THE DISTRIBUTION OF PELAGIC JUVENILE ROCKFISH OF THE GENUS *SEBASTES* IN THE UPWELLING REGION OFF CENTRAL CALIFORNIA

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ABSTRACT

Many species of central California rockfishes conclude their pelagic stage during the spring–summer upwelling period, when advection of surface waters could carry them away from nearshore postpelagic habitats. We examined the distributions of late-stage pelagic juvenile rockfish in April and May/June of 1987 and 1988, based on midwater-trawl surveys between Point Reyes and Monterey Bay, California. Distributional patterns were complex, and changed rapidly with changing oceanographic conditions and with changes in species and size composition. The smallest pelagic juveniles often appeared offshore, in the region of the upwelling front, which suggested that they had been advected offshore at some time during upwelling. However, few pelagic juveniles were found offshore of the upwelling front. Larger pelagic juveniles were often found close to shore, even when upwelling was active. This suggests that later-stage pelagic juveniles undergo behavioral changes that enable them to move toward shore or remain there in spite of upwelling. We also found evidence of more passive advection and retention of pelagic juveniles of all sizes, including onshore movement during relaxation of upwelling. It appears that relaxation of upwelling may be a sufficient but not necessary aspect of the settlement of juvenile rockfish from pelagic to postpelagic habitats. If so, advection during upwelling may not have a negative effect on the settlement and ultimate recruitment of rockfish.

RESUMEN

Muchas especies de rocot del centro de California concluyen su estadio pelágico durante el periodo de surgencias de primavera–verano, cuando la advección de las aguas superficiales podría transportarlos lejos de los hábitats post-pelágicos cercanos a la costa. Examinamos los patrones de distribución de los estadios tardíos de los juveniles pelágicos de los rocot durante abril y mayo/junio de 1987 y 1988. Los ejemplares fueron obtenidos por medio de arrastres a media agua en un área comprendida entre Punta Reyes y la Bahía de Monterey, California. Los patrones de distribución encontrados fueron complejos y cambiaron rápidamente de acuerdo a las condiciones oceanográficas y de acuerdo a cambios en la composición por especies y tallas. Los juveniles pelágicos mas pequeños se encontraron a menudo alejados de la costa, en la región asociada al frente de la surgencia, lo que sugiere que fueron transportados por la corriente de surgencia. Sin embargo, pocos juveniles pelágicos fueron encontrados del lado hacia mar adentro del frente de la surgencia. Los juveniles pelágicos de mayor tamaño se encontraron a menudo próximos a la costa, aun en los periodos de actividad de la surgencia. Lo anterior sugiere que los juveniles pelágicos cambian su comportamiento durante sus fases tardías, lo que les permite desplazarse hacia la costa, o bien, permanecer allí a pesar de la surgencia. Asimismo encontramos evidencia de un proceso mas pasivo de advección y retención de juveniles pelágicos de todas las tallas, incluyendo movimiento hacia la costa durante periodos de aflojamiento de la surgencia. Este aflojamiento podría ser un aspecto importante pero no determinante para el establecimiento de los juveniles del rocot del hábitat pelágico al post-pelágico. En tal caso, la advección durante la surgencia podría no tener un efecto negativo en el asentamiento y reclutamiento final del rocot.

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INTRODUCTION

The problems of drift and retention in marine animals with pelagic larval stages are widely recognized (e.g., Norcross and Shaw 1984; Bakun 1985, 1986; Sinclair 1988). To complete their life cycles, pelagic individuals must either remain in areas suitable for the next stage in the life cycle, or travel from the pelagic zone to these areas. Coastal upwelling systems pose a particular problem in this respect, since surface waters are transported offshore, possibly carrying propagules away from the areas inhabited by postpelagic juveniles. Parrish et al. (1981), Bakun and Parrish (1982), and Bakun (1985) suggested that the potential for offshore advection of larvae has selected for reproductive patterns that minimize the exposure of larvae to upwelling conditions, and Roughgarden et al. (1988) described the negative effect of offshore advection in barnacles.

Dozens of species of rockfish in the genus *Sebastes* inhabit the shelf and coastal zones in the region of maximum upwelling between Cape Blanco, Oregon, and Point Conception, California (Chen 1971). Many of these species bear young in winter and early spring, before upwelling begins (Kendall and Lenarz 1987; Wyllie

Echeverria 1987). However, the larvae and juveniles of many species remain pelagic well into the spring–summer upwelling period (Kendall and Lenarz 1987; Moser and Boehlert 1991), so that juveniles of these species must settle from the pelagic zone when upwelling is active (Anderson 1983; Carr 1983, 1991). Thus, while viviparity and winter spawning in rockfishes could be seen as adaptations to the negative effects of offshore advection during upwelling (Parrish et al. 1981; Ainley et al. 1993), the late pelagic stages of many rockfish are exposed to upwelling at the time they settle. If this offshore advection does affect rockfish, spatial and temporal variation in upwelling could have important effects on both year-class strength and the geographical structure of rockfish populations.

Some evidence suggests that upwelling does have an advective effect on pelagic-stage rockfish. Moser and Boehlert (1991) noted the offshore distribution of some *Sebastes* larvae, and their figures indicate relatively greater offshore distributions off northern California, where seaward jets are common. Simpson (1987) also illustrated the offshore distribution of *Sebastes* larvae in a filament of advected water associated with an offshore eddy. Brodeur et al. (1985) found *Sebastes* larvae unusually close to shore during the El Niño spring of 1983, but much farther offshore soon after an upwelling event later that summer. Hobson and Howard (1989) found that mass strandings of juvenile shortbelly rockfish near shore in northern California were correlated with onshore transport, suggesting that the usual offshore distributions were maintained by normal offshore transport. Finally, Norton (1987) has suggested that year-class strength of widow rockfish is correlated with onshore transport, and Ainley et al. (1993) found that year-class strength in the suite of species found off central California (dominated by shortbelly rockfish) was affected negatively by strong upwelling in January–February.

In this paper we examine the distribution of late-stage pelagic juvenile rockfishes off central California. Our purpose is to infer the effects of upwelling on these fish by comparing their distributions with oceanographic features associated with upwelling.

BACKGROUND

Species

The species of *Sebastes* covered in this study extrude larvae a few millimeters long in areas ranging from coastal kelp forests to the edge of the continental shelf. Most of the central California species release larvae between November and March, but the principal period of parturition varies among species, and some species have extended periods of parturition (Wyllie Echeverria 1987).

At least several species of *Sebastes* are pelagic for 3–5 months, and appear to grow at a rate of about 0.5 mm per day (Woodbury and Ralston 1991). They transform into pelagic juveniles at least 20 mm long before leaving the pelagic zone for juvenile habitats. The juvenile habitats vary among species at several scales (Love et al. 1991). Species of *Sebastes* commonly leave the pelagic zone for habitats that are shallower than those occupied by adults, often recruiting to areas quite near shore (Love et al. 1991). Observations by divers demonstrate that nearshore species show considerable specialization of microhabitats (Carr 1983, 1991; Love et al. 1991). Some deepwater species make extensive surface-to-bottom migrations (Boehlert 1977); these species were not commonly encountered as pelagic juveniles in this study. Although many species clearly leave the pelagic zone for association with the benthos, the distinction between pelagic and benthic habitat may be less clear in species such as shortbelly and chilipepper rockfish, whose postpelagic juveniles and adults form schools that associate more loosely with the bottom. Nevertheless, these species become invulnerable to midwater trawls, presumably by shifting habitat. Essentially all of the species covered in this study settle from the pelagic zone to more benthic habitats that are shoreward of their pelagic distributions.

Several aspects of the ecology of pelagic juveniles vary among species. The timing and duration of parturition, along with the duration of the pelagic stage, influence the timing and duration of their appearance as pelagic juveniles in midwater trawls and their recruitment to postpelagic habitats. A preliminary overview of the seasonal occurrence of pelagic and newly settled juveniles of species encountered frequently in our study is presented in table 1. Some species are taken in midwater trawls for limited periods; others are taken over longer periods of time. The peak seasonal occurrence of pelagic juveniles varies by a month or more from year to year.

The size of pelagic juveniles also varies among species (appendix), and the relative sizes of pelagic and settled individuals are concordant (comparing data in the appendix with Anderson 1983). Data in the appendix also show that some species are present in relatively small ranges of size while others have wider size ranges as pelagic juveniles. Because size may itself be significant in the movements of pelagic juveniles or because size may be a proxy for age and ontogeny (Woodbury and Ralston 1991), we divided the size range of each species into categories (table 2). The categories were based upon the range of sizes present and the abundance of the species. Some species were too uncommon for division into size groups, and others were common enough for only two size classes. Abundant species were typically divided into three size classes, in hopes of distinguishing distributional characteristics at the extremes of size

TABLE 1
Summary of the Relative Seasonal Occurrence of Pelagic and Newly Settled Young-of-the-Year Juvenile Rockfish off Central California

Relative peak in occurrence	Relative duration of occurrence: Brief	Extended	Variable or not assessable
Early (April)	Pygmy Copper[a]		
		Chilipepper	
	Stripetail		
	Canary		
		Shortbelly	
			Darkblotched
Intermediate (May–early June)	Blue Squarespot		
			Cowcod
		Bocaccio	
	Widow		
			Black
	Yellowtail		
Late (June or later)			"Copper complex"[b] "Rosy complex"[c]
Variable or not assessable			Brown

[a]Members of the "copper complex" (a group of species that are difficult to distinguish as pelagic juveniles) that occur early in the season are most likely copper rockfish (*S. caurinus*), which appear in kelp forests the earliest of similar-appearing species (Anderson 1983).
[b]Members of the "copper complex" occurring later in spring are probably gopher rockfish (*S. carnatus*), black and yellow rockfish (*S. chrysomelas*), or kelp rockfish (*S. atrovirens*), which settle in kelp forests in June through August (Anderson 1983).
[c]The "rosy complex" contains members of the subgenus *Sebastomus*.

and age. For the analysis of distributions in any particular set of samples, size classes may have been pooled, based on abundance (see below).

Different species of *Sebastes* also have different depth distributions as pelagic juveniles (Lenarz et al. 1991). Bocaccio are found shallower than most other species, and yellowtail, blue, and pygmy rockfish are found deeper.

Physical System

Our study area, from Point Reyes to Monterey Bay (figure 1), is oceanographically complex. During the spring–summer period, when rockfish are completing their pelagic phase, episodic northwesterly winds lead to pulses of upwelling on a scale of days. Two centers of upwelling are located within the region: a strong upwelling center at Point Reyes, and a weaker center north of Monterey Bay, off Davenport (Schwing et al. 1991). Filaments of upwelled water from these centers carry cool water offshore and to the south, and the edges of these filaments are often marked by strong frontal regions (Schwing et al. 1991). The filaments and associated fronts are frequently associated with eddies and meanders. These eddies and meanders serve to mix upwelled water with offshore water and with older mixes of upwelled and offshore waters. Freshwater outflow from San Francisco Bay enters the Gulf of the Farallons and often extends to the south. Monterey Bay frequently contains upwelled water from the Davenport upwelling center, warmed as it recirculates. Cessation of northwesterly winds leads to relaxation of upwelling, accompanied by onshore movement of offshore waters and further mixing of upwelled and other waters. Changes in circulation take place on a scale of days to weeks.

METHODS

Field

This study is based on data gathered in cruises on the R/V *David Starr Jordan* off central California during 1987 and 1988. Part of a long-term survey, these cruises sampled pelagic juvenile rockfish with a midwater trawl and gathered hydrographic data. Pelagic juveniles of many species of rockfish were relatively abundant in these years.

Fish were sampled at night with a modified Cobb midwater trawl (nominally square mouth 14 m on a side, and 9.5 mm stretched mesh cod-end liner) which was towed at depth for 15 min. at 5 kmh^{-1} (Wyllie Echeverria et al. 1990). The typical targeted depths were 37 m at most stations and 13 m at bottom depths shallower than 91 m (figure 1). Hauls at some stations were carried out at two or more depths, usually selected from 13, 37, and 117 m. The usual sampling plan was to cover a standard set of stations within a 10-night "sweep," and to sample additional sites if time permitted within the 10-day period. Typical standard stations and some extra stations are illustrated in figure 1. In 1987 and 1988, cruises were carried out in April and again in May–June. One sweep of the study area was carried out in April, and three sweeps were carried out in May–June (table 3). Rockfish and other animals were identified and enumerated, and the standard length of all rockfish or a 100-fish subsample of each species was measured.

Two sets of hydrographic data were gathered. CTD casts were made with a Sea-Bird Electronics SEA-CAT-SBE-19 profiler at each trawl station and at sets of locations interspersed between trawl stations. Raw temperature and conductivity data were processed to remove outliers and were smoothed; salinity and density were computed and then smoothed, as described in Schwing et al. (1990).

Near-surface temperature and salinity were also recorded on a 5–15 min. basis continuously during most of each cruise. Ideally, the shipboard thermosalinograph continuously measured temperature and salinity of water drawn from a through-hull connection, and the ship computer's CAMAC system periodically captured these data and information on location and other variables. When totally operational, this system provided data on

TABLE 2
Definitions of Size Classes, and the Mean Sizes, Number of Areas Occupied, and Mean Abundances of Pelagic Juvenile Rockfish (Genus *Sebastes*) Captured in Midwater Trawls, 1987–1988

		APRIL 1987			JUNE 1987									APRIL 1988			JUNE 1988					
					SWEEP 1[a]			SWEEP 2			SWEEP 3						SWEEP 1			SWEEP 2		
Species	Size Class[b] (range)	Mean SL[c]	No. of areas[d]	Mean abund. (SD)[e]	Mean SL	No. of areas	Mean abund. (SD)	Mean SL	No. of areas	Mean abund. (SD)	Mean SL	No. of areas	Mean abund. SD	Mean SL	No. of areas	Mean abund. (SD)	Mean SL	No. of areas	Mean abund. (SD)	Mean SL	No. of areas	Mean abund. (SD)
Black rockfish *S. melanops* (BLK)	All	—	—	—	40.3	5	0.117 (0.166)	37.3	7	0.187 (0.308)	34.3	4	0.099 (0.186)	—	—	—	—	—	—	—	—	—
Blue rockfish *S. mystinus* (BLUE)	S+M (<54.5)	38.9	4	0.093 (0.159)	—	—	—	—	—	—	—	—	—	41.6	10	0.870 (0.567)	—	—	—	—	—	—
	Medium (31–54)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48.3	14	1.450 (1.102)	—	—	—
	M+L (>30.5)	—	—	—	48.7	13	1.062 (0.501)	49.8	13	0.773 (0.835)	—	—	—	—	—	—	—	—	—	48.2	10	0.905 (1.005)
Brown rockfish *S. auriculatus* (BRWN)	All	23.0	8	0.271 (0.303)	—	—	—	—	—	—	—	—	—	24.4	5	0.288 (0.365)	—	—	—	—	—	—
Bocaccio *S. paucispinus* (BOC)	Small (<35.5)	—	—	—	—	—	—	28.7	5	0.164 (0.345)	26.4	5	0.215 (0.318)	31.8	5	0.152 (0.200)	—	—	—	—	—	—
	S+M (<60.5)	42.6	4	0.249 (0.478)	43.1	4	0.147 (0.253)	—	—	—	—	—	—	—	—	—	45.4	9	0.454 (0.462)	—	—	—
	Medium (36–60)	—	—	—	—	—	—	44.0	9	0.286 (0.420)	—	—	—	—	—	—	—	—	—	—	—	—
	M+L (>35.5)	—	—	—	—	—	—	—	—	—	—	—	—	56.5	8	0.418 (0.371)	—	—	—	77.0	5	0.230 (0.398)
	Large (>60.5)	—	—	—	71.6	8	0.266 (0.348)	77.5	4	0.136 (0.281)	—	—	—	—	—	—	83.2	4	0.090 (0.193)	—	—	—
Canary rockfish *S. pinniger* (CAN)	Small (<32.5)	—	—	—	26.6	6	0.147 (0.195)	26.0	11	0.287 (0.283)	—	—	—	23.9	5	0.278 (0.414)	30.2	8	0.321 (0.422)	28.1	5	0.227 (0.412)
	All	24.7	8	0.307 (0.369)	—	—	—	—	—	—	29.1	7	0.227 (0.304)	—	—	—	—	—	—	—	—	—
	Large (>32.5)	—	—	—	36.3	4	0.100 (0.185)	35.4	4	0.164 (0.336)	—	—	—	—	—	—	36.3	10	0.893 (1.028)	38.4	5	0.286 (0.595)
Chilipepper *S. goodei* (CHILI)	Small (<35.5)	32.1	6	1.025 (1.335)	—	—	—	—	—	—	—	—	—	32.4	11	1.945 (1.184)	—	—	—	—	—	—
	S+M (<59.5)	—	—	—	53.0	12	1.071 (0.892)	53.7	6	0.253 (0.443)	—	—	—	—	—	—	—	—	—	—	—	—
	Medium (36–59)	38.2	7	0.749 (1.298)	—	—	—	—	—	—	68.0 S+M+L	3	0.241 (0.520)	42.0	11	2.316 (1.787)	53.4	10	1.318 (1.810)	—	—	—
	M+L (>35.5)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	60.4	6	0.360 (0.935)
	Large (>59.5)	—	—	—	62.4	10	0.541 (0.672)	66.9	6	0.470 (0.847)	—	—	—	—	—	—	65.0	3	0.481 (1.035)	—	—	—
"Copper complex"[f] (COPPER)	All	24.7	5	0.199 (0.391)	—	—	—	—	—	—	17.8	5	0.190 (0.326)	—	—	—	—	—	—	—	—	—
Cowcod *S. levis* (COW)	All	—	—	—	—	—	—	—	—	—	—	—	—	38.6	6	0.269 (0.345)	—	—	—	—	—	—
Darkblotched *S. crameri* (DKBLT)	All	33.0	5	0.132 (0.191)	—	—	—	—	—	—	—	—	—	42.7	3	0.125 (0.278)	—	—	—	—	—	—
Halfbanded rockfish *S. semicinctus* (HLFBND)	All	—	—	—	—	—	—	43.8	4	0.065 (0.126)	—	—	—	35.4	4	0.126 (0.203)	—	—	—	—	—	—
Olive rockfish *S. serranoides* (OLIVE)	All	—	—	—	—	—	—	—	—	—	—	—	—	44.4	6	0.229 (0.326)	—	—	—	—	—	—
Pygmy rockfish *S. wilsoni* (PYGMY)	All	30.3	6	0.191 (0.260)	—	—	—	—	—	—	—	—	—	32.2	10	0.836 (0.646)	—	—	—	—	—	—

Species	Size Class (range)	APRIL 1987 Mean SL[c]	APRIL 1987 No. of areas[d]	APRIL 1987 Mean abund. (SD)[e]	JUNE 1987 SWEEP 1[a] Mean SL	JUNE 1987 SWEEP 1[a] No. of areas	JUNE 1987 SWEEP 1[a] Mean abund. (SD)	JUNE 1987 SWEEP 2 Mean SL	JUNE 1987 SWEEP 2 No. of areas	JUNE 1987 SWEEP 2 Mean abund. (SD)	JUNE 1987 SWEEP 3 Mean SL	JUNE 1987 SWEEP 3 No. of areas	JUNE 1987 SWEEP 3 Mean abund. SD	APRIL 1988 Mean SL[c]	APRIL 1988 No. of areas[d]	APRIL 1988 Mean abund. (SD)[e]	JUNE 1988 SWEEP 1 Mean SL	JUNE 1988 SWEEP 1 No. of areas	JUNE 1988 SWEEP 1 Mean abund. (SD)	JUNE 1988 SWEEP 2 Mean SL	JUNE 1988 SWEEP 2 No. of areas	JUNE 1988 SWEEP 2 Mean abund. (SD)
"Rosy complex" *Sebastomus* subgenus (ROSY)	All	—	—	—	—	—	—	—	—	—	18.2	2	0.152 (0.449)	—	—	—	—	—	—	—	—	—
Shortbelly rockfish *S. jordani* (SBY)	Small (<32.5)	29.2	8	0.824 (1.124)	24.9	4	0.215 (0.393)	25.8	6	0.622 (0.962)	24.6	7	0.897 (1.122)	29.9	9	0.645 (0.501)	—	—	—	—	—	—
	Medium (33–57)	38.3	8	1.094 (1.487)	49.4	12	1.145 (1.065)	45.8	15	1.325 (1.069)	42.9	9	0.658 (0.754)	—	—	—	54.5	12	1.531 (1.604)	49.2	8	0.392 (0.434)
	M+L (>32.5)	—	—	—	—	—	—	—	—	—	—	—	—	45.9	11	2.902 (1.546)	—	—	—	—	—	—
	Large (>57.5)	—	—	—	63.5	12	1.908 (1.806)	67.9	15	2.528 (1.960)	72.1	8	0.584 (0.721)	—	—	—	66.4	13	2.789 (1.871)	67.2	8	2.204 (2.236)
Squarespot rockfish *S. hopkinsi* (SQSPT)	S+M (<54.5)	30.3	5	0.177 (0.328)	49.1	9	0.753 (0.841)	—	—	—	—	—	—	43.2	8	0.984 (1.563)	—	—	—			
	Medium (31–54)	—	—	—	—	—	—	50.7 S+M+L	11	0.474 (0.432)	—	—	—	—	—	—	51.5	10	0.539 (0.450)	—	—	—
	M+L (>30.5)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	51.2	8	0.314 (0.390)
	Large (>54.5)	—	—	—	56.3	6	0.145 (0.194)	—	—	—	—	—	—	—	—	—	57.1	5	0.304 (0.502)	—	—	—
Stripetail rockfish *S. saxicola* (STRPTL)	Small (<32.5)	25.7	6	0.331 (0.497)	—	—	—	—	—	—	—	—	—	29.4	9	0.820 (0.861)	—	—	—	—	—	—
	All	—	—	—	40.5	12	0.659 (0.710)	37.7	7	0.188 (0.265)	—	—	—	—	—	—	37.2	11	0.474 (0.409)	33.2	4	0.097 (0.163)
	Large (>32.5)	36.2	5	0.209 (0.305)	—	—	—	—	—	—	—	—	—	35.3	8	0.947 (1.009)	—	—	—	—	—	—
Widow rockfish *S. entomelas* (WID)	Small (<35.5)	29.5	4	0.123 (0.195)	—	—	—	28.3	2	0.140 (0.396)	—	—	—	—	—	—	—	—	—	—	—	—
	S+M (<59.5)	—	—	—	54.0	11	0.834 (0.777)	—	—	—	—	—	—	40.9	7	0.298 (0.338)	—	—	—	—	—	—
	Medium (36–59)	40.9	4	0.100 (0.199)	—	—	—	53.1	15	1.133 (0.894)	—	—	—	—	—	—	51.0	13	0.986 (0.897)	50.1	9	0.790 (0.877)
	M+L (>35.5)	—	—	—	—	—	—	—	—	—	51.5	6	0.232 (0.336)	—	—	—	—	—	—	—	—	—
	Large (>59.5)	—	—	—	61.1	6	0.288 (0.489)	61.9	13	0.814 (0.731)	—	—	—	—	—	—	62.8	3	0.193 (0.497)	64.7	7	0.518 (0.713)
Yellowtail rockfish *S. flavidus* (YT)	Small (<42.5)	—	—	—	37.8	4	0.099 (0.169)	37.9	8	0.152 (0.174)	38.3	5	0.116 (0.163)	—	—	—	38.6	6	0.336 (0.652)	—	—	—
	All	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	41.3	8	0.301 (0.347)
	Large (>42.5)	—	—	—	45.9	6	0.167 (0.282)	47.9	9	0.470 (0.643)	45.1	6	0.188 (0.258)	—	—	—	45.1	9	0.474 (0.554)	—	—	—

[a]See table 3 for dates of sweeps. Readers interested in the abundances at each group of stations in a sweep can request these tables from the senior author.
[b]Adjacent size classes were combined when one or more size classes were not abundant. Mean lengths and abundances in different sweeps are presented, as employed in further analyses, only for those species/size classes (or combinations thereof) that were common enough to be analyzed.
[c]Sizes are in mm standard length.
[d]Areas occupied are the number of station groups (see description of each sweep) at which the species/size classes were present.
[e]Abundances are grand means and standard deviations of the average $\ln(x+1)$-transformed catches for each station group, averaged over all station groups.
[f]"Copper complex": *S. caurinus*, *S. chyrsomelas*, *S. carnatus*, *S. atrovirens*, and other related species.

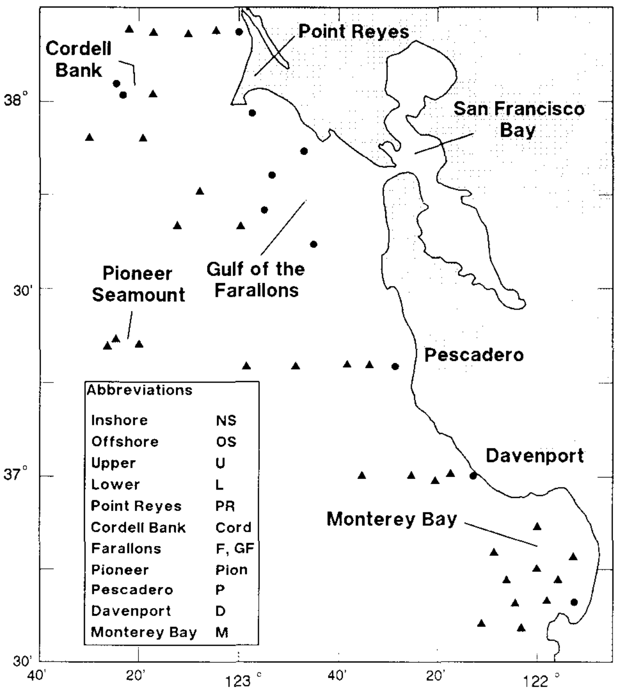


Figure 1. Map of the study area and typical midwater trawl stations. All but the stations at Cordell Bank and Pioneer Seamount were standard survey stations. The standard trawl depth was approximately 30 m at the stations marked with *triangles*, and approximately 10 m at stations marked with *circles*. Abbreviations of geographic terms that are used throughout the paper are defined in the box.

position, temperature, and salinity every 5 min. during the cruise. For use here, position was recalculated from recorded LORAN readings (rather than from SAT-NAV positions, which were subject to drift between satellite fixes), and the data set was edited to remove large blocks of data gathered when the vessel was not under way and to remove portions of the data stream that sampled trawled areas redundantly, before or after trawls actually took place. The entire system was not always operational. When the thermosalinograph was operating but the ship's computer was not, temperature and salinity from the thermosalinograph were recorded manually every 5–15 min., along with LORAN positions from the bridge. When the thermosalinograph was not working, temperature was measured by thermometer in the ship's running seawater system every 5–15 min., and 5 m salinity was determined from the CTD profiles. Temperatures and salinities thus gathered were cross-calibrated with thermosalinograph values and corrected before use.

Surface contours of temperature and salinity were computed with SURFER version 4.0 (Golden Software) using the kriging algorithm on the nearest three values in each octant surrounding smoothing points. In a continuous sweep of the study area, one pseudosynoptic map was made, but when a sweep was interrupted (particularly by strong winds that generated upwelling), contour maps were produced separately for each segment of the sweep and superimposed on each other.

