

# Life History Aspects of 19 Rockfish Species (Scorpaenidae: *Sebastes*) from the Southern California Bight

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## ABSTRACT

The authors investigated various life history aspects of 19 rockfish species (*Sebastes chlorostictus*, *S. constellatus*, *S. dalli*, *S. elongatus*, *S. ensifer*, *S. entomelas*, *S. flavidus*, *S. goodei*, *S. hopkinsi*, *S. levis*, *S. melanostomus*, *S. miniatus*, *S. ovalis*, *S. paucispinis*, *S. rosaceus*, *S. rosenblatti*, *S. rufus*, *S. saxicola*, *S. semicinctus*) from the southern California Bight. These aspects included depth distribution, age-length relationships (of 7 species), length-weight relationships, size at first maturity, spawning season, and fecundity. Growth rates of female *S. elongatus*, *S. hopkinsi*, *S. ovalis*, *S. saxicola*, and *S. semicinctus* were higher than male conspecifics. Multiple spawning per season was found in 12 species. Generally, most species spawned between late winter and early summer, though there was some spawning within the genus throughout the year. Spawning season duration ranged from 2 (*S. flavidus*) to 10 months (*S. paucispinis*). Spawning seasons tended to start earlier in the year and be of longer duration in the southern California Bight, compared to published data on central California conspecifics. Males matured at a smaller length in 7 of the 17 species studied. Maximum fecundities ranged from 18,000 (*S. dalli*) to about 2,680,000 (*S. levis*).

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## Introduction

At least 63 species of rockfishes (Scorpaenidae: *Sebastes*) inhabit waters of the northeast Pacific, from the Gulf of Alaska to California (Robins et al. 1980). Members of this remarkably speciose genus are found from the intertidal zone to at least 768 m, over virtually every bottom type and throughout much of the water column.

Since their first description in the midnineteenth century, northeastern Pacific rockfishes have been a source of interest to ichthyologists and fishery biologists. Most of the early research on this group was taxonomic and systematic. Species descriptions and group revisions predominated until Matsu- bara (1943) and Phillips (1957) brought some order to the taxonomic chaos.

Fifty-five rockfish species have been reported from the southern California Bight and perhaps 40 are common in at least part of this region. Many species are important in the sport and commercial catch (Table 1). This paper details aspects of the life histories of 19 rockfish species (Table 2) from the southern California Bight, including characteristics of their age-length and length-weight relationships, size at first maturity, spawning season, and fecundity. Sixteen of the species investigated are important sport and/or commercial fishes. A few, such as the dwarf species *S. dalli* and *S. semicinctus*, are rarely taken in fisheries, yet are very abundant in the Bight and are commonly captured in scientific survey trawl collections.

Phillips' study (1964) was one of the first efforts focusing on the biology of northeastern Pacific *Sebastes*. Since its publication, considerable effort has gone into *Sebastes* life history research, though little work had been done on the biology of many of the 19 species reported here. In particular, very little rockfish biological research has been conducted in the southern California Bight (prominent exceptions being Moser 1967a,b; MacGregor 1970; Chen 1971; Love and Ebeling 1978; Love 1980, 1981; MacGregor 1983), despite the abundance of many rockfish species and their importance to fisheries (about \$3.5 million to southern California commercial fishermen).

## Methods

### Description of the Study Area

All fishes were taken from within the southern California Bight (Fig. 1). The Bight is a 360-km long arch extending from the Mexican Border (lat. 32°32'N; long. 117°07'W) to Pt. Conception (34°25'N; 120°29'W), which has complex and shifting current patterns, abetted by eight islands and numerous submarine ridges, canyons, and basins (Reid et al. 1958, Neushul et al. 1967; Kolpack 1971; Seapy and Littler 1980; Love et al. 1985). At Pt. Conception, as the land swings eastward, the cold California Current flows to the

**Table 1.**

**Rockfish species found in the Southern California Bight (SCB), with notations on their abundance and sport and commercial importance (based on Limbaugh 1955; Carlisle 1969; Turner et al. 1969; Chen 1971; Miller Lea 1972; Feder et al. 1974; Eschmeyer et al. 1983; Love et al. 1985; Lissner and Dorsey 1986; Cross 1987; Love et al. 1987; Sunada<sup>a</sup> and Love's observations).**

