecol. Prog. Ser. 7: 125–135.
- Stephens, J.S., Jr., G.A. Jordan, P.A. Morris, M.M. Singer & G.E. McGowen. 1986. Can we relate larval fish abundance to recruitment or population stability? A preliminary analysis of recruitment to a temperate reef. CALCOFI Rep. 27: 65–83.
- Stephens, J.S., Jr., P.A. Morris, K. Zerba & M. Love. 1984. Factors affecting fish diversity on a temperate reef: the fish assemblage of Palos Verdes Point, 1974–1981. Env. Biol. Fish. 11: 259–275.
- Tsukahara, H. 1962. Studies on habits of coastal fishes in the Amakusa Islands, Part II: Early life history of the rockfish, *Sebastes marmoratus* (Cuvier et Valenciennes). Rec. Oceanogr. W. Japan Spec. 6: 49–55.
- Turner, C.H., E.E. Ebert & R.R. Given. 1969. Man-made reef ecology. Calif. Fish & Game, Fish Bull. 146. 221 pp.
- Warner, R.R. & T.P. Hughes. 1989. The population dynamics of reef fishes. Proc. 6th Inter. Coral Reef Symp., Townsville. (in press).
- Werner E.E. & D.J. Hall. 1988. The foraging rate – predation risk tradeoff and ontogenetic habitat shifts in the bluegill sunfish (*Lepomis macrochirus*). Ecology 69: 1352–1366.
- Westrheim, S.J. 1970. Survey of rockfishes, especially Pacific ocean perch in the northeast Pacific ocean, 1963–66. J. Fish. Res. Board Can. 27: 1781–1809.

Volume 30 Nos. 1-2 January 1991

CODEN EBFID3
ISSN 0378-1909

Environmental biology of fishes

Edited by R. W. Bert



Kluwer Academic Publishers