TABLE 3
Dates of Sampling Cruises on the R/V *David Starr Jordan* in 1987 and 1988

Survey	Dates
April 1987	10–22 April
May/June 1987	
Sweep 1	23 May–1 June
Sweep 2	2–12 June
Sweep 3	12–21 June
April 1988	16–22 April
May/June 1988	
Sweep 1	22 May–2 June
Sweep 2	2–11 June
Sweep 3	11–18 June

Data Analysis

In overview, our objective was to infer the effects of upwelling and other oceanographic factors on pelagic juvenile rockfish by describing their distributions relative to sea temperature and salinity. Our general procedure for each sweep was to:

a. define regional groupings of surface temperatures and salinities, as an aid in displaying the range of conditions present,
b. combine trawl stations into small groups based upon geographical proximity and similarity of temperature and salinity,
c. determine which species and size classes of rockfish to include in the analysis, removing those that were too rare to be useful,
d. compute the average abundance of each species/size class of rockfish in each group of stations,
e. use an ordination procedure to find groups of species/size classes with similar distributional patterns,
f. compute the average, over species, of the standard score of abundance for each group of species in each area, and
g. plot these standardized deviations from mean abundance on contour maps of salinity or temperature.

Plots of temperature vs. salinity were useful in displaying the range of conditions present during a sweep and in defining groups of nearby trawl stations with similar hydrographic conditions. Such plots also often revealed geographically linked sets of points indicative of differing conditions, such as upwelled water off Point Reyes vs. Davenport, or warm, low-salinity water originating offshore vs. San Francisco Bay. To simplify our display, we therefore defined geographically related sets of temperature-salinity values, drew envelopes around these points, and used these envelopes in further displays. These envelopes are not meant to imply water masses in the classical oceanographic sense, although they often work that way, but are intended to aid in the visualization of conditions. In the interest of space conservation, we present the derivation of only one set of envelopes, as an example. Curious readers may request other derivations from the senior author.

In our analysis, we used groups of nearby trawl stations with similar hydrography as our basic "sample" units, rather than individual stations. We had noted that such groups of stations typically had similar catches, but rarer species or size classes were better assessed if nearby stations were grouped. In addition, grouping nearby stations minimized the occurrence of sample units with no rockfish at all, which could not be included in ordinations. Stations were usually combined into latitudinal and onshore-offshore groups in which the latitudinal groupings normally corresponded with the sets of stations shown in figure 1: Point Reyes, Farallons (sometimes upper and lower), Pescadero, Davenport, and Monterey (sometimes upper and lower). Cordell Bank stations were usually incorporated into groups with Point Reyes or upper Farallons stations. The latitudinal groupings often differed oceanographically, but even when they did not, we kept them separate to preserve the possibility of detecting geographic variation.

Onshore and offshore groups of stations were normally defined on the basis of similarities of temperature and salinity. The temperature and salinity used to characterize each trawl station was defined as either the average of the CAMAC values recorded during a trawl (when the CAMAC system was operating), or the single measurements made at each station when the CAMAC system was not operating. Once identified, each group of stations was characterized by the average position, temperature, and salinity of stations within the group. This means of grouping stations meant that some stations changed groups when oceanographic conditions changed. We felt this appropriate, because the composition and abundance of organisms sampled in trawls at a particular station often changed with oceanographic conditions.

The abundance of various species and size classes differed seasonally and annually, so each species/size class was not always common. Species/size classes present in fewer than a third or so of the station groups were not treated separately in the analysis of distributions, because they offered little comparative information. Instead, size classes were combined when one or more adjacent size classes within a species were not common. Catches in each species/size class at each station were transformed to $\ln(x+1)$ and averaged over the stations in each station group. Hauls at standard depths (37 m, or 13 m at stations in shallow water [circles in figure 1]) were used in the main comparisons reported here.

Rather than attempting to describe the distribution of each species and size class separately, we hoped that some species and size classes would share distributional patterns that could be characterized together. We used the ordination method of detrended correspondence analysis (also known as detrended reciprocal averaging) to seek common distributional patterns. This procedure simultaneously ordinates taxa and areas, so that the relative positions of taxa on an ordination axis correspond with the relative positions of areas on the axis (Gauch 1982). The corresponding areas are those in which these taxa are relatively abundant, and the corresponding taxa are those that tend to co-occur in these areas. We used the detrended reciprocal averaging program of Pimintel and Smith (1985) to carry out the ordinations, employing the default program options and the downweighting of rare species. Jackson and Somers (1991) had found some instability of solutions with variation in one of the options in detrended correspondence analysis (the number of segments for detrending), but we found little evidence for such instability in ordination of three of our data sets in which we varied the number of detrending segments, so we used the default number of 27.

In addition to using the ordinations directly to examine distributional patterns, we used the proximity of taxa in the ordinations (supplemented by cluster analyses, which are not presented here) to group species/size classes with apparently similar distributions for further analysis of distributional patterns. We used an index of abundance for each group of species in which the index, I, was:

$$I = \frac{\sum_{i=1}^{n}\left(\frac{\bar{x}_{ij}-\bar{x}_{i\cdot}}{s_{i\cdot}}\right)}{n}$$

where $\bar{x}_{ij}$ was the average log-transformed abundance of species/size class i in the stations of station group j, $\bar{x}_{i\cdot}$ and $s_{i\cdot}$ were the average and standard deviation of the abundance of species i over all station groups, and n was the number of species/size classes in a group of species/size classes. These indices of abundance were plotted on contour maps of salinity to examine distributional patterns.

The above analyses were applied to each sweep of the study area except for sweep 3 of May/June 1988, when most pelagic juvenile rockfish had already settled. Additional analyses of specially sampled areas or of distinctive bathymetric distributions were carried out as appropriate.

RESULTS

April 1987

One sweep of the study area was completed between April 10 and April 20, 1987. A two-day seaward ex-

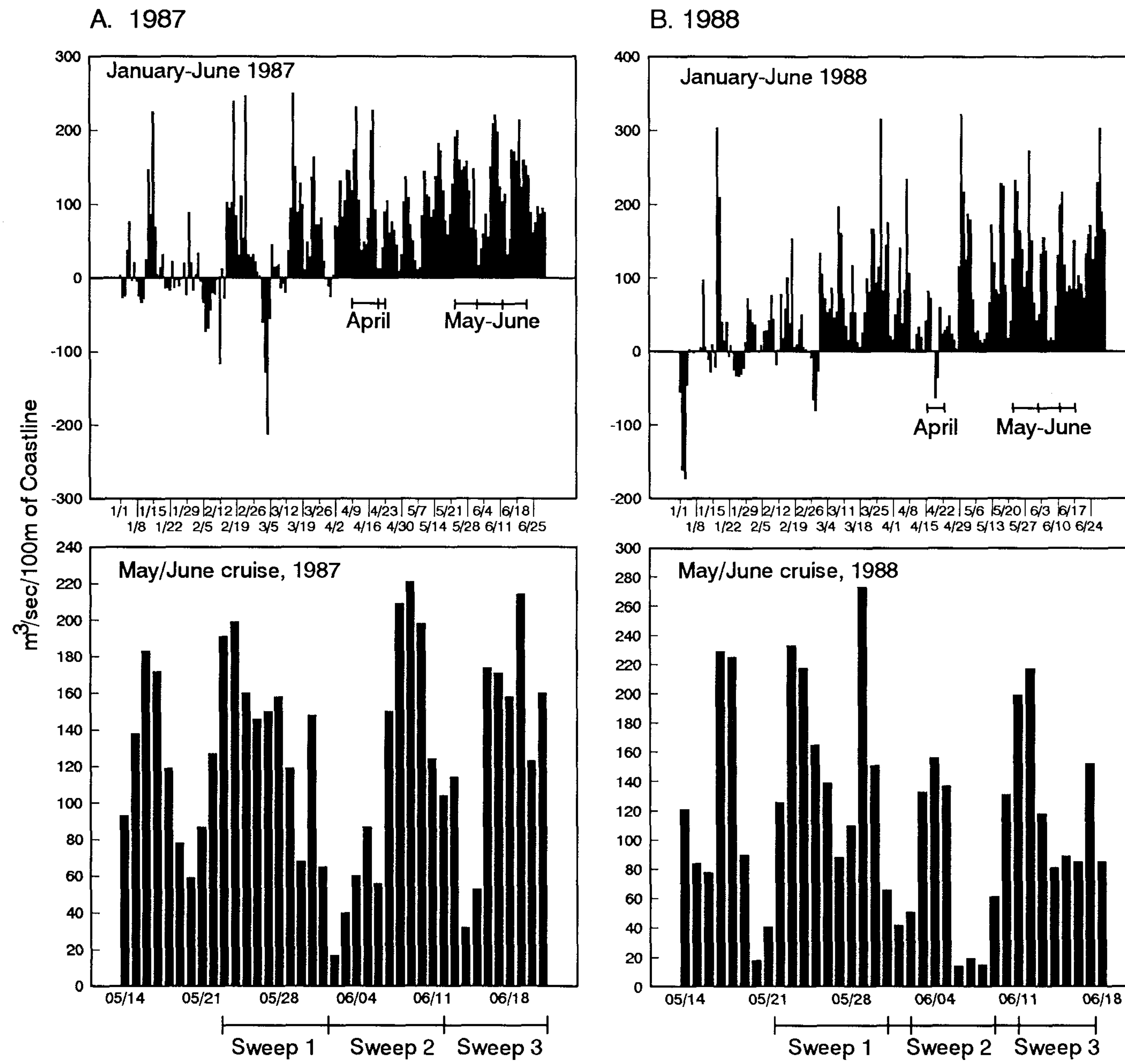


Figure 2. Bakun's upwelling index at 36° N, 122° W.

cursion was made following the regular sweep, in which one leg extended from the outer Pescadero stations past Pioneer Seamount, and the other offshore of Point Reyes.

Oceanography. Periods of upwelling-favorable winds had occurred intermittently for two months before this cruise (figure 2a). Upwelling conditions prevailed for several days immediately before the cruise and persisted for its first few days. After a short period of reduced winds, another brief windy period occurred before the end of the regular sweep (figure 2a).

Active upwelling was evident in the surface temperatures and salinities encountered during the regular sweep (figures 3 and 4). Tongues of cool, saline water extended from Point Reyes and Davenport, and relatively sharp fronts separated the recently upwelled water nearshore from warmer, less saline waters offshore in both areas. The larger Point Reyes plume extended in a convoluted pattern south of the Gulf of the Farallons, while the Davenport plume extended south in a less-pronounced pattern. Fresh water from San Francisco Bay was evident along the coast to Pescadero. The high salinities but warm temperatures in Monterey Bay suggested that the surface waters had been upwelled and subsequently warmed without mixing with offshore waters.

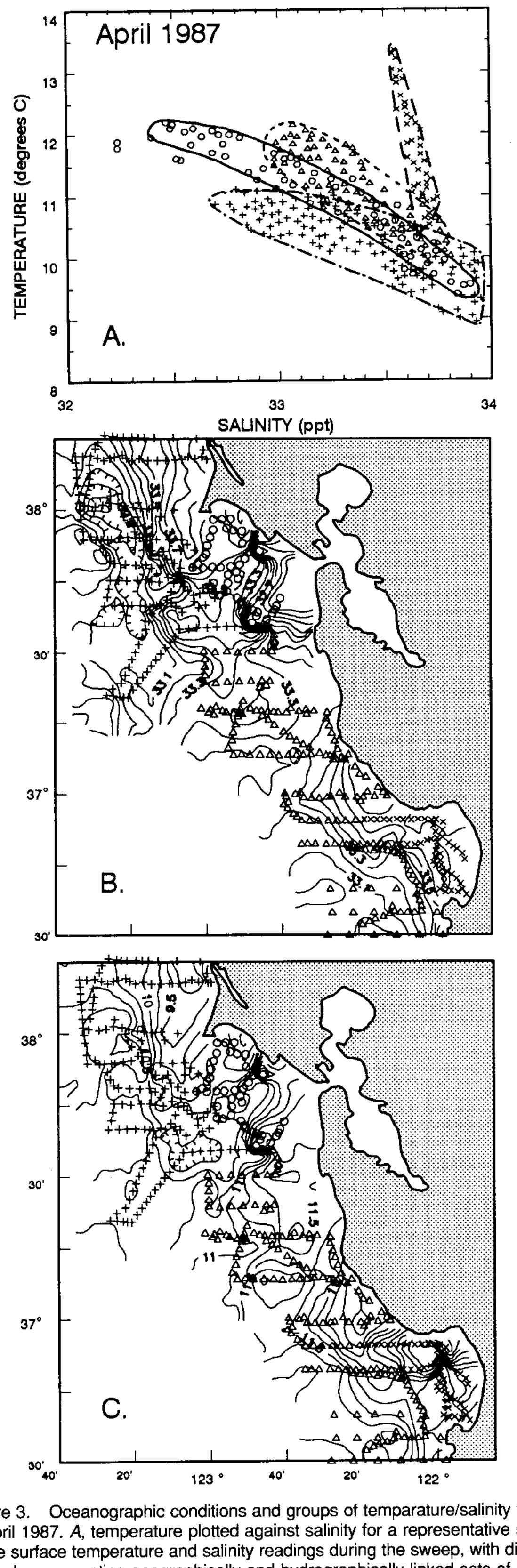


Figure 3. Oceanographic conditions and groups of temparature/salinity values in April 1987. *A*, temperature plotted against salinity for a representative subset of the surface temperature and salinity readings during the sweep, with different symbols representing geographically and hydrographically linked sets of points. The envelopes drawn around each set of points help display the range of conditions present during the sweep. The locations of the salinity and temperature readings are plotted on contour maps of salinity (*B*) and temperature (*C*).

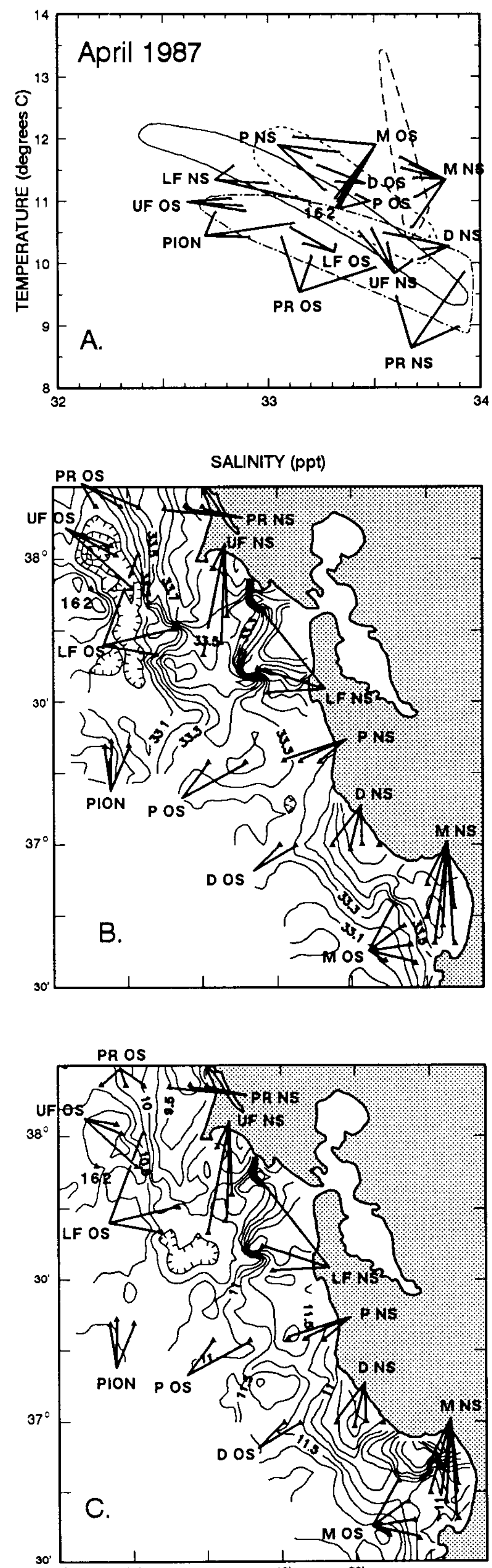


Figure 4. April 1987 trawl stations and their groupings, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Envelopes of temperature and salinity values in *A* are defined in figure 3. Abbreviations of place names are defined in figure 1.

We described four envelopes of temperature and salinity values (figure 3). Warm but saline Monterey Bay waters constituted one envelope (temperature and salinity points indicated by x's). Temperatures and salinities grading from freshly upwelled water to warmer, less-saline offshore water were defined for areas in the north (+'s) and south (triangles); northern waters were somewhat more saline at similar temperatures than the southern waters, and the most recently upwelled waters were more saline off Point Reyes than off Davenport. Waters in the Gulf of the Farallons (circles) ranged from cool and saline upwelled water to the warm, fresh outflow from San Francisco Bay. (Figure 3 and the above description illustrate the designation of temperature-salinity envelopes employed for each sweep. We will not present this procedure for the remaining sweeps, but interested readers may request diagrams similar to figure 3 for the remaining sweeps.)

We defined 13 groups of 2–6 trawl stations, based on latitudinal proximity and similarity of surface temperature and salinity (figure 4). Groups of nearshore stations tended to occur in recently upwelled water (Davenport nearshore, upper Farallons nearshore, and Point Reyes nearshore). Pescadero nearshore stations and lower Farallons nearshore stations were warmer and less saline, under the influence of the San Francisco Bay outflow. The nearshore Monterey stations reflected the isolated upwelled water characteristic of the bay. Groups of offshore stations occurred in warmer, less-saline water characteristic of the regions in which they were found.

Rockfish distributions—regular sweep. Because it took place early in the season, the April 1987 cruise yielded relatively small pelagic juvenile rockfish (table 2, appendix). Sixteen species/size classes were included in the analysis for this cruise; in only one species—the stripetail rockfish—was the large size class abundant enough to be analyzed separately, and the large size classes were absent for most species (table 2).

In the ordination of the 16 species/size classes and 13 areas, the second axis separated the Point Reyes areas from the others, based on the absence of species other than brown rockfish (figure 5). The first axis largely represented a gradient from nearshore to offshore in the areas south of Point Reyes. The upper Farallons nearshore area (UF NS) occurred at the extreme of the otherwise offshore end of axis 1 because the only taxon present there—small shortbelly rockfish—was also abundant in offshore areas. Species/size classes on the offshore end of axis 1 were relatively small: the small size classes of shortbelly, chilipepper, and widow rockfish, as well as canary rockfish and medium shortbelly rockfish, which were—on average—small in size (table 2). Little comparative size data are available for darkblotched rockfish. At the nearshore end of the gradient were the large size class of stripetail rockfish, and the copper rockfish complex. The latter fish were probably *S. caurinus*, which settle earliest among the complex of similar species (Anderson 1983). Stripetail rockfish also appear in midwater trawls relatively early in the season. Thus the species/size classes at the nearshore end of the gradient may have been ontogenetically advanced. In between were a mixture of medium and small size classes. The groupings of species/size categories for further analysis are indicated in figure 5. Brown rockfish will not be considered further.

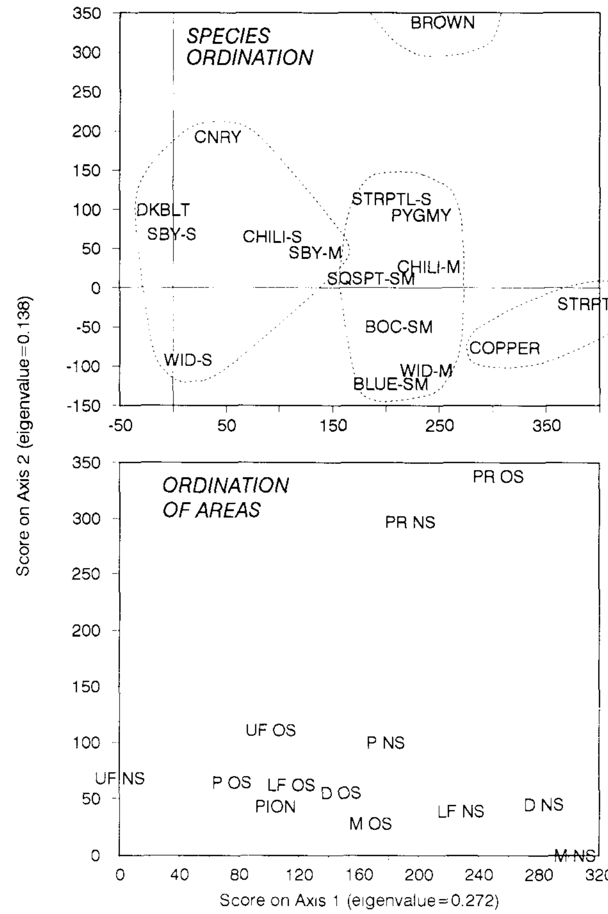


Figure 5. Ordination by detrended correspondence analysis of species and areas sampled during the April 1987 sampling cruise (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

Overall, pelagic juvenile rockfish were the most abundant in the frontal regions off Monterey and Davenport (table 4). Other offshore areas in the southern part of the study area yielded relatively high catches of a variety of species/size categories, whereas the northern areas were largely devoid of pelagic juveniles. Some species were moderately abundant in the nearshore areas that scored high on axis 1 of the ordination.

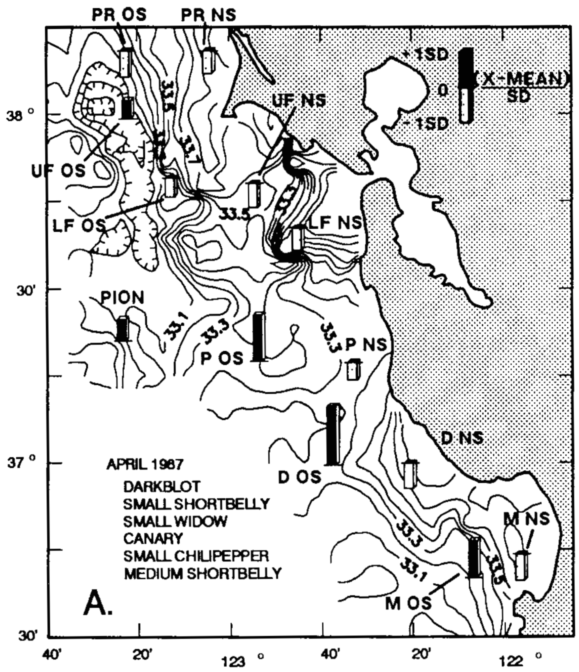
The group of fish scoring the lowest on axis 1 of the ordination was abundant in offshore areas of relatively

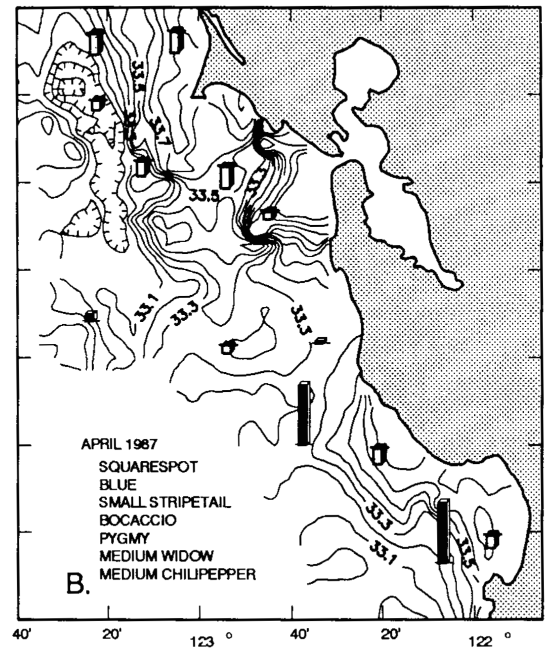
TABLE 4

Abundance of Pelagic Juvenile Rockfish in Station Groups[a], 1987–1988

APRIL 1987				JUNE 1987												APRIL 1988				JUNE 1988							
				SWEEP 1				SWEEP 2				SWEEP 3								SWEEP 1				SWEEP 2			
Area[b]	Mean abund.[c]	Taxa prs.[d]	Taxa >avg.[e]	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.	Area	Mean abund.	Taxa prs.	Taxa >avg.
M NS	0.135	5	3	M NS	0.478	13	4	M NS1	0.748	13	9	M NS	0.403	9	6	M NS	1.447	16	15	M NS	0.960	12	9	LM NS	1.056	7	6
								M NS2	0.361	10	6													UM NS	0.460	9	4
M OS	1.118	16	15	M OS	1.193	14	12	M OS1	0.145	8	0	M OS	0.310	4	3	M OS1	0.718	14	6	M OS	0.372	11	3	LM OS	0.669	7	4
								M OS2	0.604	9	7					M OS2	1.304	9	8					UM OS	0.405	11	4
D NS	0.110	6	3	D NS	0.645	10	8	D NS	0.937	13	12	D NS	0.072	4	0	D NS	0.827	14	9	D NS	1.508	9	9	D NS	0	0	0
																				D MID	0.528	13	3				
D OS	1.513	15	15	D OS	0.664	16	10	D OS	0.752	14	12	D OS	0.774	4	4	D OS	1.154	14	12	D OS	0.766	10	7	D OS	0.043	3	0
P NS	0.294	7	4	P NS1	0.656	7	5	P NS1	0.731	9	9	P NS	0	0	0	P NS	0.594	11	6	P NS	1.964	13	13	P NS	0.380	4	3
				P NS2	0.279	7	2	P NS2	0	0	0									P MID	0.099	3	0				
P OS	0.547	8	7	P OS	0.383	11	5	P OS	0.537	12	8	P OS	0.318	9	8	P OS	0.637	14	8	P OS	0.601	8	5	P OS	0.019	1	0
PION	0.510	13	10					PION	0.201	5	2																
LF NS	0.101	7	4	LF NS	0.479	13	7	LF NS	0.404	10	4	LF NS	0.236	5	4	LF NS	1.298	15	13	LF NS	0.462	10	1	GF	0.921	10	7
LF OS	0.095	4	1	LF OS	0.279	10	2	LF OS	0.311	13	4	LF OS	0.555	7	6	LF OS1	0.116	3	2	LF OS	0.666	11	5	LF OS	0.219	5	4
																LF OS2	0.660	10	8								
UF NS	0.022	1	0	UF NS	0.352	5	5	UF NS	0.688	12	9	UF NS	0.343	7	7	UF NS	0.622	6	5	UF NS	0.927	10	7				
UF OS	0.426	8	8	UF OS	1.133	14	14	UF OS	0.716	14	10	UF OS	0.457	4	4	UF OS	0.254	10	1	UF OS	1.506	12	12	UF OS	1.219	8	6
				CORD	0.435	10	5					CORD	0.392	8	7												
PR NS	0.052	2	1	PR NS	0.501	11	7	PR NS	0.913	7	7	PR NS	0.238	5	5					PR NS	0.285	6	2	PR NS	1.168	10	9
								PR MID	0.675	12	10																
PR OS	0.014	1	0	PR OS	0.039	2	0	PR OS	0.315	9	4	PR OS	0.019	1	0					PR OS	0.408	12	4	PR OS	0.614	8	5

[a]Station groupings differ from sweep to sweep, depending on conditions. The species/size groups used in each sweep are indicated in table 2.
[b]Each area is a group of stations defined by geographic proximity and hydrographic similarity (see descriptions of each sweep). See figure 1 for the definitions of the abbreviations for areas.
[c]Mean abundance (Mean abund.) is the grand mean, over species and size classes, of the average $\ln(x+1)$-transformed catches of each species/size class among the stations within each area.
[d]Taxa prs. is the number of species/size classes present in the group of stations.
[e]Taxa >avg. is the number of species/size classes present in an area at above-average abundance for all station groups within the entire sweep.