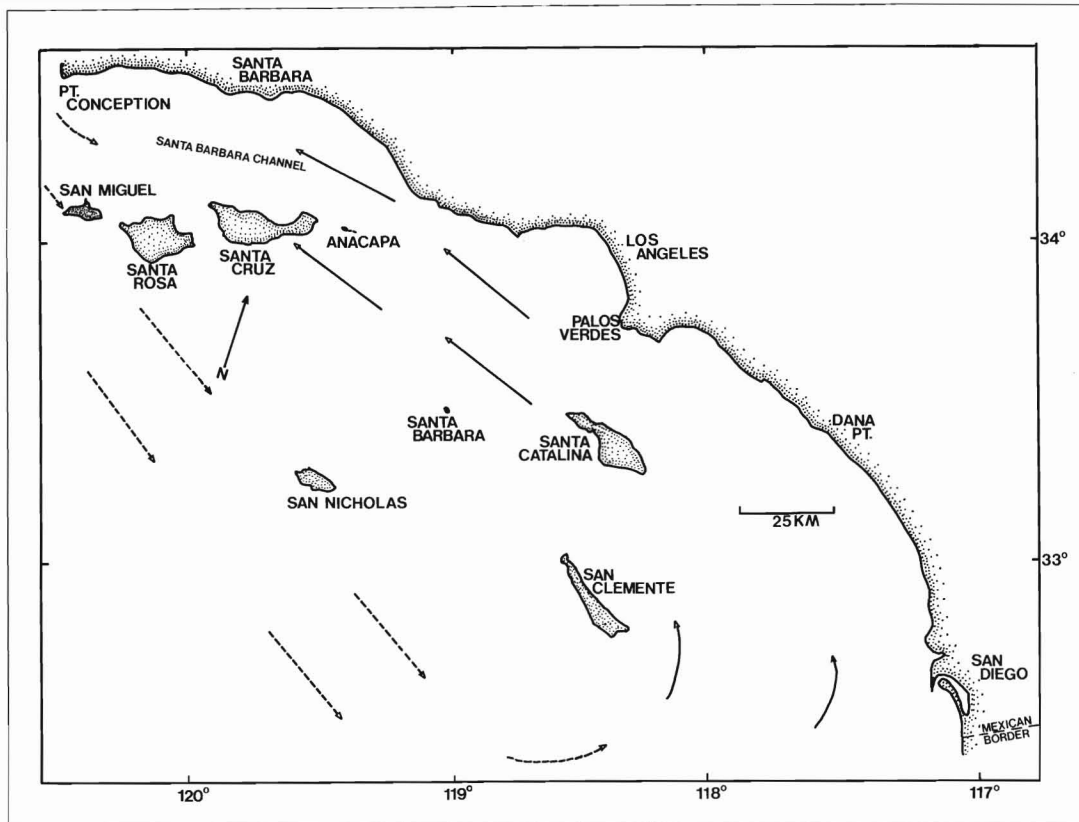
Species found within the Southern California Bight	Common in at least part of SCB	Importance		Species found within the Southern California Bight	Common in at least part of SCB	Importance	
		Sport	Commercial			Sport	Commercial
<i>aleutianus</i> —rougheye rockfish				<i>macdonaldi</i> —Mexican rockfish			
<i>alutus</i> —Pacific ocean perch				<i>melanops</i> —black rockfish			
<i>atrovirens</i> —kelp rockfish	x	x		<i>melanosema</i> —semaphore rockfish			
<i>auriculatus</i> —brown rockfish	x	x		<i>melanostomus</i> —blackgill rockfish	x		x
<i>aurora</i> —aurora rockfish	x		x	<i>miniatus</i> —vermillion rockfish	x	x	x
<i>babcocki</i> —redbanded rockfish				<i>mystinus</i> —blue rockfish	x	x	
<i>brevispinis</i> —silvergray rockfish				<i>nebulosus</i> —China rockfish			
<i>carnatus</i> —gopher rockfish	x	x		<i>nigrocinctus</i> —tiger rockfish			
<i>caurinus</i> —copper rockfish	x	x	x	<i>ovalis</i> —speckled rockfish	x	x	x
<i>chlorostictus</i> —greenspotted rockfish	x	x	x	<i>paucispinis</i> —bocaccio	x	x	x
<i>chrysomelas</i> —black-and-yellow rockfish	x	x	x	<i>phillipsi</i> —chameleon rockfish	x		x
<i>constellatus</i> —starry rockfish	x	x	x	<i>pinniger</i> —canary rockfish	x		x
<i>crameri</i> —darkblotched rockfish				<i>proriger</i> —redstripe rockfish			
<i>dalli</i> —calico rockfish	x			<i>rastrelliger</i> —grass rockfish	x	x	
<i>diploproa</i> —splitnose rockfish	x		x	<i>rosaceus</i> —rosy rockfish	x	x	
<i>elongatus</i> —greenstriped rockfish	x	x	x	<i>rosenblatti</i> —greenblotched rockfish	x	x	x
<i>ensifer</i> —swordspine rockfish	x	x		<i>ruberrimus</i> —yelloweye rockfish	x	x	x
<i>entomelas</i> —widow rockfish	x	x	x	<i>rubrivinctus</i> —flag rockfish	x	x	x
<i>eos</i> —pink rockfish				<i>rufinanus</i> —dwarf-red rockfish			
<i>flavidus</i> —yellowtail rockfish	x	x	x	<i>rufus</i> —bank rockfish	x	x	x
<i>gilli</i> —bronzespotted rockfish	x	x	x	<i>saxicola</i> —stripetail rockfish	x		
<i>goodei</i> —chilipepper	x	x	x	<i>semicinctus</i> —halfbanded rockfish	x		
<i>helvomaculatus</i> —rosethorn rockfish	x		x	<i>serranoides</i> —olive rockfish	x	x	x
<i>hopkinsi</i> —squarespot rockfish	x	x		<i>serriceps</i> —treefish rockfish	x	x	
<i>jordani</i> —shortbelly rockfish	x			<i>simulator</i> —pinkrose rockfish	x		
<i>lentiginosus</i> —freckled rockfish	x			<i>umbrosus</i> —honeycomb rockfish	x	x	
<i>levis</i> —cowcod	x	x	x	<i>wilsoni</i> —pygmy rockfish			
				<i>zacentrus</i> —sharpchin rockfish			