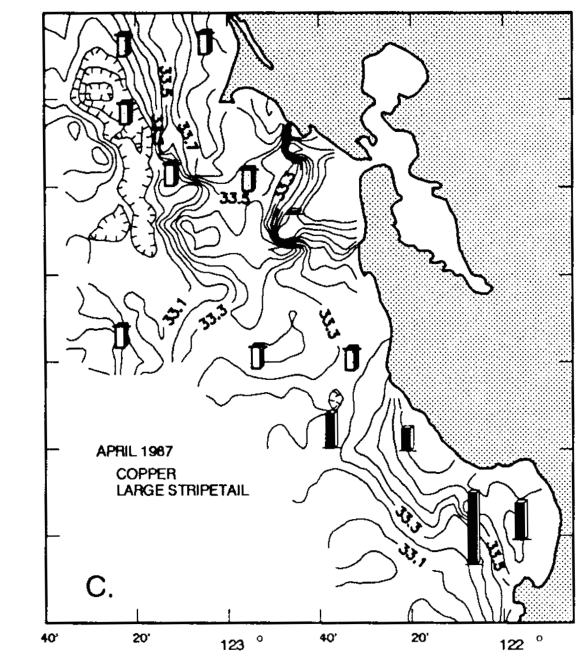


Figure 6. Relative distribution of species groups defined by ordination (figure 5), April 1987. Each bar represents the mean, over species, of the difference between the ln(*x*+1)-transformed abundance of a species in an area and its mean over all areas, divided by its standard deviation over areas. See figure 4 for station groupings. Contours are salinity (ppt).

low-salinity water, and absent in nearshore areas of recently upwelled water (figure 6a). The second ordination group, consisting of some medium size classes and earlier-settling species, was also abundant offshore in the south, and rare near shore, but it was somewhat less rare in the nearshore areas than the previous group (figure 6b). The copper–large stripetail group was abundant offshore of Davenport and Monterey, but was also above average in abundance closer to shore in these areas, in spite of upwelling. Thus the abundance patterns of these groups of species corresponded to their positions in the ordination.

Offshore Swing. A series of offshore stations was sampled after the regular sampling was completed. Beginning with the most offshore station in the Pescadero line and continuing past Pioneer Seamount, the first series of stations extended to the northwest (figure 7, line B). The second series of stations covered an east-west transect off Point Reyes (figure 7, line A). Profiles of density along each line were obtained from CTD casts. Catches of all three of the species groups tended to be above average for the entire cruise in the frontal zones separating coastal water from the more stratified offshore waters (figure 7). Catches declined offshore, especially for groups II and III (the species groups that scored higher on axis 1 of the ordination), and eventually dropped to zero for nearly all species. This indicates that pelagic juvenile rockfish may be concentrated near the upwelling front, and that the distribution of even the smallest size classes does not extend offshore indefinitely.

Summary. The absence of smaller size classes of pelagic juvenile rockfish in newly upwelled water and their presence in the fronts offshore in the April 1987 cruise suggests that earlier stages of pelagic juvenile rockfish are advected offshore during upwelling. But although earlier larvae may be distributed far offshore, the offshore swing conducted for this study suggests that the dis-

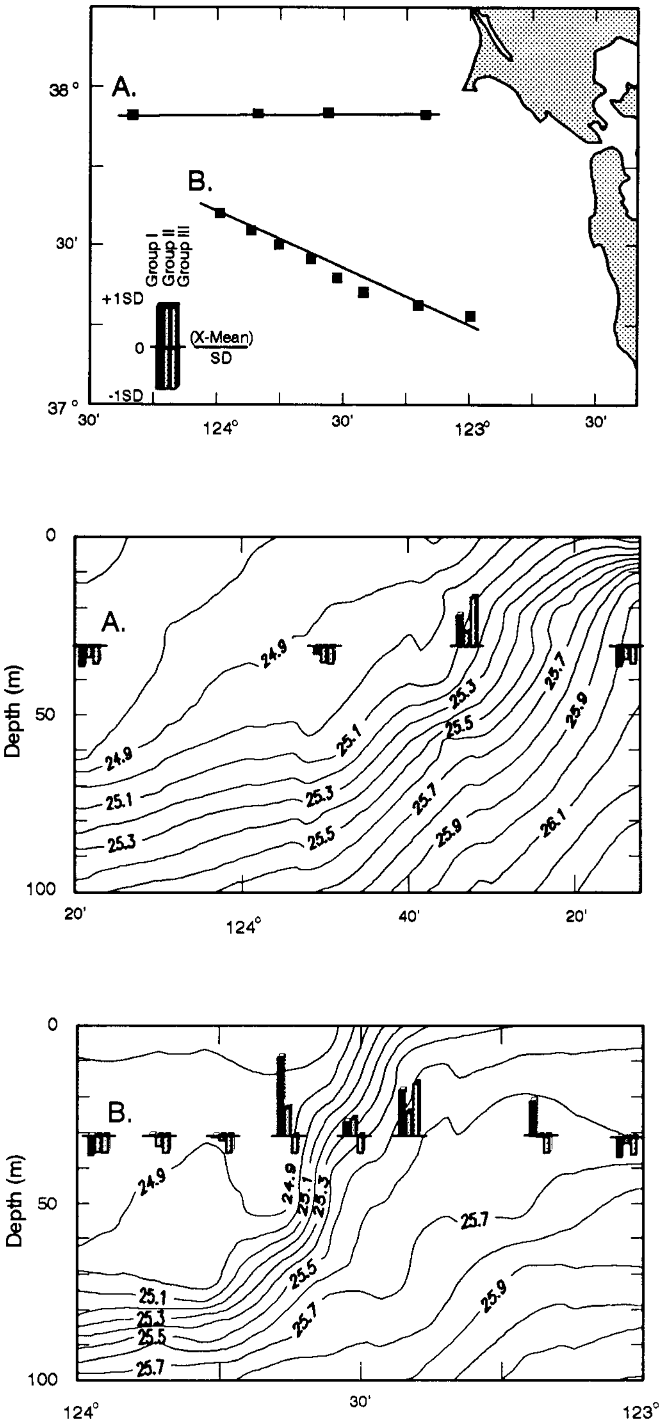


Figure 7. Distribution of pelagic juvenile rockfish offshore of the usual study area, April 1987. *Upper panel*, locations of trawl stations in northern offshore line (*A*) and southern offshore line (*B*). *Lower panels*, deviations from mean abundance of juvenile rockfish catches at stations in lines *A* and *B*, plotted on profiles of density (sigma t) as determined from CTD casts. Deviations from mean abundance were the mean among species within a group of the difference between each species' ln(x+1)-transformed abundance at a station and its mean abundance in all trawls in April 1987, divided by its standard deviation over all trawls. Groups of species were defined in the ordination (figure 5). Group I: Darkblot, small shortbelly, small widow, canary, small chilipepper, and medium shortbelly rockfish. Group II: Small stripetail, pygmy, medium chilipepper, small and medium squarespot, small and medium bocaccio, medium widow, and blue rockfish. Group III: Copper and large stripetail rockfish.

tribution of pelagic juveniles does not extend offshore indefinitely. Despite the apparent offshore advection of many pelagic juveniles, distribution also seems to be related to size or ontogenetic stage. Larger size classes and early-settling species were found close to shore in some areas of quite recently upwelled water, suggesting that the later stages are not as affected by offshore advection as the earlier stages.

May/June 1987, Sweep 1

Oceanography. Upwelling-favorable conditions occurred fairly consistently during the few weeks before the May 22–June 2 sweep of the study area in 1987, but relaxed during the few days before the cruise (figure 2a). Upwelling-favorable conditions returned for most of the sweep, relaxing toward the end (figure 2a).

Surface temperatures varied widely during this sweep, but salinities were largely greater than 33.5 ppt (figure 8). Active upwelling was evident only off Point Reyes, but the high salinities generally prevalent in the region indicated that most of the waters in the study area had been upwelled, and that this water remained largely unmixed with offshore water. Little offshore water was evident during the sweep, but a complex front bordered the recently upwelled water off Point Reyes. The relatively fresh San Francisco Bay outflow was evident off Pescadero, yielding the lowest salinities of the cruise. The southern portion of the study area, which was visited shortly after the period of relaxed winds, contained relatively warm but also saline water, with a diffuse onshore-offshore gradient. This water likely had its origin in upwelling, and had not yet mixed greatly with offshore waters.

Trawl stations were combined into 14 groups (figure 8). Nearshore areas in the north (Point Reyes and the upper and lower Gulf of the Farallons) were in recently upwelled water, although some mixing and warming had occurred in the southern part of this area. The offshore Point Reyes and Cordell Bank stations were in or beyond the northern portion of the upwelling front, while the LF OS and UF OS stations were in increasingly warm and less saline water off the southern portion of the Point Reyes upwelling front. The offshore stations off Pescadero, Davenport, and Monterey Bay were in relatively warm but still saline water, while the most nearshore stations in these areas were in slightly more saline water. The most nearshore stations off Davenport and Pescadero (D NS and P NS1) were cooler, while the nearshore Monterey stations were warmed in the manner often characteristic of Monterey Bay. The intermediate stations off Pescadero (P NS2) were influenced by the San Francisco Bay outflow.

Rockfish distributions. Pelagic juvenile rockfish were much larger during this cruise than in April (table 2, ap-

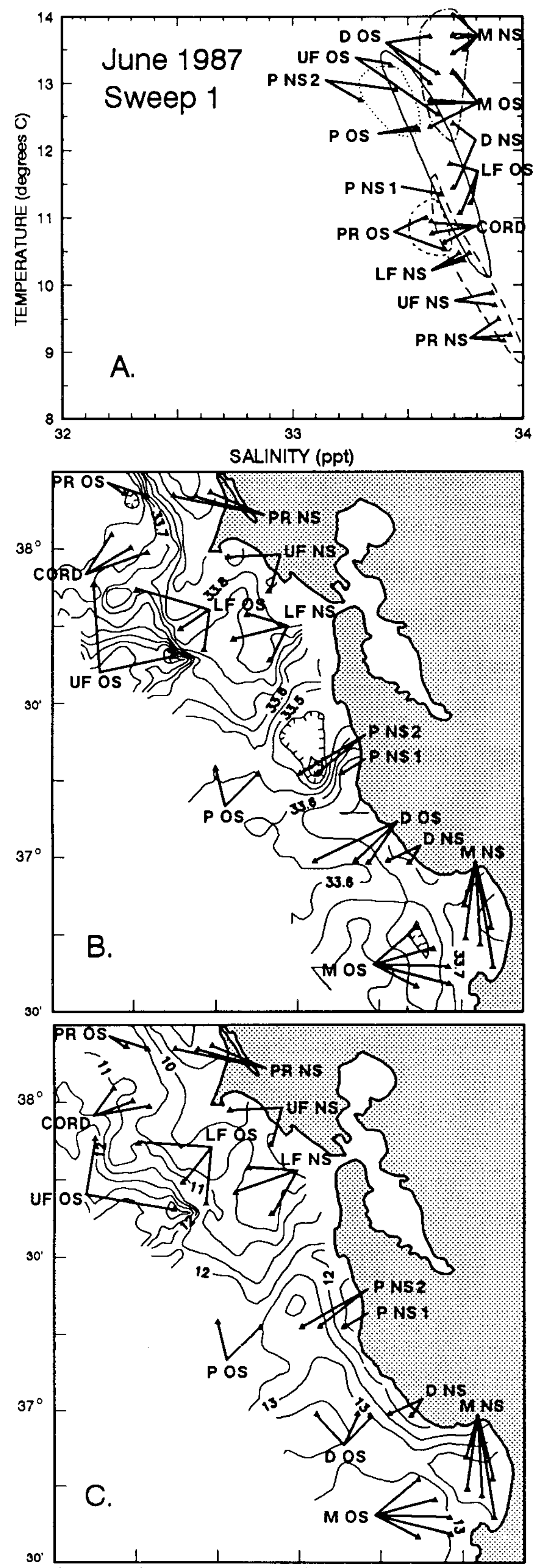


Figure 8. Trawl stations and their groupings from May/June 1987, sweep 1, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Abbreviations of place names are defined in figure 1.

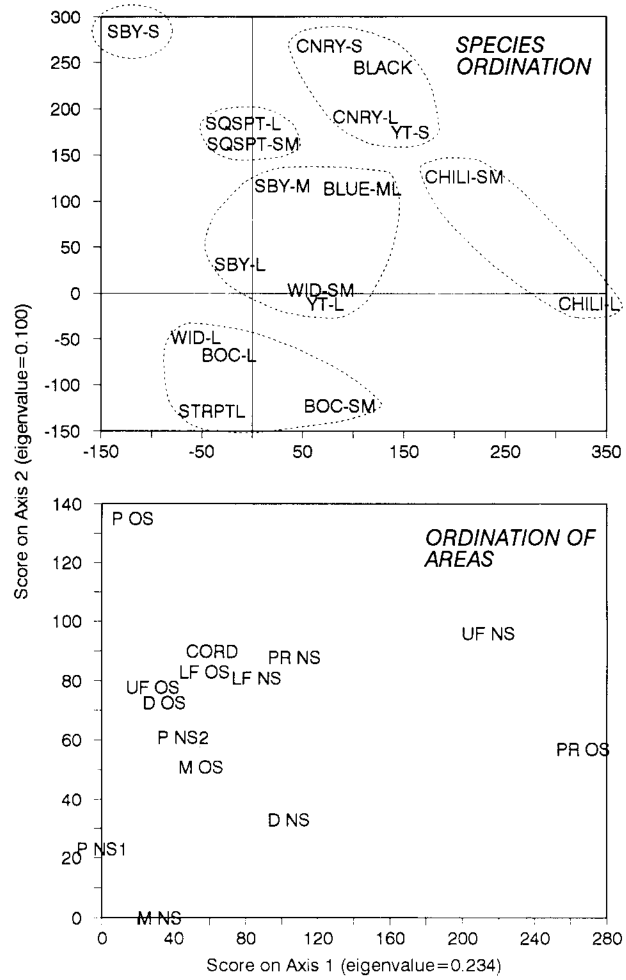


Figure 9. Ordination by detrended correspondence analysis of species and areas sampled during sweep 1 of May/June 1987 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

pendix). The large size classes of several species were abundant, and the small size classes of most species were rare or absent. Eighteen species/size classes were included in the analysis of this sweep (table 2).

Ordination of the 14 areas and 18 species/size classes resulted in a roughly triangular distribution of taxa and areas (figure 9). The high end of the first axis reflected taxa that occurred in some northern areas. The second axis reflected a roughly onshore-offshore gradient, with offshore areas scoring high and nearshore areas (particularly in the south) scoring low. Some smaller size classes, particularly small shortbelly rockfish, fell out at the offshore end of axis 2, while the predominant larger size classes occurred along the rest of axis 2. The two axes together yielded a triangular pattern with northerly, Point Reyes areas and their associated species on the right, offshore areas and their species in the upper left, and southerly nearshore areas in the lower left. Species/size categories did not fall into sharply distinctive groups. We designated six groupings for use in further analysis (figure 9), recognizing that each group contained some heterogeneity.

Overall, species were most common and abundant offshore in the Monterey, upper Gulf of the Farallons, and Davenport areas (table 4). The fewest species and lowest overall abundance were in the offshore Point Reyes area. The most nearshore area off Pescadero (P NS1) and the nearshore area in the upper Gulf of the Farallons each had relatively few species, but those species present were abundant. Some of the remaining nearshore areas (Point Reyes, Monterey, and Davenport) had fair numbers of species but lower overall abundances, while the remaining offshore areas (Cordell, Pescadero, and lower Gulf of the Farallons) generally had fewer species and lower abundances.

Small shortbelly rockfish, which fell in the upper left corner of the ordination (figure 9), occurred in only four offshore areas of warm, lower-salinity water (figure 10a). The second group defined in the ordination included a mixture of sizes, and did not occur in many areas. They tended to be found toward the north, being absent in Monterey Bay (figure 10b). They were found in some offshore areas of warm, relatively low-salinity water, but were also abundant in recently upwelled water (figure 10b). Squarespot rockfish, including the large size class, were generally abundant offshore (figure 10c). The group consisting of medium and large shortbelly rockfish, medium/large blue rockfish, large yellowtail rockfish, and small/medium widow rockfish was somewhat heterogeneous in its distribution, but as a whole was relatively abundant in the south and in some nearshore areas, as well as offshore of the upper Gulf of the Farallons (figure 10d). The group consisting of stripetail rockfish, large widow rockfish, and medium and large bocaccio tended to be abundant in the south, and in that area the group was more abundant nearshore than the other groups (figure 10e). The last group, small/medium and large chilipepper rockfish, was abundant in the recently upwelled water off Point Reyes and two areas in the south (figure 10f).

The distributions of these groups, then, showed strong latitudinal differences, but less clear evidence of ontogenetically linked differences in onshore-offshore distributions. There was some indication of smaller size classes offshore in the first two groups, and larger size classes closer to shore in the last three groups, but small canary and yellowtail rockfish were found close to shore even in recently upwelled water, and some ontogenetically advanced fish (squarespot rockfish) were not abundant close to shore. The small size classes of some species (widow, chilipepper, and squarespot rockfish, as well as the "rosy complex"), which were too rare to be treated separately in the overall analysis, were found only in the upper Gulf of the Farallons offshore area, where many taxa were abundant.

Summary. Upwelling was strong only off Point Reyes during this sweep, and most of the study area contained upwelled water of less recent origin that was relatively unmixed with offshore water. Small size classes of most species were rare or absent, but medium and large size classes were abundant. There were strong north-south gradients in the distributions of pelagic juveniles, and some indications (with exceptions) of size-related differences in onshore-offshore distributional patterns across species. A number of species were abundant in some of the offshore areas (Monterey, Davenport, and Gulf of the Farallons), but only the latter area was in a frontal zone. Overall, there seemed to be a much smaller degree of commonality in distributional patterns across taxa and size classes than in April, and a greater degree of idiosyncrasy in species distributions.

June 1987, Sweep 2

Oceanography. Upwelling-favorable conditions appeared to relax considerably near the end of sweep 1, and these conditions continued into the first several days of the June 2–12 sweep of the study area (figure 2a). Upwelling-favorable conditions returned for a few days later in the sweep, but relaxed somewhat at the conclusion of the sweep.

Hydrographic conditions during sweep 2 seemed to reflect the absence of upwelling-favorable conditions (figure 11). The upwelling plume off Point Reyes appeared to weaken and move slightly offshore; warmer, slightly less saline water occurred inshore of the diffuse remnants of the Point Reyes upwelling plume, and the sharply defined front that was offshore of Point Reyes during sweep 1 disappeared or moved out of our sampling area (figure 11, cf. figure 8). A tongue of saline but not particularly cool water, probably the remnant of previous upwelling, occurred offshore of the San Francisco Bay outflow in the Gulf of the Farallons, and extended down the coast to Pescadero. The coolest, most saline water in the study area occurred in the upper Gulf of the Farallons, which was visited just after the period of upwelling-favorable winds. Warm, low-salinity water occurred offshore in the region south of the Gulf of the Farallons, separated from the more nearshore waters by a strong front. Warm, low-salinity water also appeared offshore of Davenport and Monterey Bay, separated from the coastal waters by a strong salinity gradient and less strong temperature gradient. There was little evidence of recent upwelling at Davenport, where the usual plume of cool, high-salinity water was absent. Instead, saline but relatively warm water remained pooled along the coast and in Monterey Bay.

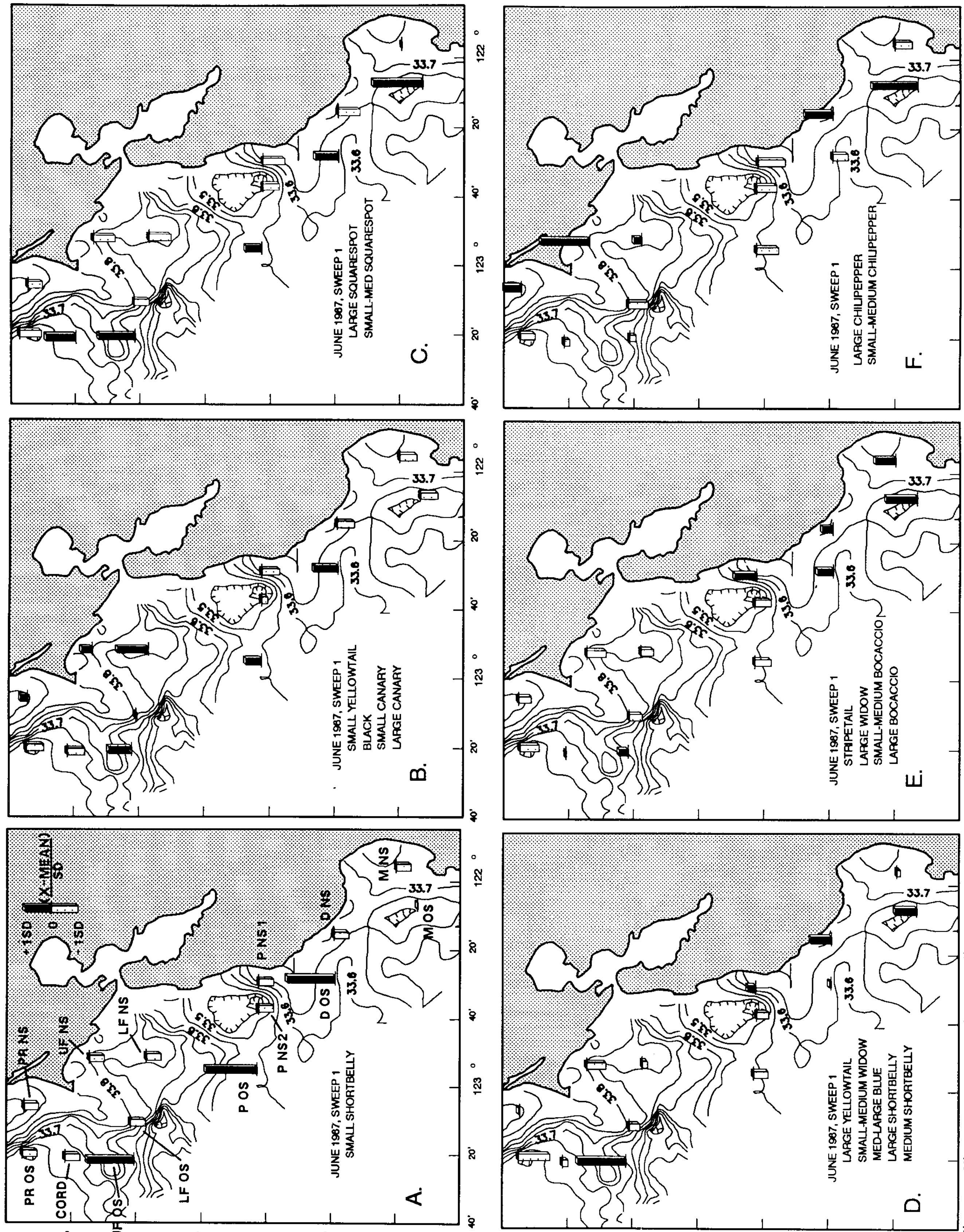


Figure 10. Relative distribution of species groups defined by ordination (figure 9), sweep 1 of May/June 1987. Explanations as in figure 6. See figure 8 for station groupings.

Trawl stations were combined into 17 groups of 1–4 stations (figure 11). Two stations in the upper Gulf of the Farallons occurred in the most recently upwelled water sampled. Other sets of stations off Point Reyes and the Gulf of the Farallons were in relatively cool water, grading to more offshore conditions in the UF OS stations. The middle stations off Point Reyes were in the core of the decaying plume, and the most nearshore station was in quite warm but moderate-salinity water. The offshore stations at Davenport, Pescadero, and Pioneer Seamount were in or beyond the frontal regions separating offshore from coastal water, and the different sets of offshore stations off Monterey Bay spanned the frontal region. Nearshore stations in the south were of moderate to high salinity, but also moderate to high temperature, indicating local warming. The middle station off Pescadero (P NS2) was in the tip of the decaying Point Reyes plume. No juvenile rockfish were captured at this station, so it was not included in the ordination analysis. However, it was included in the distributional analysis of species groups identified in the ordination.

Rockfish distributions. Overall, catches of pelagic juvenile rockfish increased during sweep 2 (table 4), and smaller size classes of several species appeared in greater abundance (table 2 and appendix). Twenty species/size groups were included in the analysis of this sweep (table 2).

The first ordination axis was very clearly an onshore-offshore gradient, and the second axis a north-south gradient (figure 12). Smaller size classes of juvenile rockfish fell to the offshore end of the first axis, and taxa falling toward the onshore end of the axis tended to be large, although not all large size classes scored low. Species/size classes were assigned to 6 groups for further analysis, as indicated in figure 12.

Overall, no single area yielded high catches of nearly all species/size categories (table 4). A number of areas had moderate to large catches of at least half the species/size categories, with the species mix varying from area to area. The nearshore area off Point Reyes had large catches of relatively few species; the LF OS area had small catches of relatively many species; and some areas (P NS2, Pioneer Seamount, and M OS1) had relatively small catches of few species (table 2).

Most of the species groups defined in the ordination had some internal heterogeneity in distribution, but the overall patterns reflected the positions of the groups and areas in the ordination. The group of relatively small fish scoring high on axis 1 had a predominantly offshore distributional pattern, well represented in the recently intruded offshore water of low salinity (figure 13a). Each of the species/size categories in this group increased in abundance from sweep 1 to sweep 2 (table 2).

The group consisting of small yellowtail, stripetail, large bocaccio, and black rockfish was ontogenetically

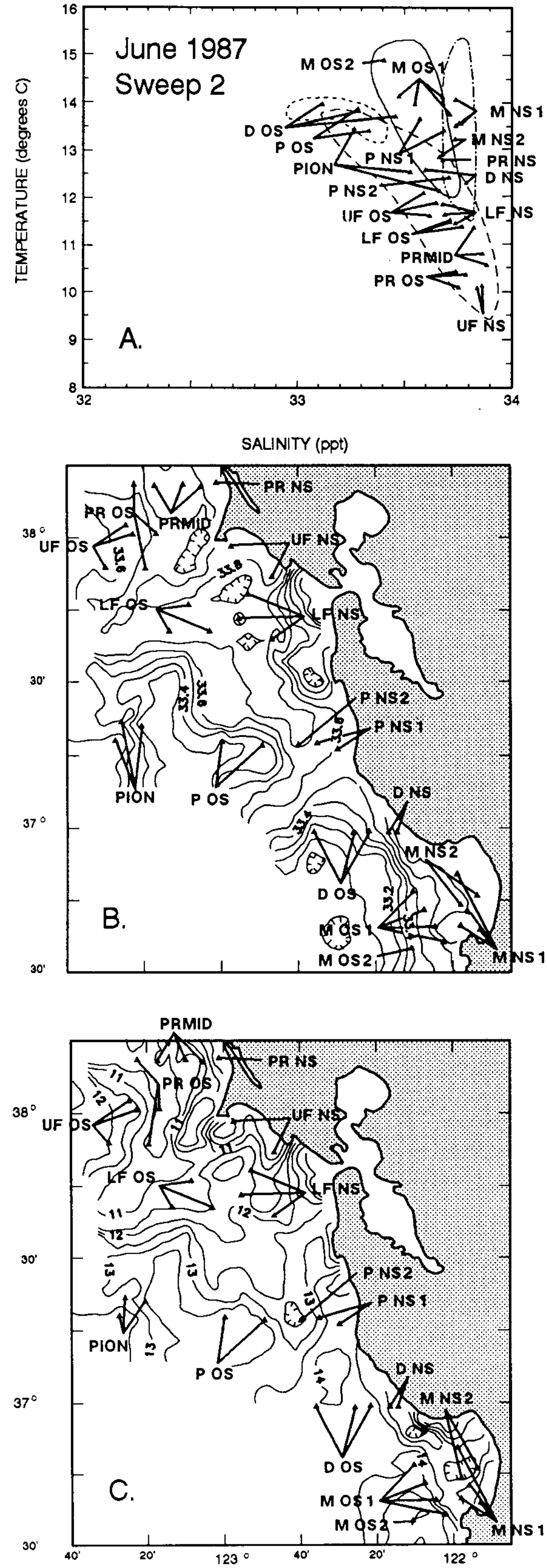


Figure 11. Trawl stations and their groupings from May/June 1987, sweep 2, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Abbreviations of place names are defined in figure 1.

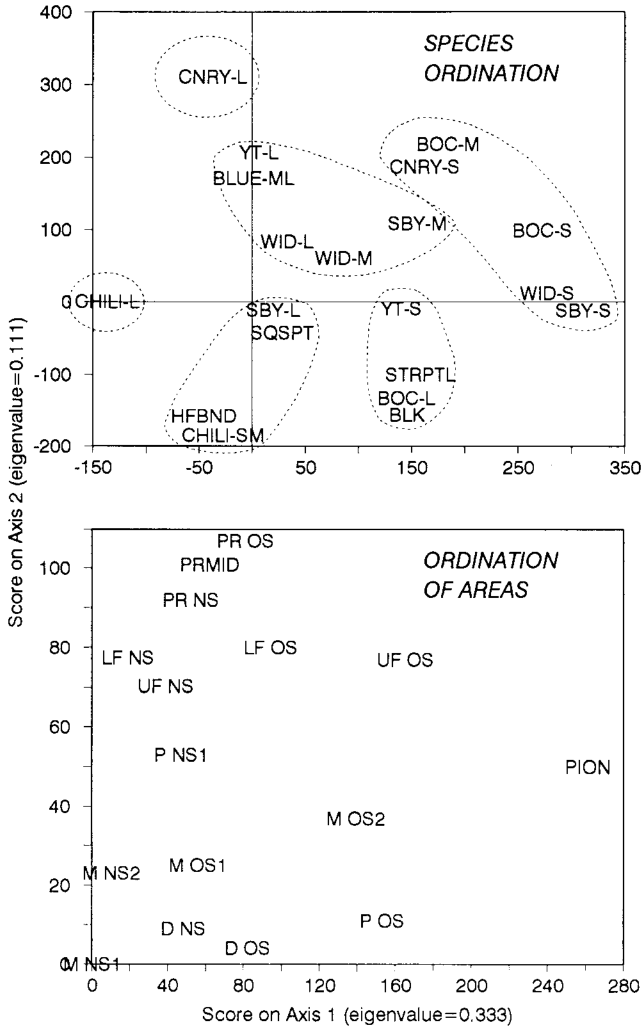


Figure 12. Ordination by detrended correspondence analysis of species and areas sampled during sweep 2 of May/June 1987 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

mixed. As a group, these taxa were abundant in the south (including nearshore areas off Monterey and Davenport), and abundant only in some offshore areas in the north (figure 13b). The distribution of the group showed no obvious relation to temperature and salinity, except for relatively low abundance in most areas of cool water in the northern part of the study area.

The group consisting of halfbanded, medium chilipepper, large shortbelly, and squarespot rockfish was relatively advanced ontogenetically. It was most consistently abundant nearshore and in the south (figure 13c). As a group, these taxa tended to be most abundant in some, but not all, of the nearshore areas of high salinity (figure 13c).

As a whole, the group consisting of medium and large widow rockfish, blue rockfish, large yellowtail rockfish, and medium shortbelly rockfish was relatively advanced ontogenetically. On average, this group tended to be abundant nearshore, except in Monterey, and only patchily present offshore (figure 13d). The areas showing near-average abundance for the group as a whole were internally heterogeneous. The offshore areas off Davenport, outside Monterey Bay, and the upper Gulf of the Farallons were notable in this respect. There was no particular relation between the abundance of this group and temperature and salinity, except that the group was relatively uncommon in low-salinity offshore waters (figure 13d).

Large canary rockfish were restricted to nearshore areas in the north with relatively cool, saline water (figure 13e). Large chilipepper rockfish were also found only in nearshore areas, but were most abundant in the south, in areas of relatively warm but saline water (figure 13f).

Summary. There was little active upwelling during or immediately before the sweep. Small size classes of several species became more abundant during this sweep, and appeared in offshore waters, often associated with an onshore intrusion of relatively warm, low-salinity water. Medium and large size classes of several species showed patchy and latitudinally separated distributional patterns, but were often abundant near shore.

Comparison of sweeps 1 and 2. The comparison of sweeps 1 and 2 suggests that relaxation of upwelling led to the onshore advection of some juvenile rockfishes, but the comparison was complicated by fish settling out between sweeps.

The increased temperatures and decreased salinities in several offshore areas (M OS2, D OS, and P OS) indicate the appearance of offshore water (figure 14a). The offshore displacement of the upwelling plume off Point Reyes led to an increase in salinity offshore, while the increase in temperature and decrease in salinity nearshore indicates advection to the nearshore region inside the plume (figure 14a).

From sweep 1 to sweep 2 several nearshore areas (PR MID, PR NS, UF NS, M NS1, P NS1, D NS) showed relatively large increases in abundance of juvenile rockfish (table 4). Several areas showed large turnovers in species composition. In several offshore areas of high species turnover (D OS, PR OS, LF OS, UF OS), average abundance increased, while in two nearshore areas (LF NS, M NS2) average abundance decreased slightly (table 4). The two offshore areas off Monterey showed large decreases in average abundance, and most species decreased. No rockfish were caught in the P NS2 area in sweep 2 (table 4).

Some early-settling species and large size classes (medium and large chilipepper, stripetail, blue, and large bocaccio) decreased in abundance from sweep 1 to sweep 2 (table 2). The difference was probably due to settlement. Some small stripetail rockfish did, however, ap-

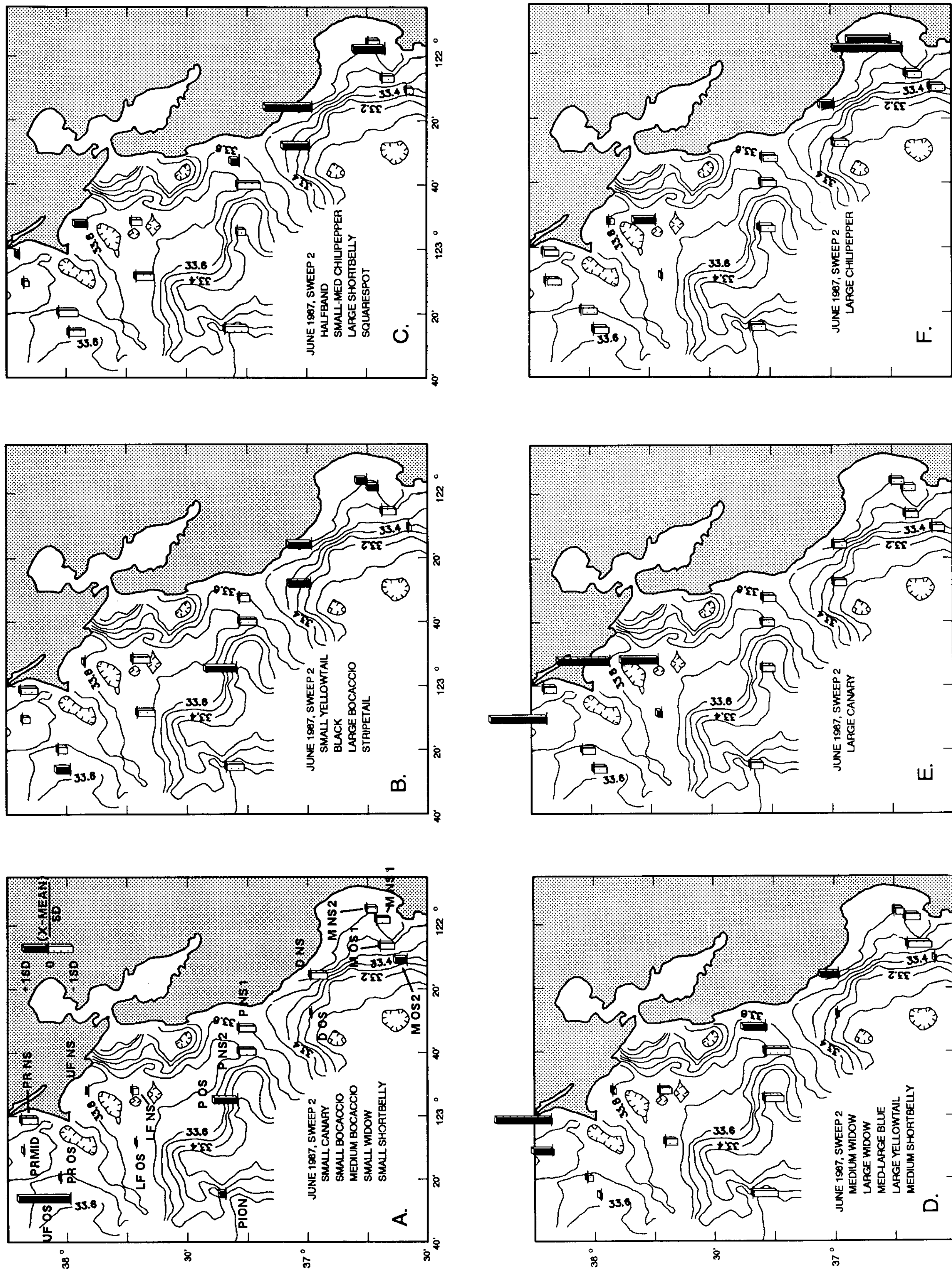
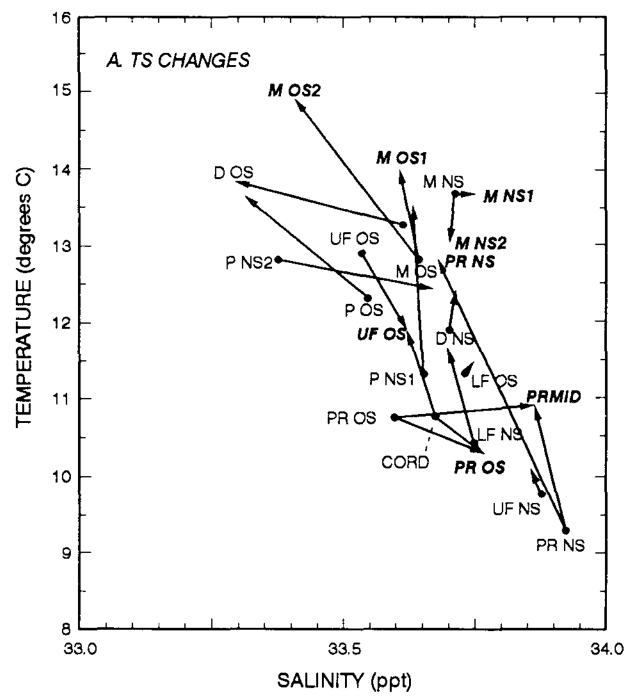


Figure 13. Relative distribution of species groups defined by ordination (figure 12), sweep 2 of May/June 1987. Explanations as in figure 6. See figure 11 for station groupings.



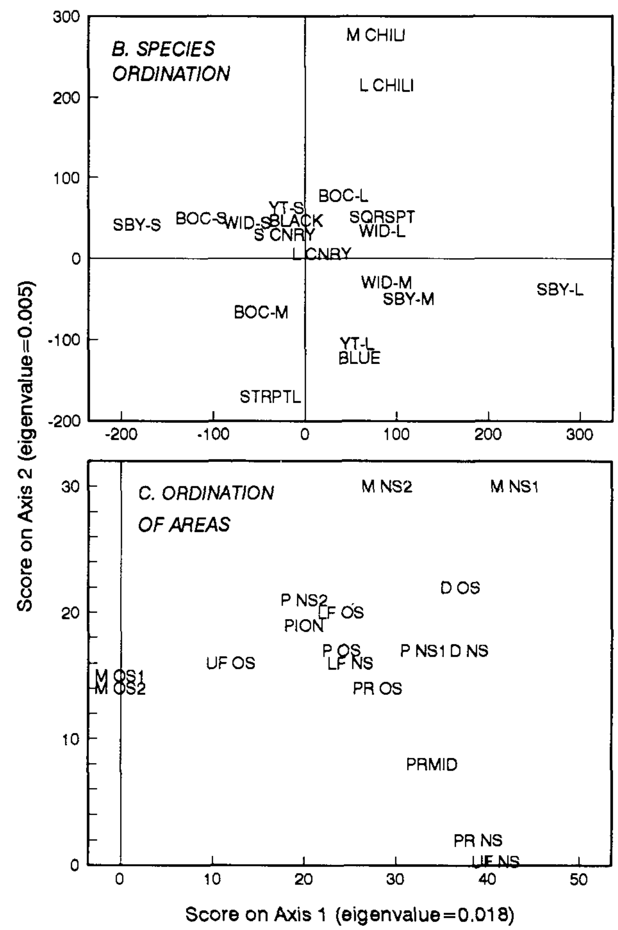


Figure 14. Comparison of sweeps 1 and 2, May/June 1987. *A*, temperature and salinity changes from sweep 1 (*solid circles at origin of arrows*) to sweep 2 (*arrow points*). Place names for sweep 1 (and for sweep 2, when station groupings remained the same) are printed in plain type, and names of new station groupings for sweep 2 are in boldface italics. New combinations of stations are indicated by diverging and converging arrows. *B*, *C*, ordination of the differences in abundance between sweeps one and two.

pear in offshore areas during sweep 2 (appendix g). Several species/size categories (large shortbelly, widow, yellowtail; medium widow, shortbelly; and small shortbelly) increased substantially in abundance between sweeps, while others (small bocaccio, widow, canary, yellowtail; medium bocaccio; large canary; and blue rockfish) increased but less substantially overall, either because they increased in fewer areas or because they were not present in many areas in either sweep (table 2). In general, then, most species/size groups other than early-settling species increased in abundance within the study areas between sweeps.

Differences in abundance between sweeps were ordinated to seek recurrent patterns of change in species abundance over areas (figure 14b,c). A cluster analysis was also carried out, giving similar results. Smaller size classes loaded low on axis 1 of the ordination, and larger size classes loaded high (figure 14b). Corresponding with the small size classes were offshore areas, where the small fish appeared and some larger fish declined in abundance (figure 14c). The second axis was largely a gradient from south to north. At the high end of the axis were species/size classes that either increased substantially in the Monterey nearshore areas or decreased (or did not increase) in the nearshore areas off Point Reyes, such as medium and large chilipepper and large bocaccio (figure 14b,c). These fish seemed to have settled out in the north, and perhaps moved inshore in the south. At the low end of axis 2 were species that increased (or did not decrease) in abundance in the nearshore areas off Point Reyes. Several species that were rare or absent off Point Reyes increased substantially in abundance in sweep 2 (large yellowtail, blue, medium and large widow, medium and large shortbelly, and squarespot rockfish). Some of these also increased nearshore in the south (squarespot, large shortbelly, and large widow).

The changes in abundance suggest three patterns of advection associated with relaxation of upwelling. First and most obvious was the appearance of small rockfish of several species in offshore areas, most often in areas where intrusion of offshore water was evident. Their appearance in these areas suggests that larvae or small juveniles had occurred offshore, and appeared in our catches as these offshore water masses moved into our study area and the fish grew to a size vulnerable to our sampling gear. The second pattern was the appearance of larger size classes of several species in nearshore areas off Point Reyes. Their increase was centered in the warm water mass that appeared close to shore off Point Reyes during sweep 2. Water masses of similar characteristics were not present nearby within the study area during sweep 1 (figures 8, 11, 14a), suggesting that this water was advected into the area during sweep 2, perhaps from the north. Thus the appearance of these fish may have been associated with advection as well. Third, larger size classes of several species increased in abundance nearshore in Monterey or other southern areas between sweeps, often declining in offshore areas. Compression of the areas of relatively high-salinity, aged upwelled water toward shore when the offshore water appeared could indicate the onshore transport of these groups during the relaxation of upwelling.

Bathymetric distributions in relaxation area. Juvenile rockfish showed unusually shallow bathymetric distributions in southern Monterey Bay during sweep 2, and this was correlated with the development of a sharp, shallow thermocline (figure 15). Although thermal stratification was evident at four stations across southern Monterey Bay, there was no corresponding halocline at these stations (figure 15). Salinity throughout the water column was lower at the most offshore of these stations (figure 15), perhaps indicating a different water mass. A strong halocline was present only at CTD stations offshore of station D, corresponding to the offshore water mass that appeared off Monterey. Thus the shallow thermocline at the stations illustrated here was probably due to local warming, and could develop because vertical mixing and upwelling had subsided (as discussed in Send et al. 1987).

Several species of juvenile rockfish were unusually abundant above the thermocline (figure 15). When present at a station, four of the ordination groups (II–V) were usually abundant in tows at 10 m depth, often more abundant than at 32 m. In addition, several species were abundant in short surface tows made at stations B and D. These bathymetric distributions were among the most unusually shallow of the bathymetrically stratified tows made between 1983 and 1988. Of these species, bocaccio usually occur in shallow water, but the others are usually most abundant at 30 m (chilipepper, shortbelly, and squarespot rockfish), or even at 100 m (widow, blue, and yellowtail rockfish; Lenarz et al. 1991). In contrast to these four ordination groups, the small size classes in ordination group I were not abundant in shallow water. They were most abundant in middepths at offshore station D (figure 15).

In summary, several species/size groups were unusually shallow in this area. The smallest size classes were the major exception to this pattern. Although we have not scanned our data for other situations in which a similar shallow thermocline developed, it is interesting that these shallow distributions coincided with the devel-

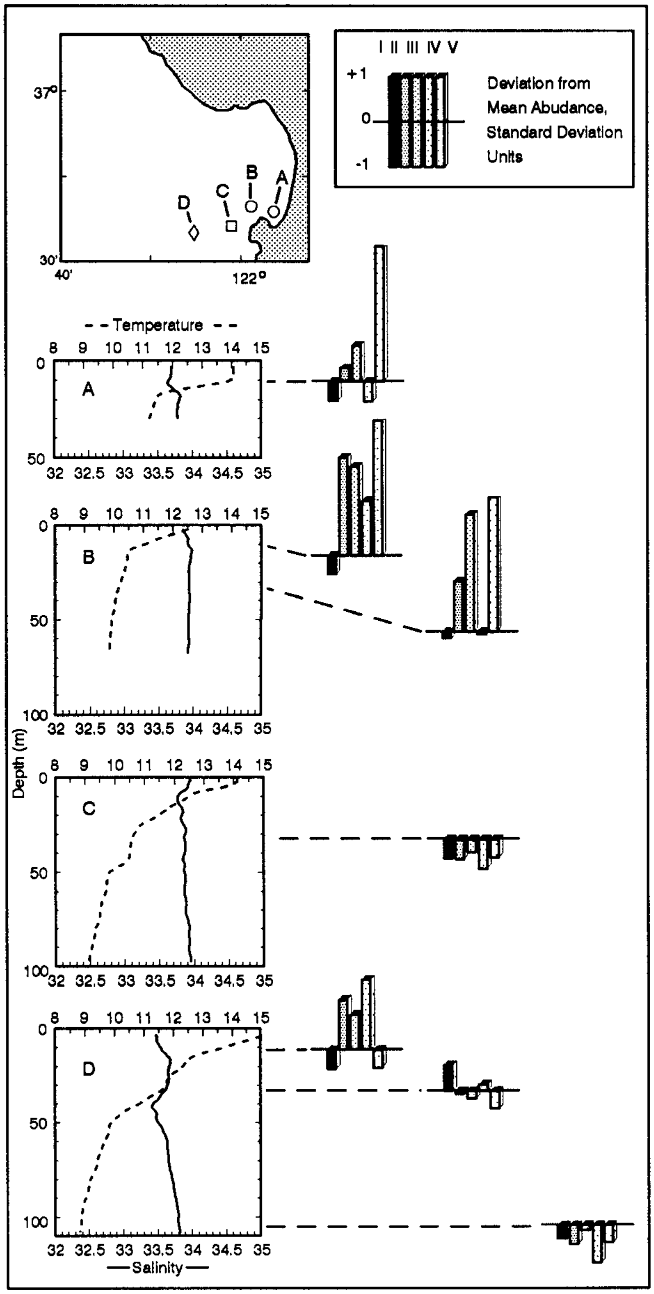


Figure 15. Horizontal and vertical distributions of pelagic juvenile rockfish in southern Monterey Bay during relaxation from upwelling, sweep 2 of May/June 1987. *Upper left*, map of stations. *Circles* indicate stations in the M NS1 group; the *square* indicates the M OS1 group; and the *diamond* indicates the M OS2 group (figure 11). *A–D*, CTD profiles at the corresponding stations, and comparative abundances of five groups of species identified in the ordination (figure 12). Bar graphs indicating abundance are aligned with the depth at which the trawls were made. Bars represent means (over species) of differences from the average abundance of each species in trawls carried out during sweep 2, scaled in standard deviation units. Group I: Small shortbelly and small bocaccio were present only at station D, and small canary rockfish were present only at station B. Group II: Small yellowtail (stations B,D), stripetail (station B), large bocaccio (stations A,B,D), and black rockfish (station B) were all absent at station C. Group III: Halfbanded (station B), medium chilipepper (stations A,B), squarespot (stations B,C,D), and large shortbelly (stations A,B,D). Group IV: Medium and large widow, medium shortbelly, blue, and large yellowtail rockfish were present mostly at stations B and D. Group V: Large chilipepper rockfish were present only at stations A and B.

opment of a sharp, shallow thermocline during the relaxation of upwelling and the apparent onshore movement of several taxa.

June 1987, Sweep 3

Oceanography. Upwelling-favorable conditions occurred during the middle of sweep 2, but declined at its conclusion and into the beginning of sweep 3, which took place between June 12 and 21 (figure 2a). After the relaxed conditions during the early part of sweep 3, quite strong winds and upwelling-favorable conditions occurred during the remainder of the sweep (figure 2a). Winds forced an interruption of sampling on June 16, in the middle of the Gulf of the Farallons. Sampling resumed on June 18, off Point Reyes. Because hydrographic conditions changed substantially within the same region before and after the interruption of sampling, temperature and salinity data were contoured separately in the periods before and after June 16 (labeled "before blow" and "after blow" in figure 16). In addition, failure of the shipboard CAMAC system during the period after June 18 forced us to rely on more widely spaced temperature and salinity data from CTD casts.

The occurrence of upwelling-favorable conditions during and before sweep 3 was reflected in hydrography (figure 16). A sharp onshore-offshore gradient in salinity occurred along the coast through most of the study area, while a similar temperature gradient was evident everywhere except in the central part of the study area (figure 16). Recent upwelling was most evident in the northern part of the study area, where salinities above 33.7 ppt and temperatures below 10°C occurred far offshore. The upwelling center off Davenport was evident, particularly in salinity, but water had evidently warmed close to shore, perhaps reflecting the passage of time since the most recent strong winds late in sweep 2 and the sampling early in sweep 3. Low-salinity offshore water masses were evident offshore of the upwelling front through much of the study area south of Point Reyes.

Trawl stations were combined into 13 groups of 1–6 stations (figure 16). Several sets of stations in the north were in recently upwelled water (PR NS, PR OS, UF NS), while others in the north were transitional (LF NS, LF OS, CORD). The UF OS and P OS stations were in offshore waters. Some groups of stations in the south were in mixed and insolated water masses (P NS, M OS, D OS); the others were in nearshore areas with high salinity and moderate temperature indicative of upwelled but insolated water (M NS, D NS). No fish were caught at either station in the P NS area, so this area was not included in the ordination of species and areas.

Rockfish distributions. Overall, catches of pelagic juvenile rockfish decreased between sweeps 2 and 3 (tables 2, 4). Several species disappeared or were found in

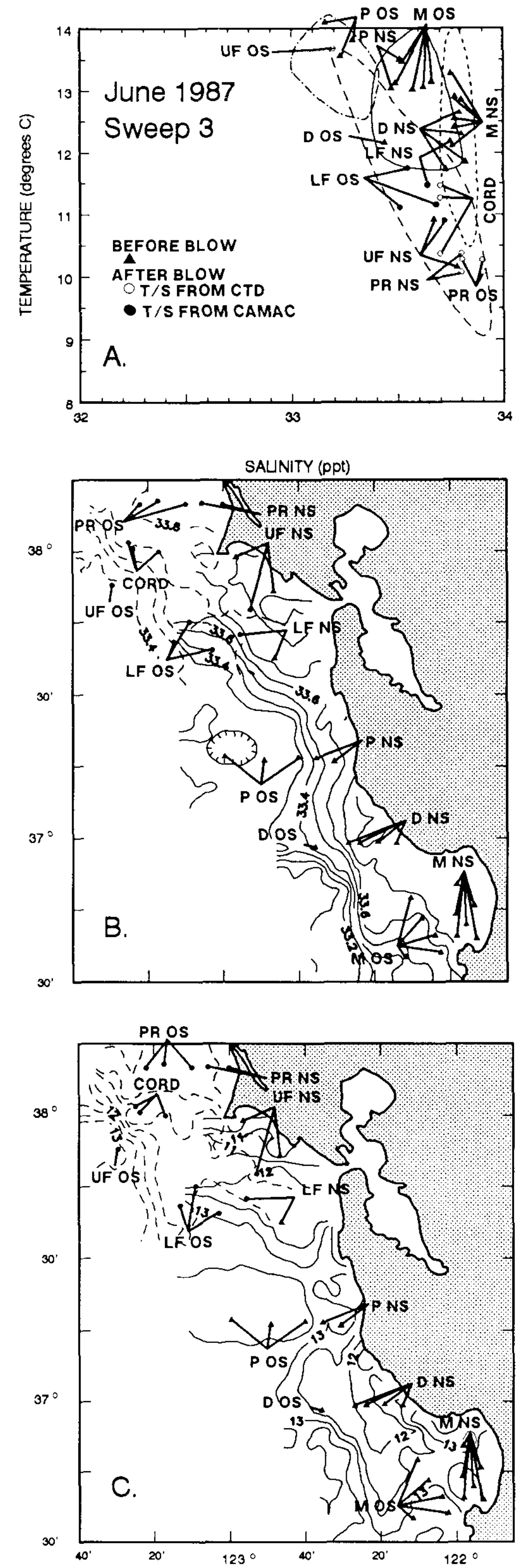


Figure 16. Trawl stations and their groupings from May/June 1987, sweep 3, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). "Before blow" stations were sampled before a windy period that forced a hiatus in sampling; "after blow" stations were sampled after, and some of the temperature and salinity data for these stations were taken from CTD rather than CAMAC. Abbreviations of place names are defined in figure 1.

only one area during sweep 3 (blue, squarespot, stripetail, and halfbanded rockfish), and several other species also decreased in abundance, particularly among larger size classes (black, bocaccio, canary, chilipepper, shortbelly, widow, and yellowtail rockfish). These declines likely indicate settlement of juveniles since sweep 2. Small size classes of several species either increased in abundance (rosy and copper complexes, and shortbelly rockfish), or stayed about the same (bocaccio, canary, chilipepper, yellowtail, and black rockfish), indicating an influx of younger fish (see appendix and table 2). Twelve species/size groups were included in the analysis of this sweep (table 2).

Ordination of the 12 taxa and 12 areas yielded an onshore-offshore gradient on axis 1 and a roughly north-south gradient on axis 2 (figure 17). Smaller taxa were associated with the offshore (high) end of the first axis, and several of the taxa falling at the other end were large (chilipepper, large shortbelly, large yellowtail), although some smaller size classes also scored low on axis 1 (mainly canary rockfish). The endpoints of axis 2 were determined by the unique distributions of canary and chilipepper rockfish. Species/size classes were grouped as indicated in figure 17 for further analysis.

No single area yielded large catches of many species (table 4). The UF NS and M NS areas, which fell out in the upper left quadrant of the ordination (figure 17), had moderate catches of a number of species in addition to those scoring high on ordination axis 1. The P OS, LF OS, and CORD areas also had a number of species in moderate abundance, but lacked some of the larger size classes and had some of the small species. The D OS, UF OS, and (to a lesser extent) M OS areas had large catches of just a few species. Of these, the M OS and UF OS areas in particular yielded mainly small species/size classes, and loaded high on axis 1. The LF NS, D NS, and PR OS areas had few species, and those in low abundance. These areas fell out in the lower left quadrant of the ordination (figure 17).

The group of small rockfish loading high on ordination axis 1 displayed an offshore distributional pattern, occurring largely at or beyond the front between high- and low-salinity water (figure 18a). Most members of this group were probably new to the study area since sweep 2. The copper and rosy complexes consisted of very small fish (table 2), and the small shortbelly rockfish and bocaccio were smaller on average than in sweep 2 (table 2, appendix b,e). It seems likely that most of these fish had occurred in offshore waters, and grew to a size retained by our gear by the time of this sweep. The species within the copper complex most likely to have been caught during this sweep were *S. chrysomelas*, *S. carnatus*, or *S. atrovirens*, the late-recruiting members of this group (Anderson 1983). Similarly,

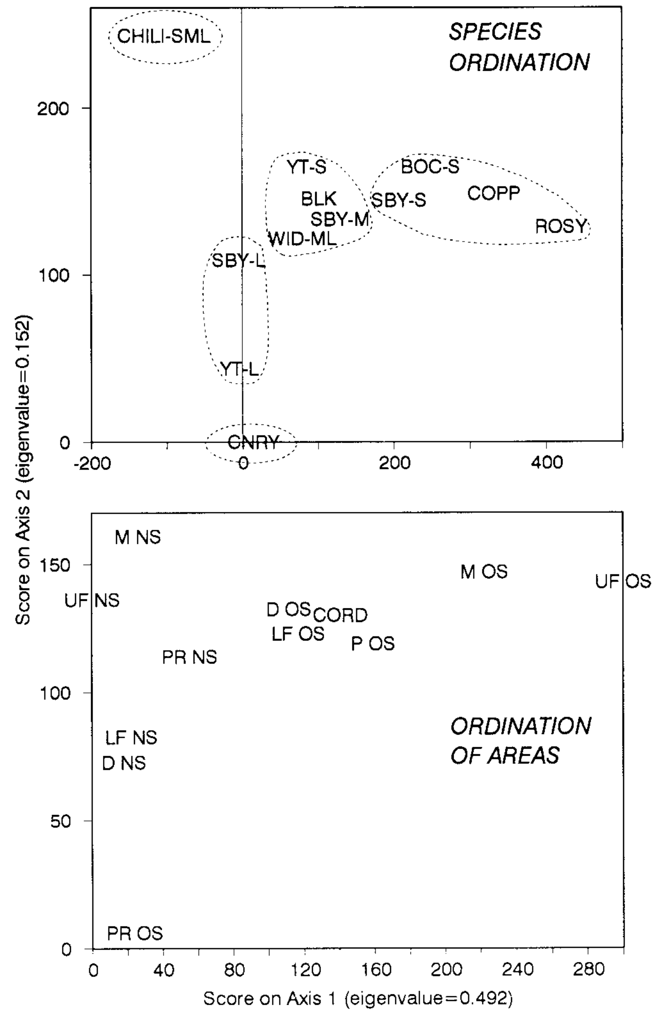


Figure 17. Ordination by detrended correspondence analysis of species and areas sampled during sweep 3 of May/June 1987 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

members of the subgenus *Sebastomus* (the rosy complex) are late spawners (Chen 1971). The small shortbelly rockfish and bocaccio captured here were probably the result of late spawning in these species.

The distribution of the second group defined by ordination—medium shortbelly, black, small yellowtail, and widow rockfish—was somewhat heterogeneous (figure 18b). Abundant in some offshore and transitional areas, at least some members of the group were also abundant in some nearshore areas of recent upwelling. The group was also heterogeneous with respect to size and ontogeny.

The large yellowtail–large shortbelly group occurred in some offshore areas, but as a whole these taxa were abundant near shore, especially toward the north (figure 18c).

The canary rockfish present during this sweep were relatively small (table 2, appendix d). This species was uncommon south of the Gulf of the Farallons, but in

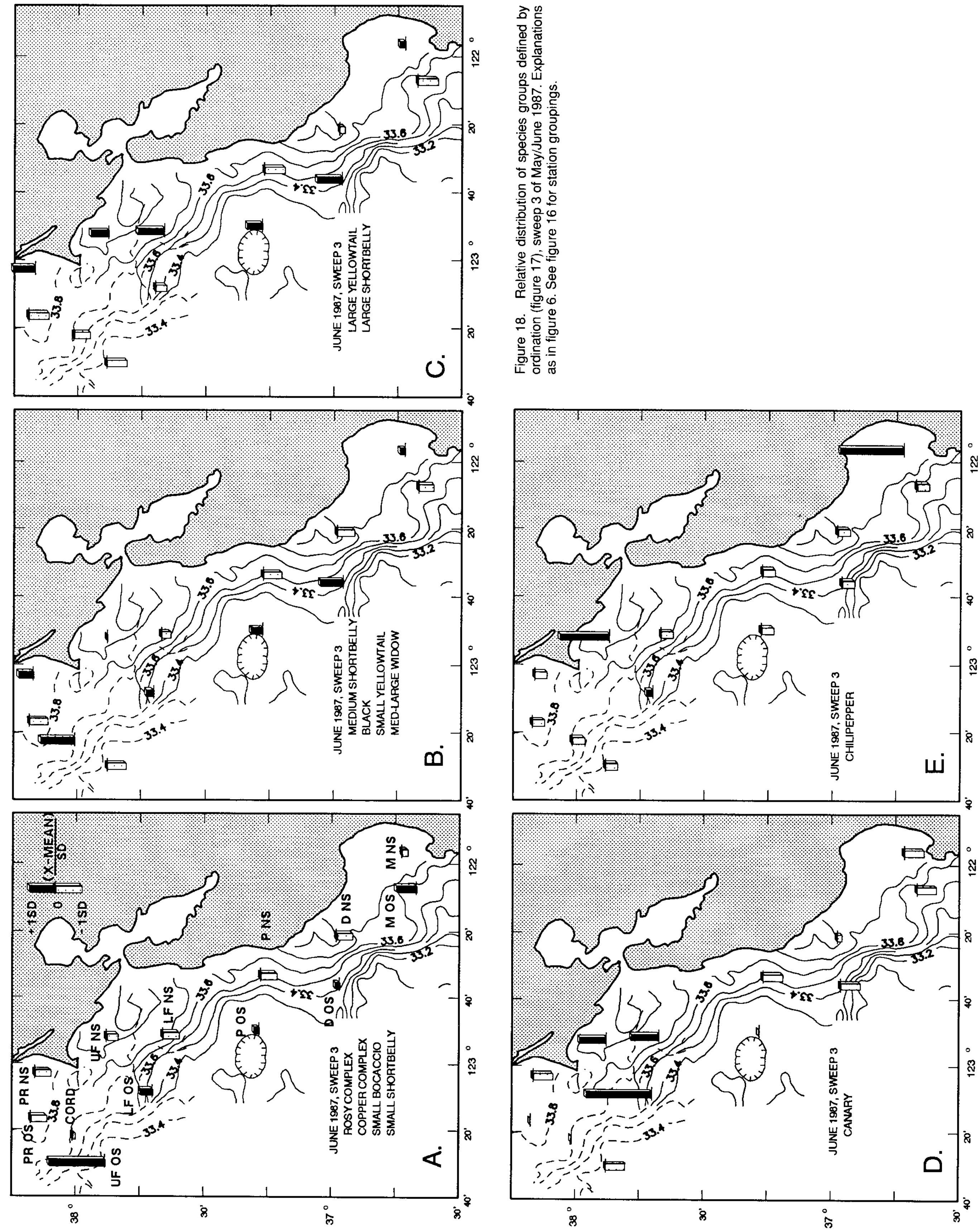


Figure 18. Relative distribution of species groups defined by ordination (figure 17), sweep 3 of May/June 1987. Explanations as in figure 6. See figure 16 for station groupings.

the north was common both offshore and nearshore, even in recently upwelled water (figure 18d).

The chilipepper rockfish present during this sweep were mostly medium to large in size (table 2, appendix c). This species was abundant mostly in the nearshore regions of the Gulf of the Farallons and Monterey Bay, in high-salinity water (figure 18e). The few small chilipepper rockfish present were at the LF OS area.

Summary. Sweep 3 was marked by a resumption of upwelling, the apparent settlement of large numbers of juvenile rockfish, and the appearance offshore of very small juveniles of some species. Remaining larger fish tended to be closer to shore, even in recently upwelled water. However, small juveniles of canary and yellowtail rockfish were not restricted to offshore distributions.

April 1988

The April 1988 cruise was relatively brief (six nights of sampling from April 16 to 22). As a result, the Point Reyes stations were not sampled, and other areas such as Cordell Bank and Pioneer Seamount were skipped as well, reducing the geographic coverage during this sweep. In addition, data from some stations were not used because of problems with the net.

Oceanography. Winds had been upwelling-favorable episodically through March and the first week of April, but these winds relaxed considerably during the week before the cruise, and downwelling-favorable conditions prevailed during much of the cruise (figure 2b).

Neither the ship's computer nor thermosalinograph was operational during this cruise, so surface temperature and salinity values were determined from CTD casts and measurements of water temperature with a thermometer. CTD readings (from the upper few meters of the water column) were obtained from about 80 points, including all trawl stations. The temperature of water in the ship's running seawater system was measured with a thermometer at each of these points, and at one or two points between each CTD station. Thermometer and CTD temperatures were cross-calibrated where both were measured, and the mean difference between the two was applied to all thermometer readings. In an additional difference from the treatment of previous sweeps, the temperature and salinity of each trawl station was determined from one value, the CTD reading, rather than from the average of 5-minute thermosalinograph values recorded during the trawl.

Because of both the limited geographic scope of sampling and the lack of recent upwelling, rather uniform oceanographic conditions were found during the April 1988 cruise (figure 19). Relatively high-salinity water (>33.6 ppt) occurred along the coast, even forming a plume-type structure off Davenport (figure 19), indicating that upwelling had occurred at some time before

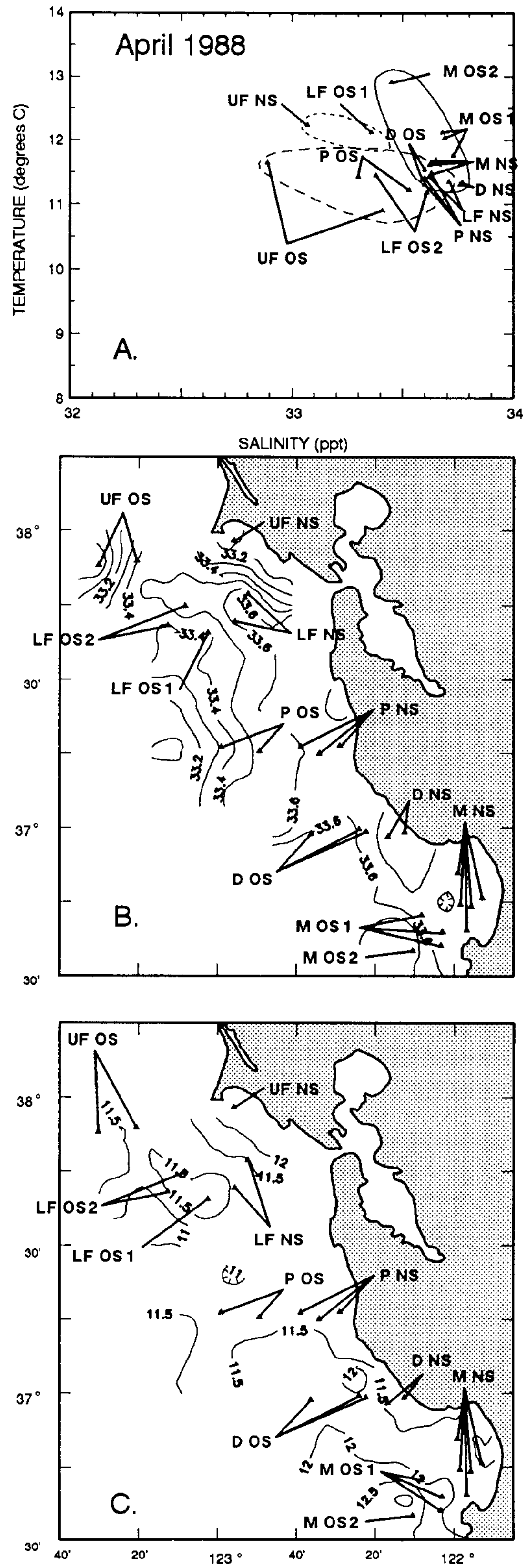


Figure 19. Trawl stations and their groupings from April 1988, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Abbreviations of place names are defined in figure 1.

the cruise. But the relatively warm temperature and rarity of very high salinities suggest that upwelling had not been recent, that the upwelled water had been warmed at the surface, and that little active advection due to upwelling was taking place during this cruise. There were some gradients to lower-salinity (but still cool) water offshore in the central and northern portions of the study area, but onshore-offshore fronts were not particularly strong. A tongue of somewhat warmer and lower-salinity water intruded from the south into the region offshore of Monterey Bay. The freshwater plume from San Francisco Bay was evident in the northern Gulf of the Farallons. These waters were underlaid (as were those of much of the study area) by cool, saline water typical of upwelling conditions.

Trawl stations were combined into 12 groups of 1–5 stations each (figure 19). Three of these contained only one station each—two because of unique oceanographic conditions (LF OS1 and M OS2), and one because hauls from a nearby, similar station were unusable (UF NS). Several of the areas had similar water characteristics: M NS, D NS, LF NS, P NS, and D OS were all in areas of relatively saline water at the lower range of temperatures present during the sweep, and were probably in slightly aged upwelled water that had not mixed to a great degree with offshore water (D OS showed the most mixing and D NS the least). M OS1 was in slightly warmer, but still saline, water, and M OS2 was in an apparent offshore intrusion of warmer, less saline water. P OS and LF OS2 were near a diffuse offshore front separating the more saline nearshore water from less saline offshore water, and the UF OS stations straddled a more pronounced offshore front in the northern portion of the study area. At the UF NS area, fresh San Francisco Bay plume waters overrode cool, saline waters below. The single LF OS1 station was difficult to classify. Its surface characteristics were most like the bay plume region, but more saline. It may have been located in a pocket of relatively warm offshore water.

Rockfish Distributions. Because it was early in the season, the April 1988 cruise yielded few of the large size classes of pelagic juvenile rockfish, and greater numbers of small and medium fish, but most species were larger than in April of 1987 (table 2, appendix). Eighteen species/size classes were included in the analysis of this sweep (table 2).

Seven of the 12 areas ordinated fell together in a rather tight cluster (figure 20). Three of the remaining areas were isolated in the ordination, forming three of the four axis extremes, and each of these (LF OS1, M OS2, and UF NS) consisted of only one station each. A weak onshore-offshore gradient ran diagonally from the lower left to the upper right of the ordination. This was slightly correlated with fish size, since some of the taxa scoring

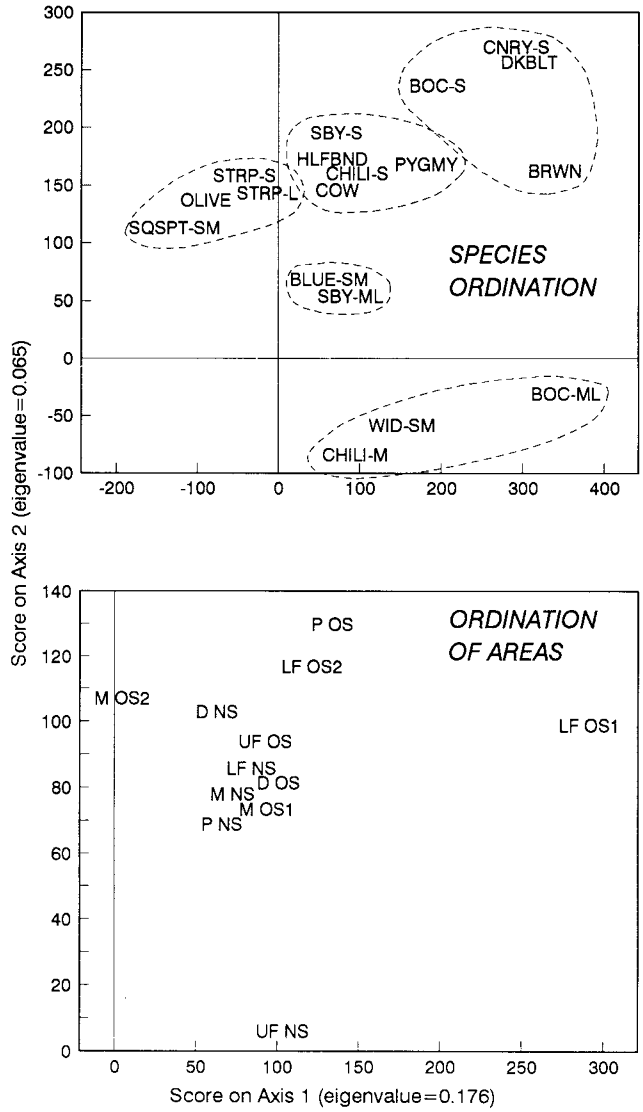


Figure 20. Ordination by detrended correspondence analysis of species and areas sampled during April 1988 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

low on axis 2 (medium chilipepper and medium-large bocaccio) were relatively large, and several of the smaller groups scored high on axes 1 and 2. However, much of the arrangement of species in the ordination was related to their occurrence in the areas lying at the extremes of the ordination axes. Thus, the ordination revealed little larger-scale structure in the assemblage of juvenile rockfish during this cruise. Five groups of taxa were defined for further analysis, as indicated in figure 20.

Three areas near the center of the ordination (M NS, LF NS, and D OS) had relatively high catches of several species/size classes (table 4). The M OS2 area, which was at the low end of ordination axis 1, had large catches of fewer species. The UF NS area, which was at the low end of axis 2, had few species, but most of those were above average abundance for the study area. The LF OS1 area, which was the high extreme of axis 1, had low catches of very few species. The remaining areas had intermediate numbers of species, in low to moderate abundance. Among these were the P OS and LF OS2 areas that formed the other extreme to UF NS on axis 2 of the ordination.

The trio of medium chilipepper, small-medium widow, and medium-large bocaccio, which fell in the lower right corner of the ordination, was distinctive in its abundance in the UF NS area and its rarity in lower-salinity offshore areas (figure 21a). This group was among the larger fish present during the sweep. The group of small bocaccio, darkblotched, small canary, and brown rockfish included relatively small fish that fell in the upper right corner of the ordination. As a group, they were found in several of the lower-salinity offshore areas, and tended to be rare in nearshore areas (except LF NS, where many species were abundant; figure 21b). This group was better represented at the UF OS area than any other group. The group consisting of small and large stripetail, small-medium squarespot, and olive rockfish, which occurred low on axis 1 of the ordination, was abundant largely in the southern part of the study area (figure 21c). Members of this group were abundant at M OS2 in the tongue of warmer, less saline water, but were also abundant in the higher-salinity areas of D NS and M NS. This group represented a mix of sizes. The group consisting of small shortbelly, halfbanded, cowcod, small chilipepper, and pygmy rockfish included some small size classes (as well as the early-recruiting pygmy rockfish), but was found in the higher-salinity areas in the southern part of the study area and in the LF NS area (figure 21d). It was rare in lower-salinity offshore areas. The last group (medium-large shortbelly and small-medium blue rockfish) was widespread, and unusual in its abundance at both the UF NS and M OS2 areas (figure 21e). This group may have had a north-south bipolarity in its pattern of abundance, but showed no distinctive onshore-offshore pattern of distribution nor any particular relation to temperature and salinity.

Summary. The April 1988 cruise was unusual in the narrow ranges of geography, oceanographic conditions, and size classes encountered. The cruise took place during a major relaxation period that followed an extended period of upwelling. This, in combination with the reduced set of stations sampled, led to a rather tight clustering of stations with regard to oceanographic conditions. Because the cruise was early in the season, large size classes of juvenile rockfish were rare. However, the timing of the recruitment season seems to have been earlier in 1988 than in 1987, so small pelagic juveniles were not particularly abundant either. Most areas had similar catches of species and size classes, perhaps related to their similar oceanographic conditions. Where catches and conditions differed, there was some indication of onshore-offshore differences in distribution that were related to size and ontogeny among taxa. But there was no strict segregation of small size classes offshore and large size classes onshore.

June 1988, Sweep 1

The first sweep of the study area in May/June 1988 was carried out between May 22 and June 2. Sampling at the regular suite of stations was completed on the night of May 30–31. Following the regular sampling, two nights (5/31–6/1) were spent sampling an upwelling filament offshore of the Gulf of the Farallons.

Oceanography. Two periods of upwelling-favorable conditions occurred between the relaxed wind conditions of April and the initiation of this sweep (figure 2b). Immediately before this sweep, several days of upwelling-favorable conditions gave way to relaxed conditions, and these prevailed at the beginning of the sweep. But strong upwelling-favorable conditions returned shortly into the sweep, and reoccurred toward the end of the sweep (figure 2b).

The ship's thermosalinograph was operational during this sweep, but not its computer, so temperature and salinity readings were recorded manually at each CTD and trawl station, and at one or two points between these stations. The temperature and salinity values associated with each trawl station, then, were single points instead of averages of several values recorded during the trawl. Changing weather and other interruptions of the regular schedule led to discontinuities in the quasi-synoptic acquisition of oceanographic data, so the data from Monterey Bay and the Gulf of the Farallons were contoured separately.

The upwelling-favorable conditions present during this sweep were evident in the temperature and salinity patterns observed (figure 22). Salinity exceeded 33.7 ppt in most nearshore areas, and temperatures below 11°C were common, all indicating recent, active upwelling. Upwelling centers were evident off Davenport and below Point Reyes (figure 22). Upwelled water from Davenport formed a front with less-recently upwelled water to the north, and spread across Monterey Bay to the south. The nearshore portion of Monterey Bay, which was sampled before the first upwelling-favorable period during the sweep (figure 2b), was characterized by relatively warm but saline water, which presumably originated with earlier upwelling (figure 22). A lens of relatively fresh water from San Francisco Bay extended downcoast to the vicinity of Pescadero. Recently upwelled water occurred in the Gulf of the Farallons and off Point Reyes, with a filament extending offshore south of Point Reyes. The only truly offshore water was found off Point Reyes,

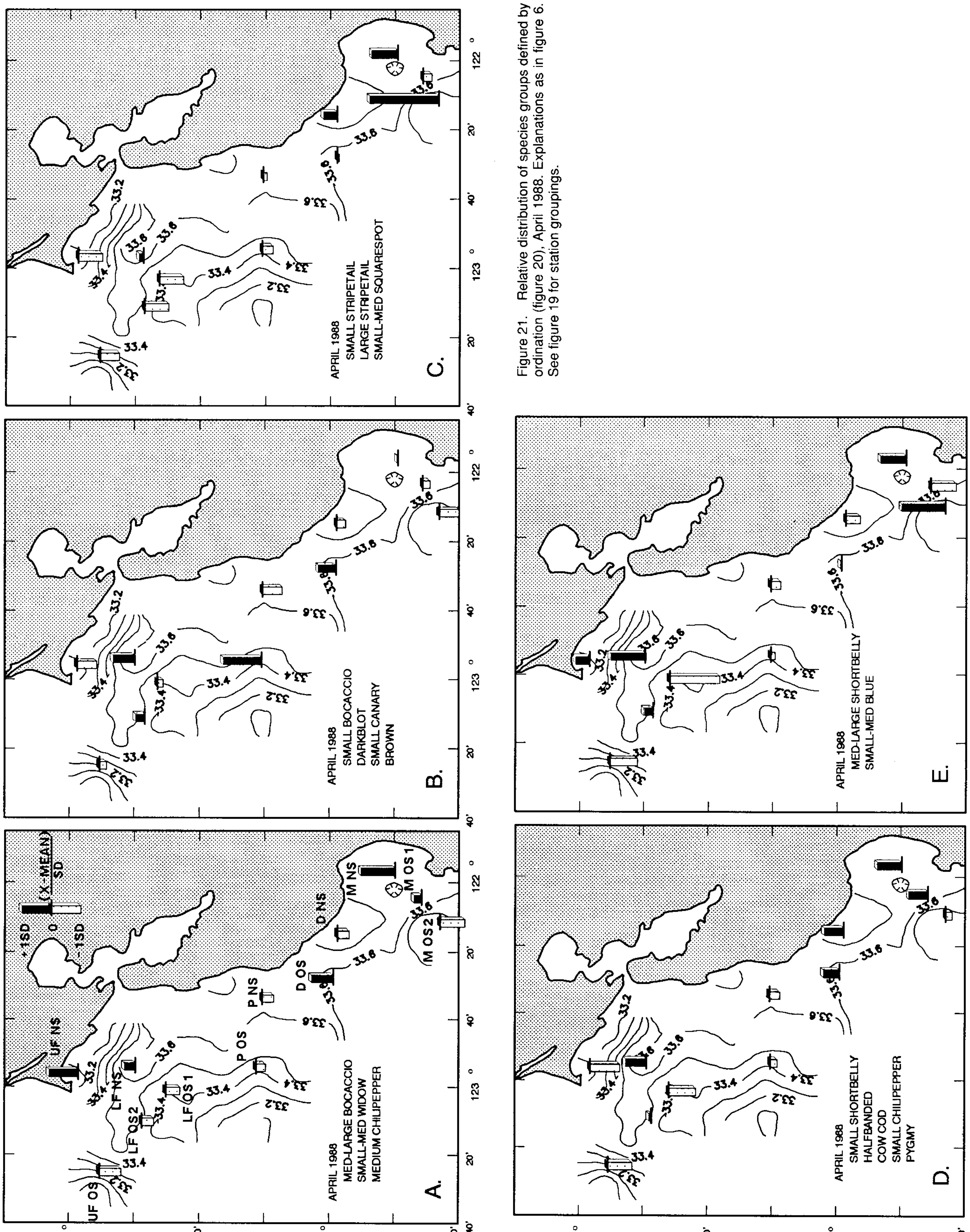


Figure 21. Relative distribution of species groups defined by ordination (figure 20), April 1988. Explanations as in figure 6. See figure 19 for station groupings.

where a very strong front separated upwelled water inshore from quite low-salinity, warm water offshore.

Trawl stations were combined into 14 groups of 1–6 stations each (figure 22). The M NS stations in Monterey Bay were in upwelled but insolated water, which was cooler in the south. The M OS stations were in saline but cooler water that had likely been advected south across Monterey Bay in the most recent episode of upwelling. The D NS, D MID, and D OS groups graded from very recently upwelled water inshore to less-recently upwelled water offshore. The P NS station was in somewhat recently upwelled water north of the Davenport center. Offshore, this graded into the San Francisco Bay plume (P MID), and then into somewhat mixed coastal/offshore water (P OS). In the Gulf of the Farallons, the LF NS stations were at the edge of the most recently upwelled water from Point Reyes, and the UF NS stations were in very recently upwelled water. The LF OS stations graded from somewhat recently upwelled water to mixes with lower-salinity offshore water south of the filament off Point Reyes, while the UF OS station was nearly in the center of this filament. The PR NS stations were in recently upwelled water along the coast, while the PR OS stations were at and beyond the front separating upwelled water from the low-salinity water mass offshore.

Rockfish distributions. Small size classes of pelagic juvenile rockfish were rare during this sweep, and medium and large size classes were abundant for many species (table 2, appendix). Even in species such as canary and yellowtail rockfish, where small size classes were abundant enough to analyze, the mean size of small fish was large (table 2). Sixteen species/size classes were included in the analysis of this sweep (table 2).

Ordination of the 14 areas and 16 taxa suggested a triangular arrangement, with southerly nearshore areas at the apex on the right, offshore areas in the upper left, and northerly areas (mostly nearshore) in the lower left (figure 23). Larger size classes of several species clustered at the right of the ordination, associated with the southern nearshore areas. Several widespread taxa, many of which were of medium size, occurred in the center of the ordination. Three other taxa, small to medium in size, occurred in the upper left of the ordination, associated with some offshore areas. Two other taxa (large canary and small yellowtail rockfish) had idiosyncratic distributions, both being below average in abundance in the southern nearshore areas and some offshore areas, but relatively abundant in some of the northern areas.

Overall patterns of abundance among areas influenced the ordination. The three nearshore areas in the south had large catches of a large subset of the species present (including some species that occurred nowhere else), while the UF OS area, which was near another corner

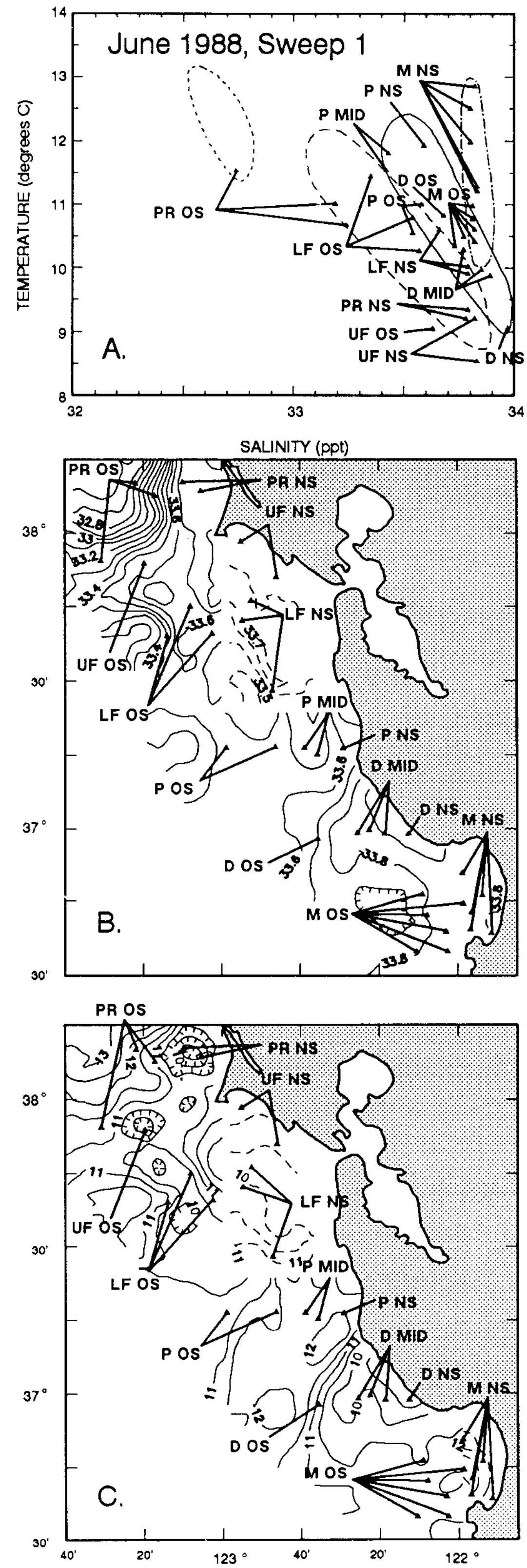


Figure 22. Trawl stations and their groupings from May/June 1988, sweep 1, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Monterey Bay and the Gulf of the Farallons were contoured separately (*dashed contour lines*) because of interruptions in sampling. Abbreviations of place names are defined in figure 1.

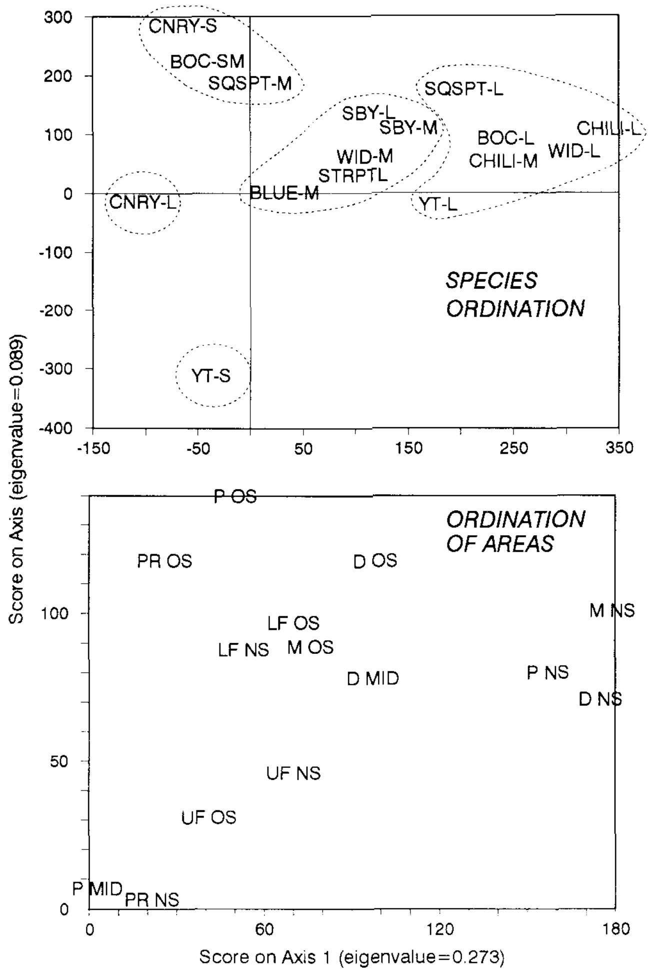


Figure 23. Ordination by detrended correspondence analysis of species and areas sampled during sweep 1 of May/June 1988 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

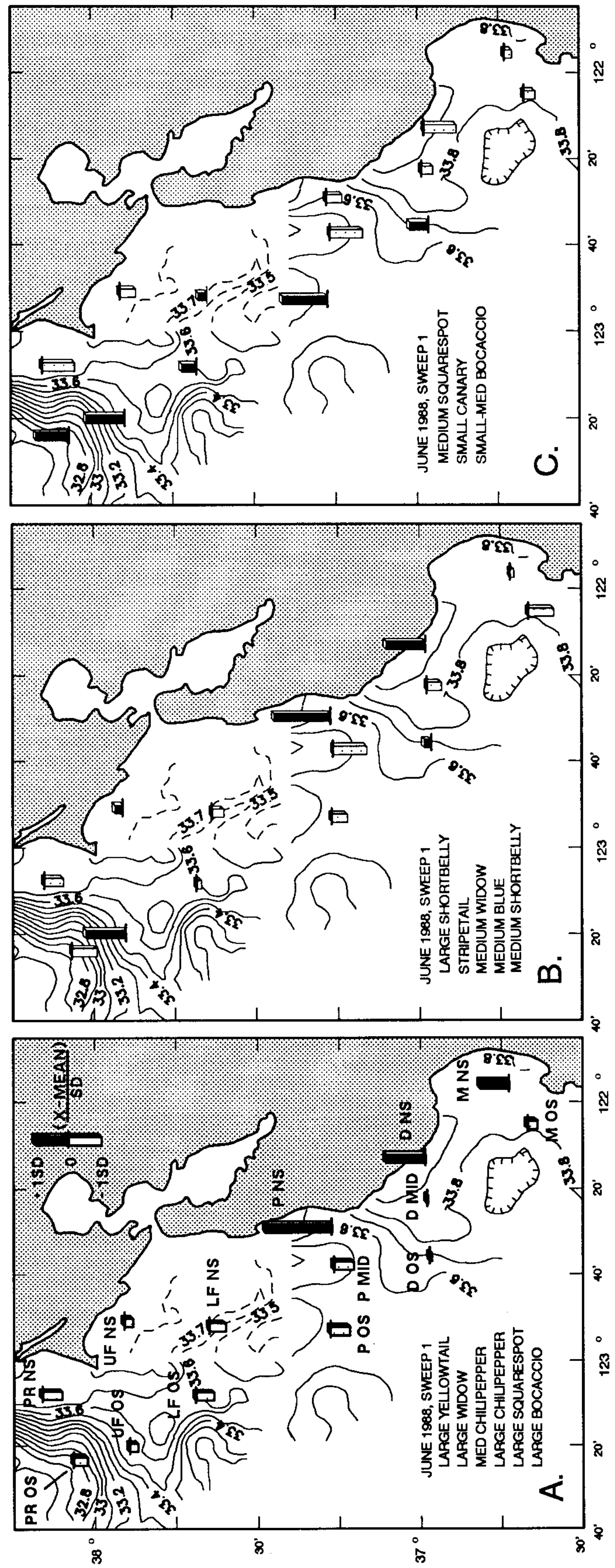
of the ordination, had large catches of another large subset of the species present (table 4). The P OS area, which was at the upper left apex of the ordination, yielded fewer species, but of those, most were relatively abundant. The P MID and PR NS areas had relatively small catches of few species. The presence of two somewhat uncommon taxa (large canary rockfish and small yellowtail rockfish) in one or both of these areas probably led to the prominent position of these areas in the ordination. We should note here that the most-inshore station off Point Reyes was not sampled during this sweep. The most-nearshore stations in other areas often had large catches, and we believe that the most-nearshore station off Point Reyes may also have yielded large catches, had we sampled it. We identified five groups of species/size classes for further analysis (figure 23).

The group of mostly large (or early-settling) taxa falling on the right of the ordination was most abundant in the nearshore areas to the south, both in less recently upwelled waters off Pescadero and Monterey, and at the very base of the active upwelling center off Davenport (figure 24a). Some, but not all, of the members of this group were also present farther offshore in the Davenport upwelling plume. The group in the center of the ordination, which included medium and large size classes and an early-settling species (stripetail rockfish), typically occurred in a large number of areas (table 2). As a group, however, they were most abundant in nearshore areas north of Monterey, and in the upwelling filament off Point Reyes (figure 24b). They were abundant near shore in the upwelling center off Davenport, and all but the stripetail rockfish were abundant in the newly upwelled water below Point Reyes. Thus their onshore-offshore distribution was similar to that of the first group, but this group occurred farther north. The group in the upper left corner of the ordination consisted of smaller size classes (two medium size classes and one small), and occurred largely in lower-salinity waters located offshore (figure 24c). Large canary rockfish were most abundant in the northern portion of the study area, both within the upwelling filament offshore of Point Reyes and in the more recently upwelled water above and below the point (figure 24d). Small yellowtail rockfish were also most abundant in the north, particularly in the upwelling filament off Point Reyes (figure 24e). Unlike other small fish, the small yellowtail rockfish were abundant in some nearshore areas, even in recently upwelled water below Point Reyes.

Summary: main sweep. Current upwelling was quite evident during this sweep of the study area. Despite this, large size classes of several species were found close to shore, even in the most recently upwelled water. We think that large catches of pelagic juveniles may also have been made at the most nearshore station off Point Reyes. Some of the smaller size classes were found farther offshore, in more oceanic water or in mixed water that had been upwelled less recently. The results of this sweep suggest that under some conditions large size classes can either maintain station close to shore, or move closer to shore in spite of upwelling.

In contrast to the idea that offshore transport in upwelling does not affect late-stage pelagic juveniles, larger size groups of a few species (most notably canary rockfish) were abundant in the plume of upwelled water extending off Point Reyes (figure 24). A similar effect did not seem to occur in the Davenport upwelling center, since the offshore areas within this plume (D OS at the edge of the plume, and M OS within) did not generally yield large catches of larger size groups, particularly in comparison to the inshore areas (figure 24).

Distributions in Point Reyes upwelling plume. Portions of two days and nights (5/31 and 6/1) were spent conducting hydrographic surveys and trawl samples near the



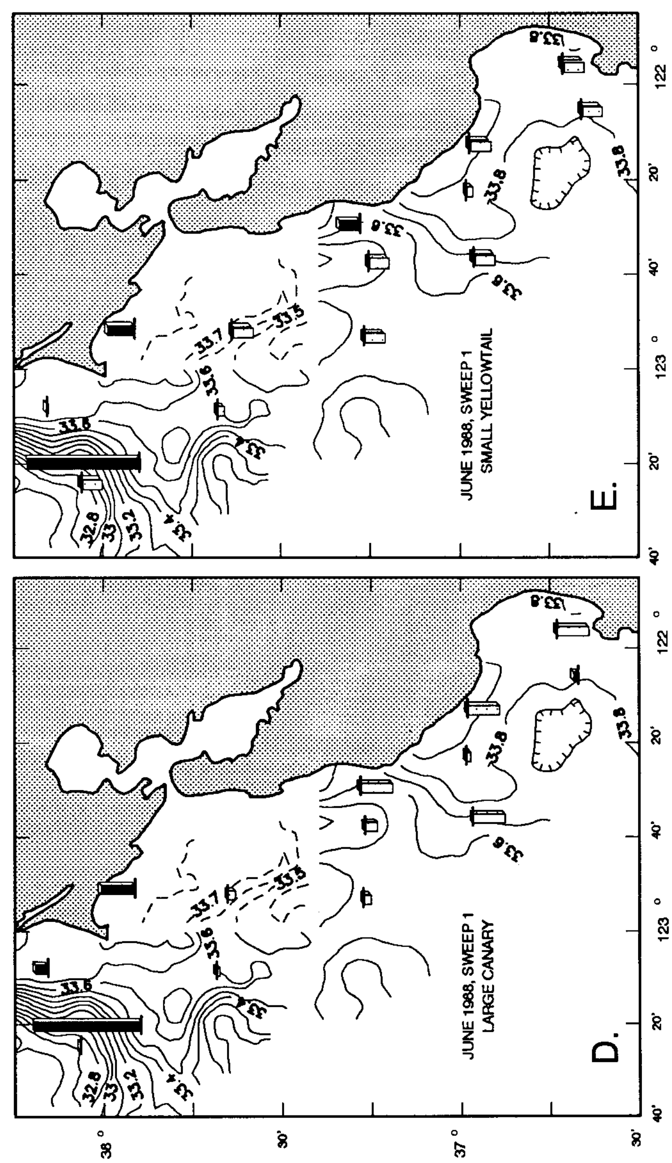


Figure 24. Relative distribution of species groups defined by ordination (figure 23), sweep 1 of May/June 1988. Explanations as in figure 6. See figure 22 for station groupings.

offshore end of the upwelling filament off Point Reyes. A core of cool, saline water extended over 55 km offshore of the Farallon Islands, and over 35 km offshore of the UF OS station sampled during the regular sweep (figure 25). Sharp gradients in temperature and salinity separated these waters from warmer, less saline waters on the south side of the plume (figure 25). On the north side of the plume, salinities dropped rapidly, but cool temperatures extended more broadly north. CTD casts in the core of the plume (figure 26, cast F) indicated only slight thermal stratification above 20 m. Nearer the southern edge of the plume (figure 26, cast E), salinity in the upper 50 m was much lower than in the core, and temperatures were slightly warmer, with sharp thermal stratification above 10 m. South of the plume (figure 26, casts A,B), the water column was strongly stratified, with a pycnocline at 40 m. Here, temperature converged with the core of the plume below 60 m, and salinity converged at about 100 m. To the north, (figure 26, cast D), complex thermal stratification with a sharp thermocline at 10 m yielded cooler temperatures above 50 m than found in the same depth range south of the plume; warmer temperatures below 50 m; and consistently lower salinities than south of the plume. This area bordered the low-salinity, offshore water mass evident off Point Reyes in the main part of the sweep. The core of the plume showed many indications of high productivity: green water, large amounts of krill, and abundant pinnipeds. Waters to the south of the plume were especially different: quite blue, and lacking the other indications of productivity.

Pelagic juvenile rockfish were sampled at three bathymetrically stratified stations on the night of 5/31–6/1 (figure 25, stations A, E, and F), and in single, standard-depth trawls at three stations on the night of 6/1 (stations B, C, and D). Station F was at the core of the plume; station E was at its southern edge; stations A and B were in blue water south of the plume; and stations C and D were north of the plume's core.

Catches of pelagic juvenile rockfish were highest in the core of the plume, and the three species/size groups that had been abundant in the northern portion of the study area during the regular sweep were also the most abundant in the plume (figure 25, station F). Catches of the two other species/size groups were at or just below average for the rest of the sweep. In the three abundant groups, catches were highest at 30 m and 110 m of depth. Catches of all groups were lower at the southern edge of the plume (figure 25, station E), and no juvenile rockfish were caught in the four trawls made in blue water south of the plume (figure 25, stations A and B). Catches were near to above average at the two stations north of the plume core (figure 25, stations C and D), where only small yellowtail rockfish were abundant.

These trawls suggest two main points. First, at least some pelagic juvenile rockfish can be advected offshore during upwelling. In fact, one adult olive rockfish was caught in trawls at the core of the plume; we think it lost contact with reefs off the Farallon Islands and was carried away. This advection is apparently not just a surface phenomenon, because pelagic juveniles were found well into the water column. Second, as found in the April 1987 survey, pelagic juveniles large enough to be captured in our gear may be rare in offshore water masses beyond the influence of some coastal processes. No pelagic juvenile rockfish were found in the blue water mass to the south of the plume, just as pelagic juveniles declined in abundance offshore of the coastal/offshore fronts in April of 1987.

June 1988, Sweep 2

The second sweep of the study area was carried out between June 2 and June 11. The regular portion of the sweep was completed on the night of June 8–9. Some offshore stations were sampled on the night of June 10–11.

Oceanography. Following the largely upwelling-favorable conditions during the regular portion of sweep 1, relaxed conditions prevailed immediately before sweep 2 (figure 2b). A brief period of moderately favorable conditions for upwelling occurred near the beginning of sweep 2, followed by relaxed conditions during the remainder of the regular portion of sweep 2 (figure 2b). Thus this sweep was largely characterized by conditions unfavorable for upwelling.

The thermosalinograph was operating during most of this sweep, but the ship's computer never was. When the thermosalinograph was operating, temperatures and salinities were recorded manually as in sweep 1. The thermosalinograph was not operating for a portion of this sweep, during which time near-surface temperature and salinity values were determined from CTD casts at trawl and CTD stations, and temperature was recorded by thermometer in the ship's running seawater system at points between trawl and CTD stations. Temperatures recorded by thermometer were calibrated to CTD readings (as in the April 1988 cruise).

Overall, oceanographic conditions during sweep 2 reflected the relaxation of upwelling. Evidence of previous upwelling could be found in the high-salinity waters present along the coast south of Point Reyes during sweep 2 (figure 27). But the absence of water cooler than 10°C (figure 27a,c) reflected the rarity of upwelling during the sweep. The coolest and most saline water was found in the northern, offshore portion of Monterey Bay, which was sampled during the period of the sweep that was most favorable for upwelling. The tongue of newly upwelled water present off Davenport during the first sweep (figure 22) was not evident during sweep 2,

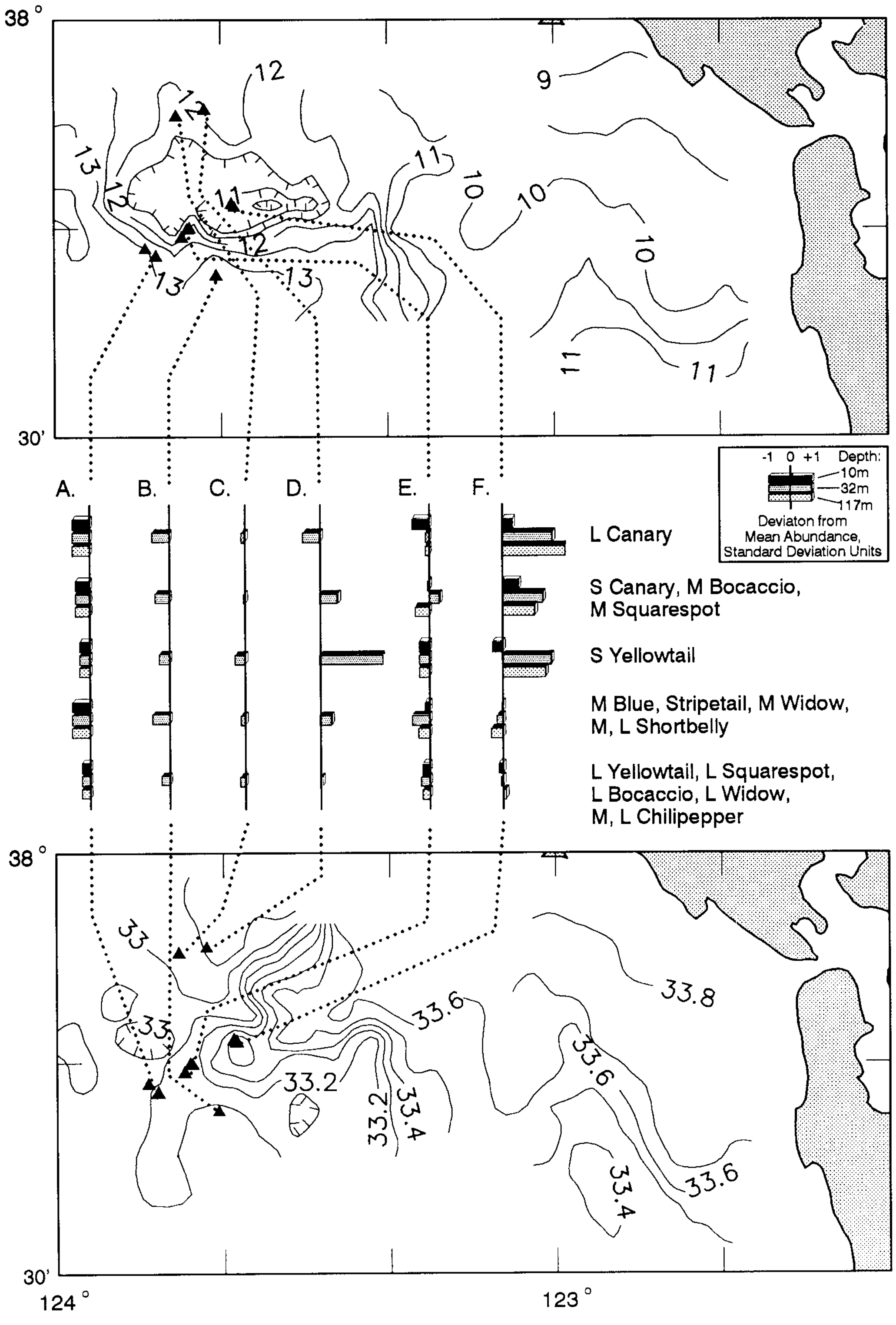


Figure 25. Distribution of pelagic juvenile rockfish in an upwelling plume, sweep 1 of May/June 1988. Positions of trawl and CTD stations are indicated by *triangles* on contour maps of surface temperature (*upper panel*) and salinity (*lower panel*). Comparative abundances of pelagic juvenile rockfish are presented in *bar graphs*, in which species are grouped according to the ordination of species and areas during the regular sweep (figure 23). The size of each bar is the average (over species in that group) of the difference between the ln(x+1)-transformed abundance of a species at that station and the mean of that species over all stations in sweep 1, divided by its standard deviation over stations. Bars in groups of 3 represent bathymetrically stratified trawls at a station.

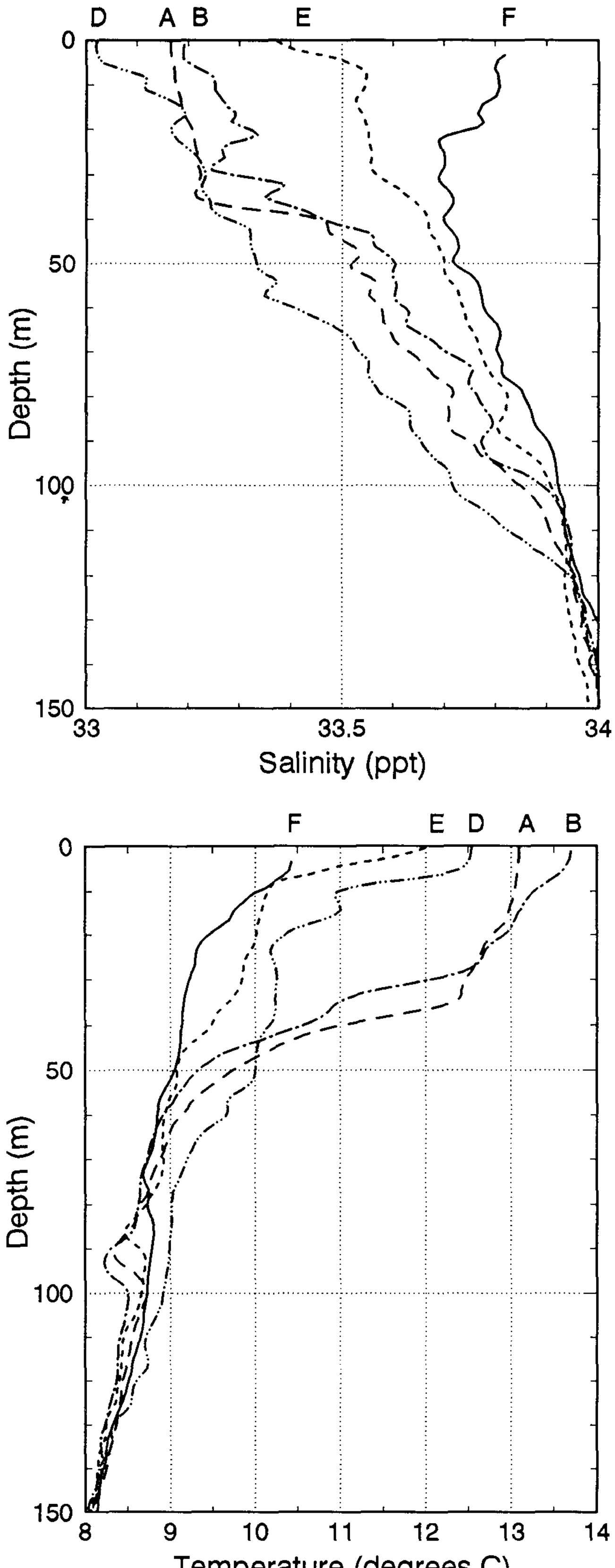


Figure 26. Profiles of salinity and temperature at five of the stations (A, B, D, E, F) depicted in figure 25.

and may have drifted across and into Monterey Bay. Local warming was evident in southern Monterey Bay (figure 27). The newly upwelled water present south of Point Reyes during sweep 1 (figure 22) likewise seems to have drifted south by sweep 2, as the most extensive mass of high-salinity water above Monterey Bay ranged from Pescadero into the southern Gulf of the Farallons (figure 27). This water had also warmed since sweep 1. The tongue of upwelled water present offshore of Point Reyes during sweep 1 was less extensive during sweep 2. The body of warm, low-salinity water present in the offshore area north of Point Reyes during sweep 1 was again present during sweep 2, but was closer to shore (figures 22, 27). Fronts indicating intrusion of offshore water were also evident from the Gulf of the Farallons to Pescadero, and offshore of Davenport (figure 27).

Trawl stations were combined into 13 groups of 1–4 stations each (figure 27). The stations within Monterey Bay (LM NS and UM NS) were in saline water that had warmed. The outer Monterey Bay stations were slightly less saline, but as cool as (LM OS) or cooler than (UM OS) the nearshore stations. The UM OS stations in particular may have been associated with the decaying plume of upwelled water from Davenport. The D NS station was in cool and saline water similar to the UM OS stations. The D OS stations were in waters of moderate salinity and temperature, indicating mixing of upwelled and nonupwelled water and local warming. The P NS station was on the inshore side of the mass of upwelled water that apparently had drifted south from the Gulf of the Farallons, and the P OS stations were near the offshore edge of this mass. The stations in the Gulf of the Farallons similarly were in coastal waters of moderately high salinity but moderate temperature. One station was at the edge of the freshwater outflow from San Francisco Bay. The LF OS stations were at and beyond the offshore front, and the UF OS stations were in the remnants of the Point Reyes upwelling plume. The PR NS stations were in mixed coastal waters, and the PR OS stations in the front and offshore water mass.

Rockfish distributions. All species except widow rockfish decreased in abundance from sweep 1 to sweep 2 (table 2), a decline that we attribute to settlement. As in sweep 1, individuals of most species were relatively large, with few small size classes present (table 2, appendix). Mean size of most taxa increased from sweep 1 to sweep 2, due to growth, appearance of larger fish within the study area, loss of smaller fish, or some combination of these factors. Mean size decreased only in squarespot, canary, and yellowtail rockfish (appendix d,i; table 2). Twelve species/size classes were included in the analysis of this sweep (table 2).

Although 13 groups of trawl stations were designated on the basis of oceanographic and geographic similarity, one of these areas yielded no pelagic juvenile rockfish and two others yielded very small catches. These three areas (D NS, P OS, and D OS) were not included in the ordination, but were included in further analyses. Ordination of the remaining 10 areas and 12 species/size classes showed little general pattern, but instead seemed to be determined by the idiosyncratic distributions of different taxa (figure 28). Areas in the center of the ordination (UM NS, UM OS, GF, and PR NS) contained most species and size classes, at moderate to high relative abundances (table 4). Extreme areas in the ordination were characterized by the presence of one or a few particular species, with little concordance in the variation of species composition over areas. Areas at the right of the ordination (P NS and LF OS) were distinctive in the abundance of canary and yellowtail rockfish, which were uncommon or absent in other areas (figure 28). The upper left corner of the ordination was determined by the restriction of chilipepper rockfish to the LM NS area. The lower left corner of the ordination was determined by the abundance of three large size classes in three offshore areas (LM OS, UF OS, and PR OS). Unlike other sweeps, in this sweep larger taxa seemed to be associated with offshore areas. Species/size classes were assigned to four groups for further analysis, as indicated in figure 28.

The group of taxa on the right of the ordination (small and large canary rockfish, and yellowtail rockfish), were somewhat heterogeneous in their distributions, but shared a tendency to occur in the northern portion of the study area, particularly in the LF OS area (figure 29a). Large canary rockfish and yellowtail rockfish were also unusually abundant in the P NS area. As a group, they were also abundant in the PR NS and GF areas, where many species were found. The distribution of this group showed little relation to oceanography, except a tendency to be rare in the most saline waters and in the southern portion of the study area (figure 29a). The group in the middle of the ordination was abundant along with most other species in the PR NS, GF, and UM NS areas, and also in the PR OS and UF OS areas (figure 29b). The group seemed to have a disjunct distribution, being most consistently abundant in the northern portion of the study area, but also inside Monterey Bay. Its distribution bore no obvious correlation with oceanography: it was abundant both in low-salinity offshore waters and in high-salinity nearshore waters. This group consisted of medium to large size classes. The mostly large taxa in the lower left corner of the ordination were abundant with other taxa in the PR NS area, but were unusual in their abundance in the UF OS and LM OS areas (figure 29c). Two of these taxa (large widow and shortbelly rockfish) were also somewhat abundant in the PR OS area (where bocaccio also were taken, but in shal-

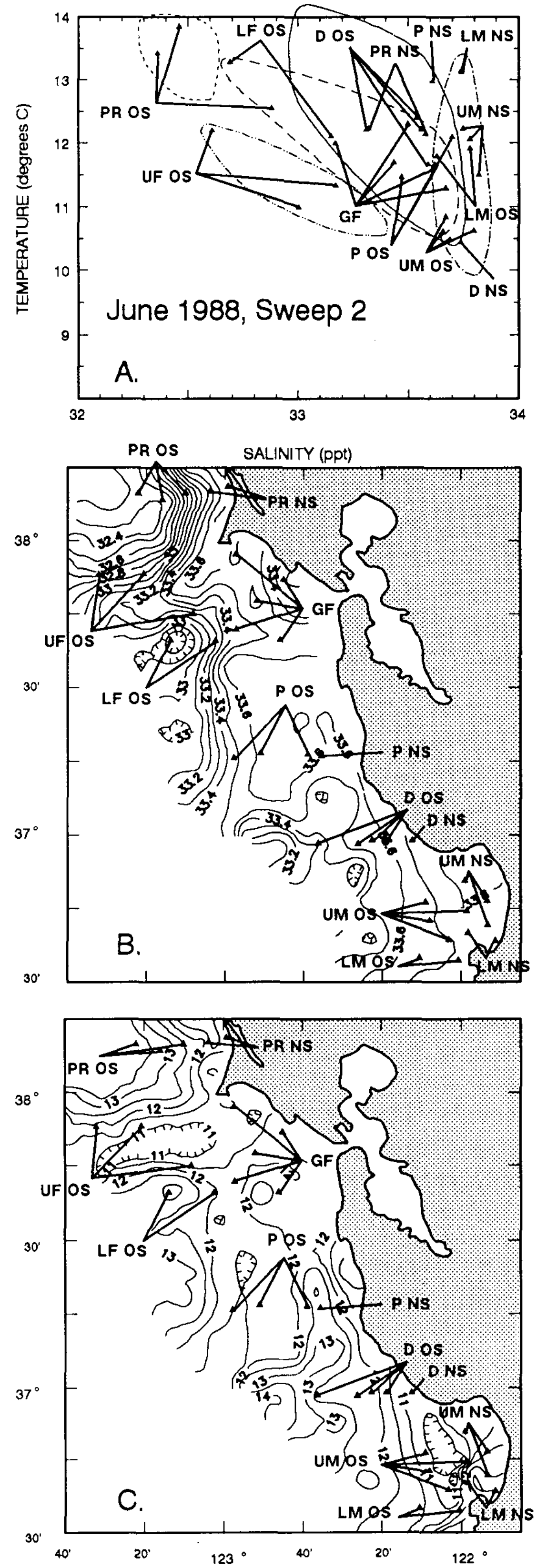


Figure 27. Trawl stations and their groupings from May/June 1988, sweep 2, plotted on temperature vs. salinity (*A*), salinity contours (*B*), and temperature contours (*C*). Abbreviations of place names are defined in figure 1.

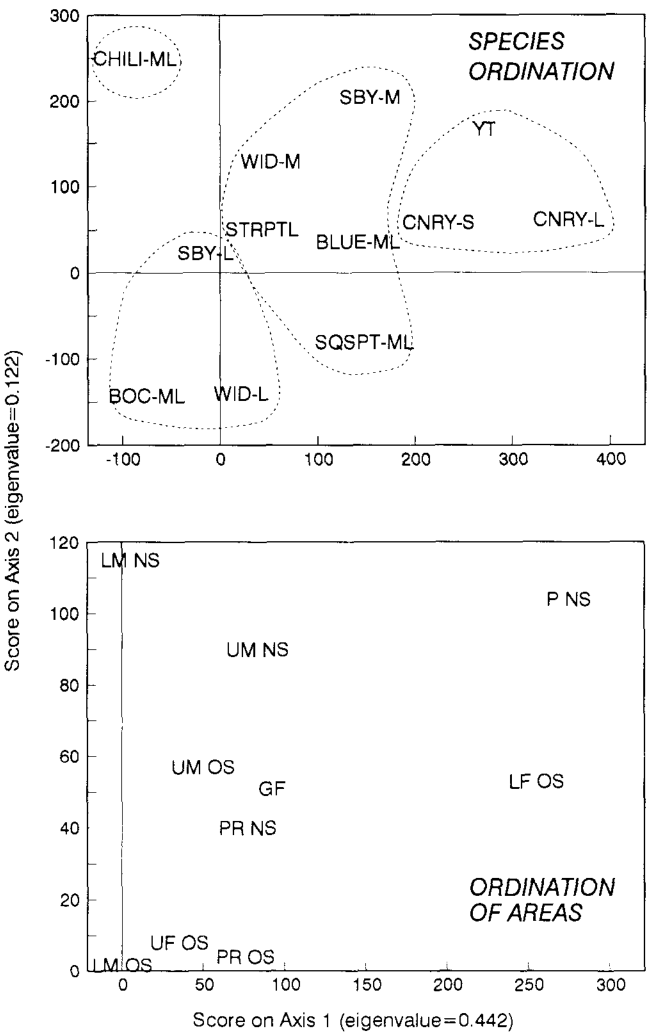


Figure 28. Ordination by detrended correspondence analysis of species and areas sampled during sweep 2 of May/June 1988 (tables 2, 4). See table 2 for abbreviations of species names and figure 1 for abbreviations of place names.

low trawls). This group, then, did not follow the pattern evident in other sweeps, and was relatively abundant offshore. However, it was also abundant in some areas of higher salinity, such as LM NS and LM OS. The final group, chilipepper rockfish, was abundant only in the LM NS area (figure 29d).

In some cases, more sense can be made of the distributions of fish during sweep 2 by comparing them to sweep 1 (figure 30). Both yellowtail and canary rockfish decreased greatly in abundance between sweeps (figure 30). Each had been only moderately abundant in the most southern portion of the study area during sweep 1, and both species decreased even more in sweep 2, presumably settling. Both species had been common in the northern part of the study area during sweep 1, and some fish remained in the general region. Small canary rockfish may have appeared in the PR NS area. We have no particular explanation for the unique occurrence of these species in the LF OS and P NS areas. In general, we see these species as having settled in large numbers between sweeps, leaving the remaining pelagic fish distributed patchily.

Members of the next group (blue, squarespot, medium shortbelly, and medium widow rockfish) had typically been present but not abundant off Point Reyes, and abundant to varying degrees in the offshore and inshore areas in the Gulf of the Farallons region, particularly in the Point Reyes plume (UF OS) during sweep 1 (figure 30). Most had been abundant in the nearshore areas off Pescadero and Davenport, and were present but not abundant nearshore and offshore in Monterey Bay. All of these taxa decreased in abundance by sweep 2—medium widow the least, and medium shortbelly the most. Typically they disappeared from the area of offshore intrusion at LF OS and disappeared or decreased substantially in the Pescadero and Davenport areas. Advection may have been responsible for the decline at LF OS, and advection or settlement at Davenport and Pescadero. Some members remained in Monterey Bay (particularly the cool water mass in upper Monterey Bay), perhaps advected from Davenport and not yet settled. Most members of this group apparently increased in abundance off Point Reyes, particularly in the nearshore area, and most remained abundant in the UF OS area. Thus the main pattern in this group was a decrease in abundance in the southern nearshore areas except Monterey Bay, and an increase in abundance off Point Reyes.

Large shortbelly, large widow, and bocaccio rockfish tended to show similar patterns of change (figure 30). Bocaccio decreased in abundance substantially between sweeps, while large shortbelly decreased less and large widow actually increased slightly in overall abundance. Like the previous group, members of this group disappeared in the area of the offshore intrusion at LF OS, and declined greatly off Pescadero and Davenport. They remained in some of the Monterey Bay areas. All increased, to greater or lesser degrees, off Point Reyes, and remained abundant in the remnants of the Point Reyes plume (UF OS).

Chilipepper rockfish essentially disappeared from the study area, apparently settling in most regions, particularly off Pescadero and Davenport (figure 30). Chilipepper rockfish remained abundant in large shoals (along with large shortbelly rockfish) in southern Monterey Bay.

Thus several groups that had been abundant off Pescadero and Davenport during sweep 1 had settled or been advected. We think that most had settled, but that remnants may have been advected into Monterey Bay (particularly those in the cool water masses in the northern portion of the bay) and remained pelagic. Large

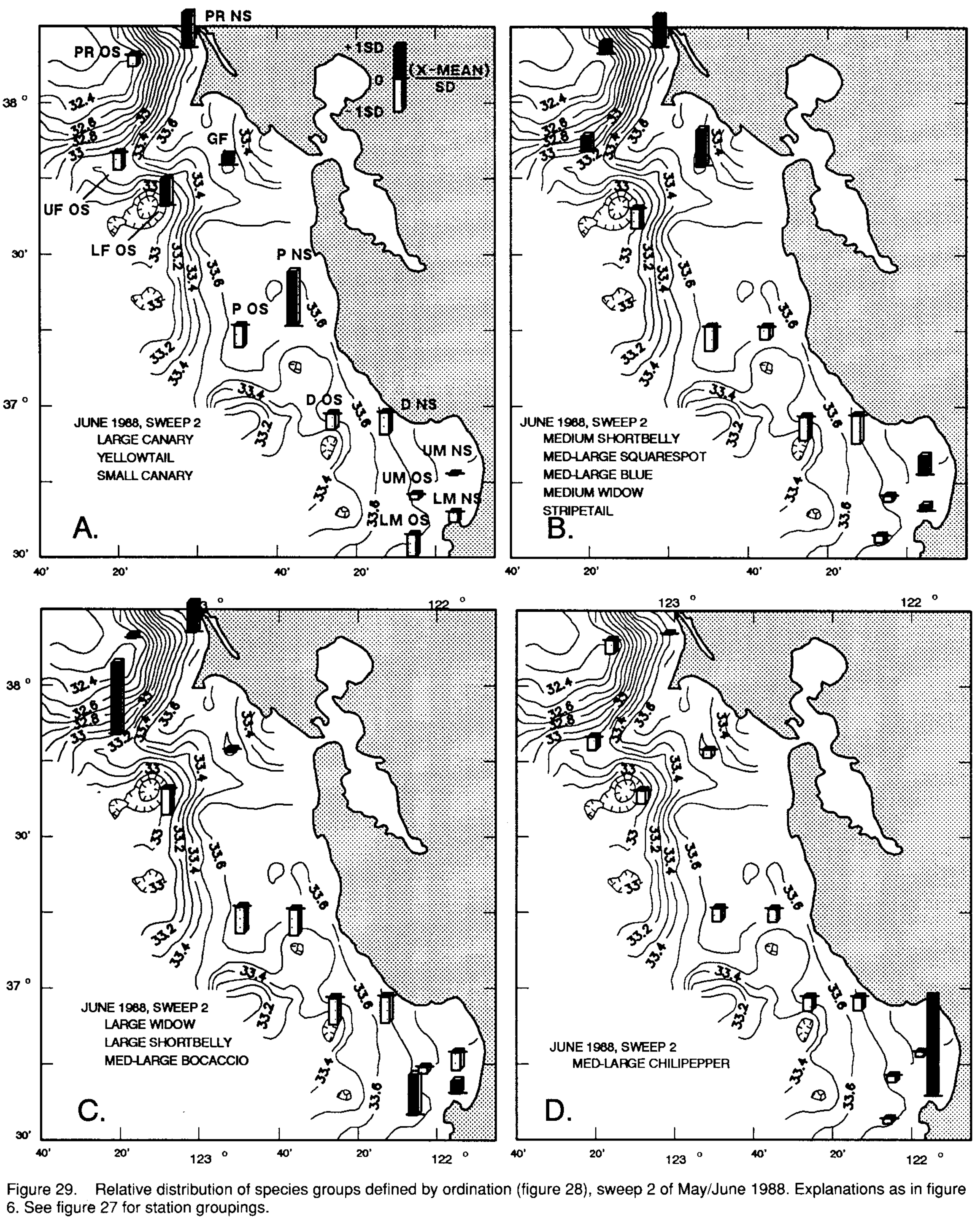


Figure 29. Relative distribution of species groups defined by ordination (figure 28), sweep 2 of May/June 1988. Explanations as in figure 6. See figure 27 for station groupings.

chilipepper and shortbelly rockfish formed large shoals in southern Monterey Bay during both sweeps. Perhaps this area is a nursery for postpelagic shortbelly and chilipepper rockfish. Many taxa remained abundant in the Point Reyes plume, indicating either a preference for conditions in this region or retention in an eddylike feature. Some increase in the abundance of large size classes in this area may have been due to growth of smaller fish. Several species increased in abundance off Point Reyes, both in the coastal waters nearshore and in the low-salinity water mass offshore. Nearshore, it is possible that the increase was more apparent than real, because the most shoreward station there was not sampled during sweep 1 (when many of the most shoreward stations yielded large catches) and had large catches in sweep 2. But this does not explain the increased catches

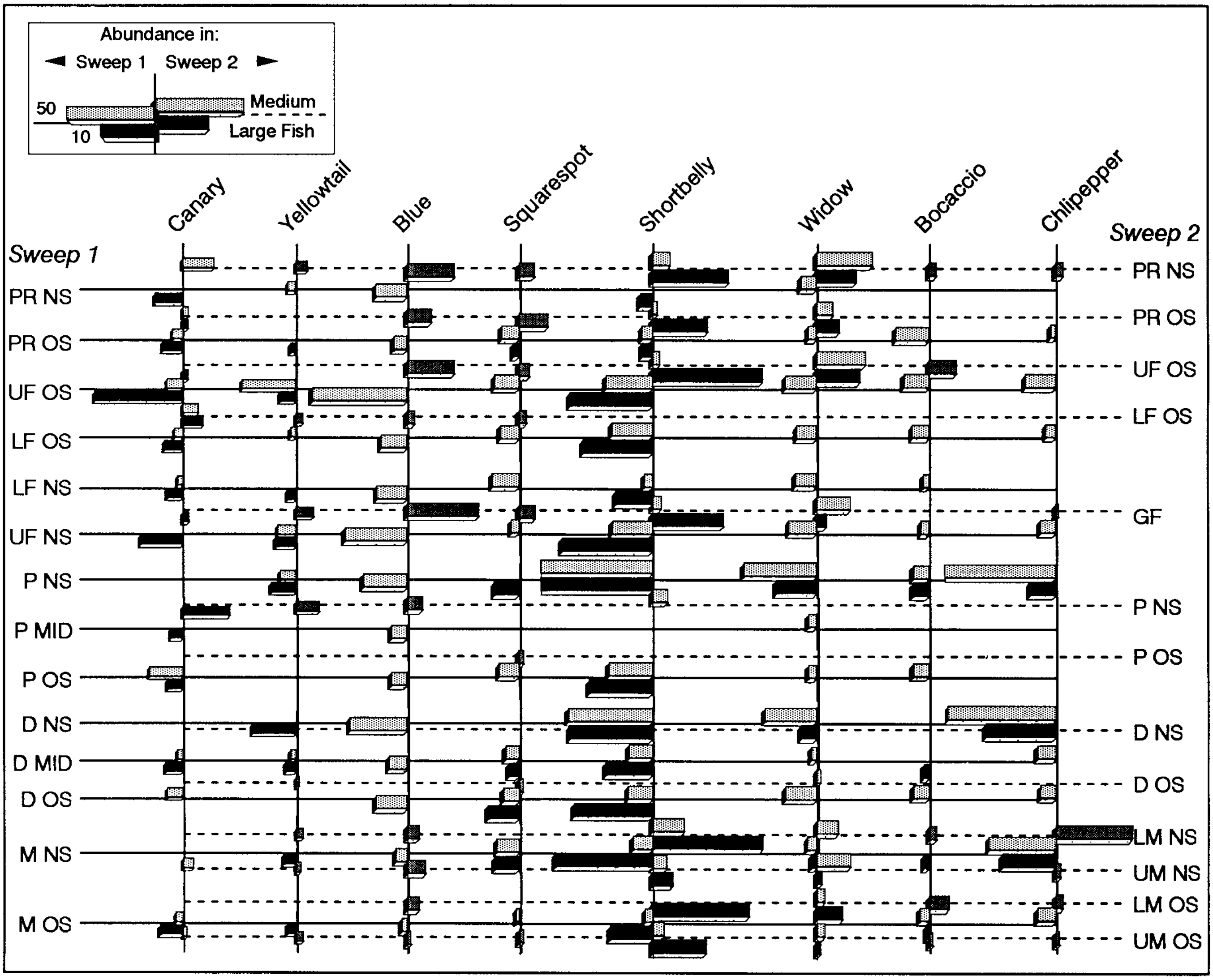


Figure 30. Comparison of pelagic juvenile rockfish abundances in sweeps 1 and 2 of May/June 1988. Station groups for sweep 1 are listed on the left, and the *aligned bars* (along the *solid horizontal lines*) extending to the left beneath each species indicate the species' abundance in the corresponding area. Station groups for sweep 2 are listed on the right. *Bars extending to the right* beneath each species (along the *dashed horizontal lines*) indicate the species' abundance in the corresponding area in sweep 2. *Pairs of bars* for one species indicate the smaller (*shaded upper bar*) and larger (*solid lower bar*) size classes for that species, if present, in that sweep. Species represented by only one size class are indicated with *one bar of intermediate shading*, aligned directly with the *horizontal line* linking areas. See table 2 for size classes. Scale is in number of fish per trawl, as transformed by ln(x+1).

offshore. In fact, the most offshore station had the largest catches, and these high catches occurred throughout the water column. We do not have a ready explanation for the apparently increased abundance of large fish in this offshore area.

Several stations were sampled offshore of the UF OS station during the two nights following the regular sweep, at longitudes between 123° 40' W and 124° 00' W. These were in an offshore water mass of low salinity and warm temperature (see figure 27 for nearby water mass characteristics). Like some of the other samples taken offshore of the upwelling front (April 1987; June 1988, sweep 1), these stations yielded few to no pelagic juvenile rockfish.

Summary. Because upwelling was not active and most pelagic juvenile rockfish were relatively large, gradients of oceanography and ontogeny were not large during sweep 2 of 1988. The size-related distributional patterns seen in some of the other sweeps were not evident at this time. In fact, little cohesive distributional pattern was found. In general, the 1988 year class was ontogenetically advanced: pelagic juveniles were relatively large in April and June, and their birthdates were earlier than in the previous 5 years (Woodbury and Ralston 1991). Many of the pelagic juveniles present during sweep 1 (often close to shore) seem to have settled by sweep 2, leading to large reductions in abundance in some areas (particularly Pescadero and Davenport). Pockets of pelagic

TABLE 5
Summary of Major Patterns in the Distribution of Pelagic Juvenile Rockfish, 1987–1988

Sweep	Range of oceanographic conditions	Range of fish sizes	North-south gradient?	Nearshore-offshore gradient?	Other notes
April 1987	Large gradient. Newly upwelled water to offshore water.	Most fish small; some advanced.	Some. Most species in south.	Yes. Small fish offshore; some early settlers nearshore.	Even small fish rare offshore of fronts.
June 1987 Sweep 1	Little gradient. Active upwelling in north; little offshore water.	Mostly medium–large fish; few small size classes.	Yes. A gradation.	Some. Smallest size group offshore, but mixed differences in some other species.	
June 1987 Sweep 2	Relaxation of upwelling; intrusion of offshore water.	Large gradient. Remaining large fish; appearance of small fish.	Yes. A gradation.	Yes. Smallest size classes in newly intruded offshore water; larger size classes near shore.	Increased abundance of larger fish near shore; shallow depth distributions in these areas.
June 1987 Sweep 3	Gradient from upwelled to offshore water.	Large gradient. Remaining large fish; appearance of small fish.	Yes.	Yes. New small fish offshore; larger fish near shore. Some small fish also near shore.	
April 1988	Small. No recent upwelling; little offshore water.	Mostly small to medium fish.	Did not sample northernmost areas.	Some differences within species, but some small fish nearshore.	
June 1988 Sweep 1	Active upwelling; little offshore water.	Mostly medium to large fish; few small fish.	Yes.	Large fish abundant near shore, even in recently upwelled water; some smaller size classes farther offshore.	Northerly-distributed juveniles abundant far offshore in upwelling plume off Point Reyes.
June 1988 Sweep 2	Relaxed upwelling; offshore intrusions.	Mostly medium to large fish; few small fish.	Yes, but some disjunct distributions in remains of upwelled water in north & south.	No. Idiosyncratic distributions of remnants of large year class.	

juveniles remained in the study area, in Monterey Bay and in the decaying upwelling plume off Point Reyes. Maybe these fish just had not settled yet, and it is possible that they were retained in areas unsuitable for settlement. The apparent increase in abundance of some species in nearshore and offshore areas of Point Reyes remains puzzling. The increase may have been (but was not necessarily) apparent rather than real in the nearshore area, since the most nearshore station was not sampled in sweep 1. However, the increase in the offshore area, which was very low-salinity offshore water, has no evident explanation. In general, we think that this sweep represents the remnants of a large year class that had mostly completed its pelagic stage.

DISCUSSION

The system we have studied is complex and dynamic. Physical conditions change in a matter of days; the propensity of the physical system to behave in certain ways changes seasonally; and the entire system changes from year to year. Furthermore, the pelagic juvenile rockfish we sampled are a transitional stage, which appeared in our sampling gear as a function of the timing of parturition and survival of larvae, and which left the pelagic zone as a function of ontogenetic changes. Because of these factors, each of our sampling sweeps was like a separate anecdote, offering different physical conditions and different size and species composition of pelagic juvenile rockfish.

In our survey of distributions in two years we found some patterns that we cannot account for on the basis of the data at hand, such as idiosyncratic distributions of some species. Perhaps this should be expected, because we did not know the spatial aspects of parturition and subsequent dispersal and survival of larvae, all of which may differ from species to species. However, we did find two recurrent patterns of differences in distribution among species and size classes that suggest consistent factors affecting the distribution of pelagic juvenile rockfish just prior to settlement (table 5).

First, at least some north-south gradient in species composition or abundance was evident in six of the seven sampling sweeps through the area, and the one sweep without such a gradient was abbreviated, lacking the most northerly stations (table 5). Second, clear gradients in fish size, from small fish offshore to larger fish nearshore, were present in four of the seven sweeps, with some indications of such a gradient in two additional sweeps (table 5). The sweeps with little onshore-offshore gradient in fish size (June 1987, sweep 1; April 1988; June 1988, sweep 2) either lacked strong onshore-offshore gradients in oceanographic conditions or lacked a wide range of fish sizes (table 5). We think that the north-south gradient may be either an effect of larger-scale factors (such as the geographic ranges of species) or a manifestation of local effects. We think that the onshore-offshore gradient in fish size is due to offshore transport of small fish during upwelling, and to ontogenetic changes that make larger fish less susceptible to offshore transport or enable them to actually move toward shore. Our data also suggest that relaxation of upwelling conditions can affect the onshore-offshore distribution of fish.

Some species recurred in the northern portion of the study area, suggesting that some of the latitudinal differences in species composition observed in this study were the result of large-scale geographic factors. The most consistently northern species was the canary rockfish, which was often abundant in the northern part of the study area and was rarely abundant in the southern part. The yellowtail rockfish was also abundant in the north, but not to the same extent as canary rockfish. These patterns occurred in both 1987 and 1988, suggesting that the repeated observations were not due merely to serial correlation of consecutive samples. No species occurred as predominantly in the south, although stripetail rockfish and bocaccio were more abundant in the south during some sweeps from each year of sampling. Persistent geographical differences in the distribution of species as pelagic juveniles may reflect the geographical ranges of the parent populations. Both canary and yellowtail rockfish have northerly distributions, although other species occur to the north as well. Alternatively, different portions of the region may persistently support the survival or retention of the larvae and juveniles of particular species, due to recurrent local conditions.

Some of the differences in geographical distribution of pelagic juvenile rockfish did appear to be local effects. This was best illustrated by apparent changes in distribution observed between sweeps. For example, larger size classes of several species were most abundant near shore in the southern portion of the study area during sweep 1 of May/June 1988, and by sweep 2 had apparently settled in the south, but increased in abundance in the north, perhaps due to advection from other areas (figure 30). Thus the apparent northerly distribution during sweep 2 was an artifact of local settlement and advection, not an effect of large-scale geographical factors. Remnant patches of species that have mostly settled may also suggest geographical trends, but these distributions may really be due to local retention or to the proximity of postpelagic habitat, as illustrated by the distribution of chilipepper rockfish in sweep 3 of June 1987 (figure 18d) and in sweep 2 of June 1988 (figure 29d).

The apparent relationship between fish size and onshore-offshore distribution manifested itself in different ways. One manifestation was the restriction of most small fish to offshore regions, beyond the upwelling front. This was evident in the April 1987 cruise, and in sweeps 2 and 3 of June 1987. In these sweeps, very early-stage pelagic juveniles, some appearing for the first time in our trawls, occurred only offshore. As discussed below, we think that such distributions are the result of offshore advection of larvae and early juveniles of *Sebastes*. Another manifestation was the occurrence of larger size classes close to shore, even in upwelling centers. This was most evident in sweep 1 of May/June 1988. Observations like this suggest that later-stage individuals can reach the nearshore zone or remain there, even when upwelling is active. The last manifestation was the actual comparison of distributions within species, which often (but not always) showed that where the distributions of smaller and larger size classes differed, the larger size classes were closer to shore (or in more recently upwelled water), and the smaller size classes were farther from shore, in offshore water or mixes of offshore and upwelled water.

These size-related distributional patterns were not universal. In several sweeps, some species did not fit the general pattern (such as the offshore distribution of large size classes near Point Reyes during sweep 2 of June 1988, and several cases in which small size classes occurred close to shore). Cases such as these will conflict with the hypothesis we develop in this paper. Other exceptions to the general pattern occurred when ranges of fish size or oceanographic conditions were narrow, and in that sense may be exceptions that prove the rule (table 5). For example, little offshore water was present in the study area during sweep 1 of May/June 1987, and small size classes were not common, so size-related patterns were not the major type of variation in distribution found during the sweep. Similarly, large size classes were not common in April of 1988, and upwelling had not been active, so the absence of upwelling may have led to the lack of onshore-offshore differences in the distributions of size classes.

The occurrence of small size classes offshore, beyond the most recently upwelled water, suggests that larvae and early juveniles had been advected offshore during upwelling. The species of rockfish encountered in this study give birth to larvae from the shoreline (e.g., blue rockfish and the "copper complex") to the shelf break (e.g., shortbelly rockfish), so we would expect early larvae to occur in various areas over the shelf. But despite possible differences in the distributions of earlier larvae, the small pelagic juveniles sampled in this study showed similar distributions. These distributions suggest a common causal factor, which we think is offshore advection during upwelling. The appearance of new groups of small pelagic juveniles offshore, often near the upwelling front (as in April of 1987 and sweeps 2 and 3 of June 1987), suggests that they had not been present in the upwelled water that came to occupy surface waters over the shelf, and if they had been in waters over the shelf before upwelling, they were advected offshore.

The decline in abundance of even small pelagic juveniles offshore of the upwelling front suggests that factors such as habitat selection, passive advection, or differential survival of larvae or juveniles may occur offshore of the upwelling front. Our best data for the offshore decline in abundance came from April 1987, when small pelagic juveniles were abundant in and near the upwelling front, yet few were found in an extensive offshore excursion beyond the upwelling front. The absence of pelagic juveniles in the blue water mass south of the upwelling plume sampled after sweep 1 of May/June 1988 fits the same pattern, as does the rarity of pelagic juveniles in the offshore stations sampled in the same region after sweep 2 of June 1988. However, the general rarity of small pelagic juveniles during May/June of 1988 leaves open the possibility that small juveniles were not available. Nevertheless, there was a strong contrast in the abundance of juvenile rockfish within and without the upwelling front in that area. Larval surveys suggest that *Sebastes* larvae may occur dozens of kilometers offshore (Moser and Boehlert 1991), so the rarity of small juveniles offshore of the upwelling front is interesting. Since our sample size was small, perhaps the pattern is not general. If it is general, the pattern suggests that the upwelling front is important to larvae or early-stage pelagic juveniles. Larvae or juveniles may seek the conditions present in the front, or individuals away from the front may not survive.

The frequent occurrence of larger pelagic juveniles close to shore, even when upwelling is active, suggests that ontogenetic changes allow these fish to reach the nearshore zone, or to remain there once they are present, in spite of upwelling. Their distributions stand in contrast to those of smaller fish, which were often offshore during upwelling. Larger size classes were very abundant near shore in sweep 1 of May/June 1988, when upwelling was quite active. In April of 1987, when most of the pelagic juveniles were relatively small and distributed offshore, a few early-settling species were found closer to shore in recently upwelled water. It seems unlikely that these large fish were simply survivors of larvae and smaller juveniles retained near shore, since we rarely found small juveniles near shore.

We suspect that the changes in distribution in larger fish are not related to size per se, but to ontogenetic stage, since distributional differences occurred between size classes in most species, independently of differences in size across species. Furthermore, the relative sizes of pelagic and newly settled individuals are concordant over species. Thus, "copper," canary, and stripetail rockfish are relatively small as pelagic juveniles (table 2, appendix), and are also relatively small as newly settled individuals (Anderson 1983). Yellowtail and blue rockfish are larger as pelagic juveniles (table 2, appendix), and are also larger as newly settled individuals (Anderson 1983). This alone suggests that pelagic juvenile rockfish reach species-specific stages at which they become competent to settle. The nearshore distribution of larger pelagic juveniles further suggests that this "competence" brings behavioral changes that facilitate inshore movement or retention. We do not know what these behavioral changes are, but discuss possibilities below.

While the more nearshore distribution of larger pelagic juveniles suggests active, behaviorally influenced movements, some of our data suggest passive transport of even larger size classes. We have already discussed the apparent offshore transport of larvae and early-stage juveniles during upwelling. We also have some evidence, both specific and circumstantial, for passive movement during relaxation of upwelling, and for passive movement associated with apparent entrainment in frontal features.

Fish distributions changed with a substantial relaxation of upwelling near the beginning of sweep 2, 1987. An obvious change was the appearance of small size classes of several species with the intrusion of low-salinity offshore water masses into the study area. While Send et al. (1987) argued for little cross-shelf transport during relaxation from upwelling, we think that the apparent onshore displacement of the upwelling front and appearance of low-salinity water was due to relaxation of factors forcing the front offshore. This shift apparently brought with it small pelagic juveniles that had been offshore of our study area. We also observed apparent alongshore advection of water and associated pelagic juveniles. With the decay and offshore displacement of the cool, recently upwelled water off Point Reyes, a new body of warmer but still saline water appeared near shore, and apparently carried with it large numbers of some species of rockfish. The association of alongshore advection with relaxation of upwelling was documented by Send et al. (1987). Finally, we saw apparent increases in nearshore abundance of several larger size classes in the southern part of the study area. With the onshore movement of the upwelling front, the band of high-salinity water along the coast had narrowed, and we suspect that this may have concentrated some fish closer to shore. Also associated with some of this was the unusually shallow depth distribution of many taxa in the newly developed thermocline. In sum, these direct observations demonstrate three types of change in distribution of pelagic juvenile rockfish associated with relaxation of upwelling. The lack of marked on/offshore stratification of size classes during sampling periods without active upwelling (such as April 1988, and to a lesser extent sweep 1 of May/June 1987) provide some indirect evidence for the effect of upwelling relaxation. The lack of offshore transport in upwelling, the mixing of offshore and nearshore water masses, and perhaps advection, may have created conditions that allowed the mixing of earlier- and later-stage pelagic juveniles.

We also have evidence suggesting that even large pelagic juveniles can become associated with or entrained in oceanographic features that are related to upwelling. We saw several instances in which a number of species were abundant in frontal areas, such as the Davenport-Monterey area during April of 1987. Our best-studied example of this was the upwelling plume offshore of Point Reyes during 1988. Several taxa were abundant near the base of this structure (but still 30 km offshore of Point Reyes) during both sweeps 1 and 2, and the same groups were abundant in the core of the plume another 25–30 km offshore after sweep 1. Many species abundant in the plume were also abundant near shore in the Gulf of the Farallons and off Point Reyes, so nearshore populations were not evacuated by offshore transport. However, the abundance of pelagic rockfish 50–60 km from shore suggests advection, and the persistence of part of this assemblage for at least one week suggests that the assemblage was retained. Incidentally, the correlation of rockfish distributions 100 m deep with the surface features we measured indicates that offshore advection of organisms during upwelling is not always limited to the classical 20–30 m Ekman layer, and in fact the features we observed at the surface were often evident to at least 30 m of depth (figure 7; Johnson et al. 1992). Advection and retention may have been an entirely passive process, in which fish were simply caught up in the current, or it may also have involved habitat selection by juveniles for conditions present in the advected water mass, but the result was nevertheless entrainment and retention of these fish. Without major changes in fish behavior (and perhaps even with behavioral changes), these fish would tend to travel with the structure.

The appearance of some taxa of pelagic juveniles near shore off Point Reyes in sweep 2 of June 1987 (described above) may illustrate the movement of entrained juveniles within a water mass, even though we do not know the source of the water mass or juveniles. On a different scale, the patchy and sometimes disjunct distributions of some species in sweep 2 of 1988, after many of the pelagic juveniles had settled, bear signs of the retention of nonsettled fish in particular water masses. For example, many species had been abundant in the newly upwelled water north of Monterey Bay during sweep 1, but essentially disappeared (mostly due to settlement, we assume) by sweep 2. However, remnants of these species' populations were found in Monterey Bay, where we have evidence for remnants of the cool, saline water mass that had been the Davenport upwelling plume during the previous sweep. We suggest that this water mass had drifted into Monterey Bay with the cessation of upwelling-favorable conditions, and carried with it some of the fish that had been present previously, but had not yet settled.

We have therefore found evidence both for the importance of passive entrainment and transport of pelagic juvenile rockfish and for ontogenetic changes in distribution that suggest a degree of independence from upwelling in later-stage individuals. It is apparent that younger pelagic juveniles may become aggregated near the upwelling front when upwelling has been active, and that later-stage pelagic juveniles may also be found in association with upwelling-related features. Distributions of pelagic juveniles may also move in association with changes in these features, and mixing may reduce onshore-offshore differences in fish abundance. These observations suggest that the fate of pelagic juveniles may depend on oceanographic conditions. The nearshore distribution of larger size classes, however, suggests that the fate of later-stage individuals does not depend on oceanographic conditions, at least in the same ways as implied above.

We think it would be useful to examine the distribution of rockfish larvae before and after the spring transition, which initially generates the distinction between the nearshore and offshore water masses seen in spring and summer (Send et al. 1987). The fate of larvae transported far offshore (up to hundreds of kilometers) remains unknown. Our smaller-scale data suggest that successful larvae either are associated with or come to be associated with the upwelling front, but we do not know whether this association is general, and we do not know when it begins. In addition, it would be interesting to know whether, and how, later larvae and early pelagic juveniles come to be associated with geographically restricted portions of the upwelling front, since these associations could influence the geographic extent of successful recruitment. In any case, we proceed with the working hypothesis that the larvae and early-stage pelagic juveniles of coastal *Sebastes* species are offshore of the upwelling front, and must move or be moved tens of kilometers closer to shore in order to find habitats suitable for the next stages in their life cycle.

Passive transport, often associated with relaxation of upwelling, may be sufficient for some nearshore movement of pelagic juveniles. This transport could occur in several ways. First, displacement of the upwelling front during relaxation may bring early-stage juveniles located in and beyond the front closer to shore, as we observed in sweep 2 of June 1987. Second, cessation of upwelling may also allow mixing of upwelled and offshore water, introducing pelagic juveniles to the coastal water mass, where they may become mixed and remixed with additional pulses of upwelling and relaxation (which create new fronts between recently and less-recently upwelled water, as described by Send et al. 1987). Such changes could have accounted for the reduced onshore-offshore gradients in fish composition in April of 1988 and in May/June 1987, sweep 1. Third, plumes of upwelled water and the associated fronts themselves may be advected along and toward shore, as suggested by Schwing et al. (1991) and inferred for barnacle larvae by Farrell et al. (1991) and Roughgarden et al. (1991). Finally, relaxation may bring about direct cross-shelf transport of mixed coastal water, as suggested in the southern portion of our study area in sweep 2 of June 1987. Hobson and Howard (1989) suggested that cross-shelf transport during relaxation was responsible for mass strandings of juvenile rockfish in June of 1988. In a sense, the spatial and temporal heterogeneity of the coastal upwelling system may provide opportunities for pelagic juveniles to move into the nearshore region more or less passively. However, the effect of upwelling relaxation may be different in rockfish than in barnacles, where successful recruitment seemed to occur during periods of relaxation from upwelling that lasted weeks (Farrell et al. 1991; Roughgarden et al. 1991). Since the pelagic stage of barnacles lasts only a few weeks, successful recruitment might depend on periods of relaxation that encompass most of the pelagic stage, so that larvae are never advected far from shore. In contrast, the extended pelagic stage of rockfish may allow larvae and juveniles to be transported offshore but still experience several relaxation events during their late pelagic existence.

But although passive transport may be sufficient to account for the nearshore transport and settlement of juvenile rockfish, it may not be necessary, or it may not be the entire story. The onshore-offshore differences in fish size that we observed strongly suggest that ontogenetic changes in behavior influence distribution and may allow for settlement even in the absence of relaxation of upwelling. Regardless of the role passive transport may play in the onshore movement of pelagic juveniles, the abundance of late-stage pelagic juveniles close to shore even under intense upwelling conditions strongly suggests that later-stage individuals are affected by upwelling differently from earlier-stage individuals. Thus we do not believe that settlement of juvenile rockfish is as dependent on movement of the upwelling front as it is in larval barnacles (Farrell 1991; Roughgarden et al. 1988, 1991).

We do not know what behavioral changes take place in later-stage pelagic juveniles. An obvious possibility is movement deeper into the water column, where transport may be onshore rather than offshore (Bakun 1986). Later metamorphic stages of the flatfishes *Citharichthys sordidus* and *C. stigmaeus* both occupy deeper positions in the water column and are found closer to shore than earlier metamorphic stages off central California in spring and early summer (Sakuma 1992). But although the ontogenetic changes in depth distributions that Sakuma observed were quite clear, Lenarz et al. (1991), using data from the same sampling survey as Sakuma, were unable to find specific evidence for increasing depth distributions in larger rockfish (although they found deeper distributions in May/June than in April).

Another possibility is that later-stage pelagic rockfish undergo behavioral changes that allow them to take advantage of frontal structures or conditions associated with relaxation in a way that facilitates shoreward transport. One such mechanism may have been illustrated by the unusually shallow distribution of later-stage pelagic juveniles above the thermocline off Monterey during the relaxation event in sweep 2 of June 1987. In such a bathymetric position, individuals may be carried closer to shore in cross-shelf transport, if it occurs, or may be subject to shoreward transport in internal waves (Shanks 1983). Shenker (1988) and Doyle (1992) have noticed large numbers of pelagic juvenile rockfish in the neuston, raising the possibility that a shift to shallow water may be a regular part of the late pelagic existence of rockfish. But this behavior would only be successful when upwelling is not active, and we know that later-stage pelagic juveniles are found close to shore even when upwelling is active. Furthermore, we have not observed any widespread tendency for shallow distributions in late-stage pelagic juveniles (Lenarz et al. 1991). Clearly, however, surveys of the depth distributions of different-stage individuals under a variety of circumstances would be a valuable area for future study. Other behavioral changes are also possible (including young fish swimming toward shore, if they have a means of determining the direction of shore), some of which may not have occurred to biologists yet. We recommend recognizing the problem and focusing some direct study on obvious alternatives like changes in depth distribution, but keeping an open mind and conducting studies of sufficient generality to detect the unexpected. The entire process of settlement may be multistage, requiring fish first to move into the nearshore region and then to actually find shore and suitable settlement habitats. The process is likely to be imprecise, depending on sensory cues that are available in the immediate environment of the fish and that trigger simple changes in swimming activity. It is also likely that the behaviors will differ among species.

At this point, then, we are unable to determine the relative roles of passive transport processes and more active behavioral changes in the onshore movement of pelagic juvenile rockfish. At one extreme, entrainment, transport, and mixing associated with fronts and other upwelling-related features could be of primary importance in the recruitment of rockfish, much as these processes seem to be important in barnacles (Farrell et al. 1991; Roughgarden et al. 1991). At the other extreme, advection and entrainment in upwelling-related features may indeed happen in rockfish, but most fish manage to settle anyhow. Here, association with upwelling-related structures may influence the geography of settlement and may entrain a few unlucky individuals, but may not have a large negative effect on settlement. We suspect that the latter case may be nearer the truth, particularly since unpublished data so far seem to indicate a good correlation over years between the abundance of pelagic juveniles and settled juveniles (S. Ralston and D. F. Howard, unpublished; D. venTresca, pers. comm.). Continued analysis of the pelagic stage, particularly the distribution of larvae and early juveniles around the spring transition, and the horizontal and vertical changes in distribution of later-stage pelagic juveniles, will be valuable in distinguishing the effects of passive and active factors in rockfish settlement. Another useful approach might be to compare the timing of settlement with oceanographic conditions, perhaps using settlement marks on rockfish otoliths (Haldorson and Richards 1987; Amdur 1991).

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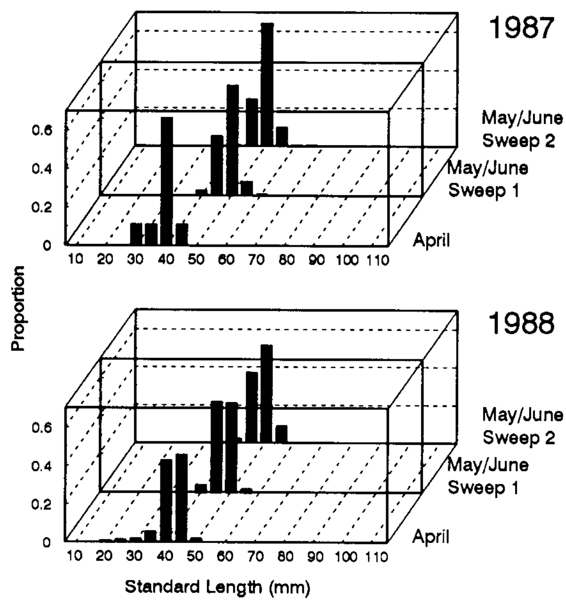
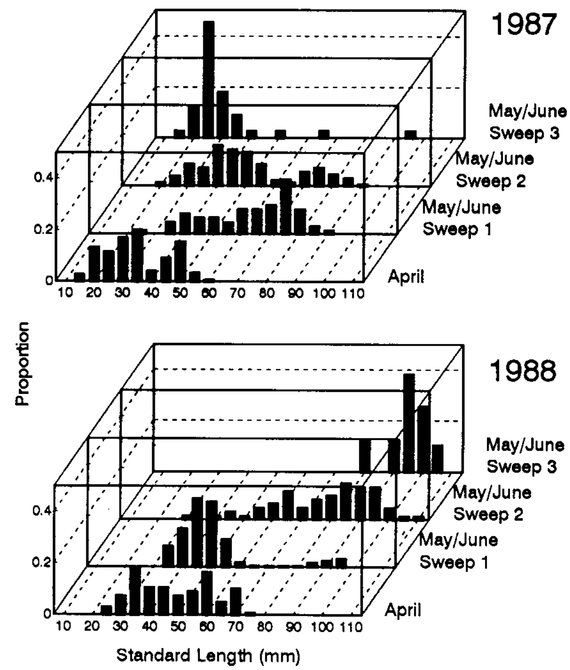
APPENDIX

Length-frequency distributions of pelagic juvenile rockfish in midwater trawls, 1987-1988. See table 3 for dates of cruises and sweeps of the study area.

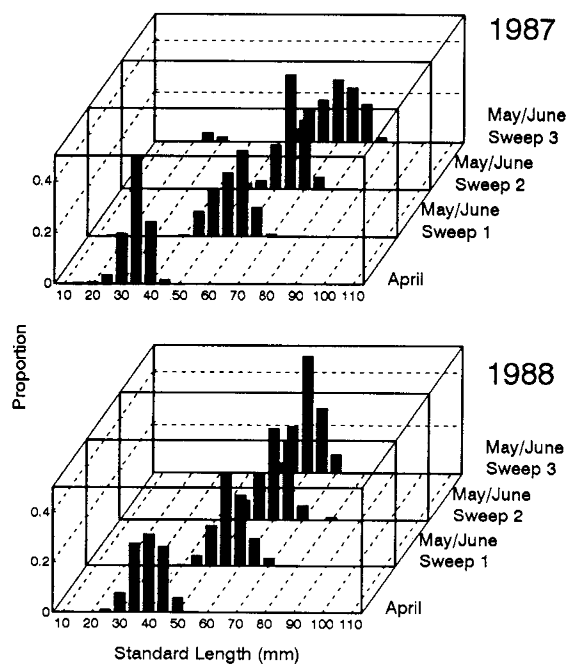
A. Blue Rockfish



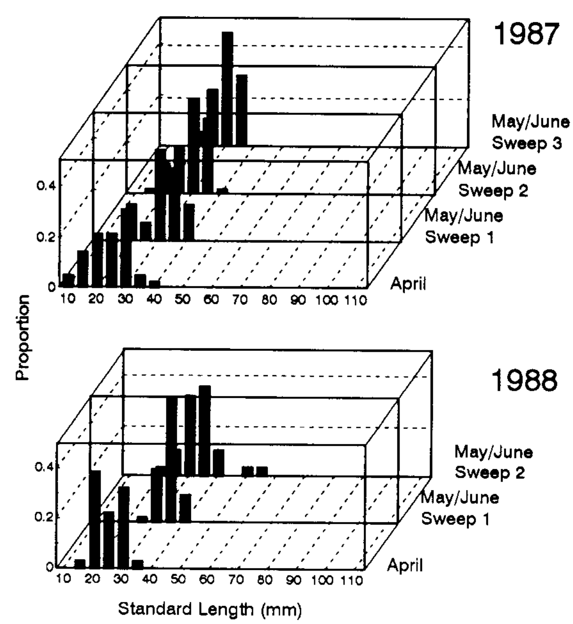
B. Bocaccio

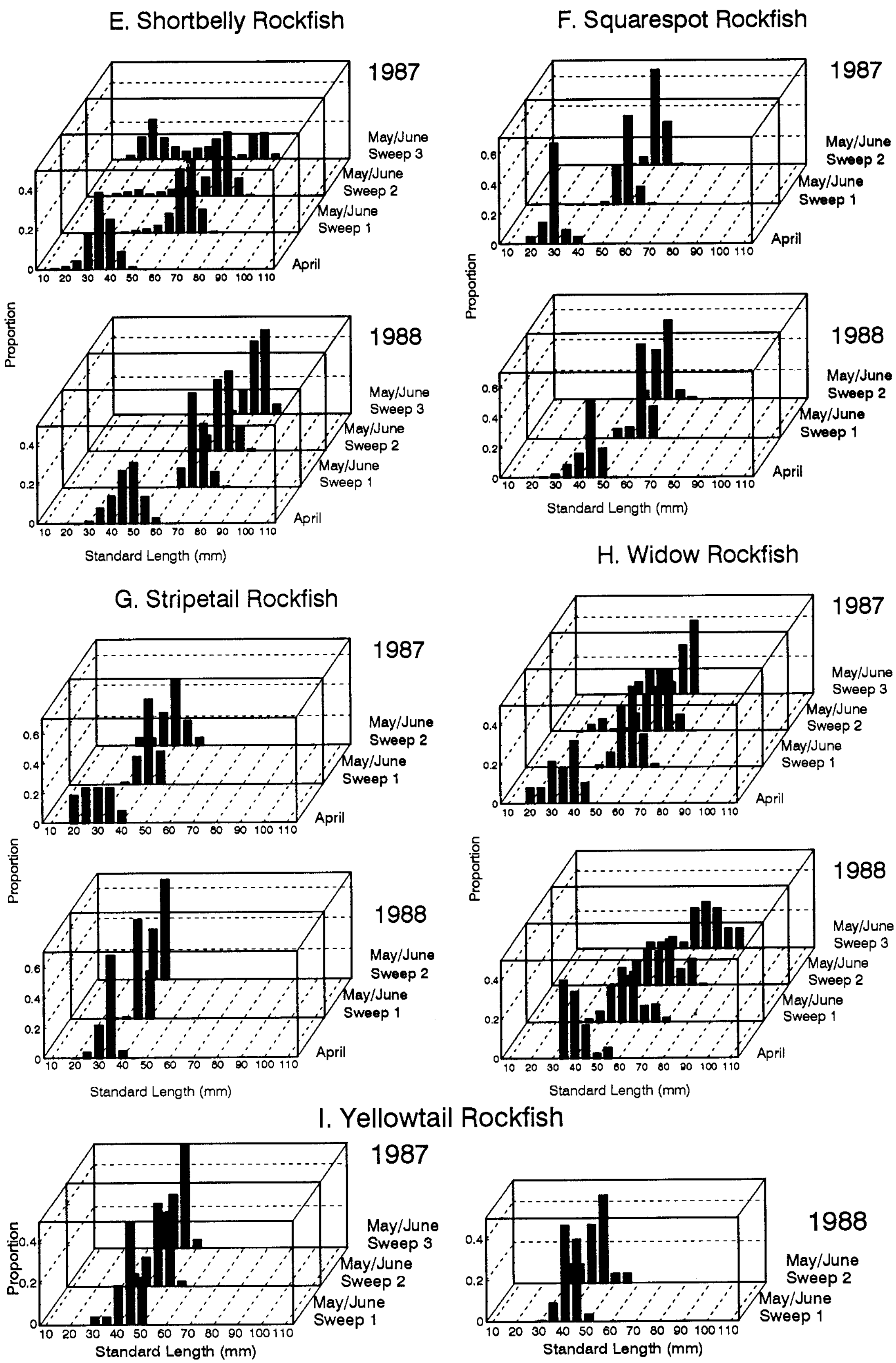


C. Chilipepper



D. Canary Rockfish




E. Shortbelly Rockfish
1987
May/June
Sweep 3
May/June
Sweep 2
May/June
Sweep 1
April
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Proportion
1988
May/June
Sweep 3
May/June
Sweep 2
May/June
Sweep 1
April
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Standard Length (mm)
F. Squarespot Rockfish
1987
May/June
Sweep 2
May/June
Sweep 1
April
0.6
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Proportion
1988
May/June
Sweep 2
May/June
Sweep 1
April
0.6
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Standard Length (mm)
G. Stripetail Rockfish
1987
May/June
Sweep 2
May/June
Sweep 1
April
0.6
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Proportion
1988
May/June
Sweep 2
May/June
Sweep 1
April
0.6
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Standard Length (mm)
H. Widow Rockfish
1987
May/June
Sweep 3
May/June
Sweep 2
May/June
Sweep 1
April
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Proportion
1988
May/June
Sweep 3
May/June
Sweep 2
May/June
Sweep 1
April
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Standard Length (mm)
I. Yellowtail Rockfish
1987
May/June
Sweep 3
May/June
Sweep 2
May/June
Sweep 1
Proportion
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Standard Length (mm)
1988
May/June
Sweep 2
May/June
Sweep 1
0.4
0.2
0
10 20 30 40 50 60 70 80 90 100 110
Standard Length (mm)