<sup>a</sup>J. Sunada, Calif. Dep. Fish Game, 330 Golden Shore, Suite 50, Long Beach, CA 90802.

**Table 2.**

**Maximum length, peak abundance depth, and degree of substrata association of the 19 rockfish species discussed in this paper.**

Species	Maximum length (cm)	Adult depth preference (m)	Substrata association	Species	Maximum length (cm)	Adult depth preference (m)	Substrata association
<i>chlorostictus</i>	50	90-179	Benthic	<i>melanostomus</i>	61	440-520	Transitional
<i>constellatus</i>	46	90-149	Benthic	<i>miniatus</i>	76	150-239+	Transitional
<i>dalli</i>	20	60-89	Benthic	<i>ovalis</i>	56	90-149	Midwater
<i>elongatus</i>	38	150-239+	Transitional	<i>paucispinis</i>	91	210-239+	Midwater
<i>ensifer</i>	25	180-239+	Benthic	<i>rosaceus</i>	28	60-119	Benthic
<i>entomelas</i>	53	150-239+	Midwater	<i>rosenblatti</i>	48	210-239+	Benthic
<i>flavidus</i>	66	120-149	Midwater	<i>rufus</i>	51	210-239+	Midwater
<i>goodei</i>	56	180-239+	Midwater	<i>saxicola</i>	30	180-239+	Midwater
<i>hopkinsi</i>	29	60-119	Midwater	<i>semicinctus</i>	25	120-149	Midwater
<i>levis</i>	94	180-239+	Transitional				



**Figure 1.**

The southern California Bight, site of the present study. Included are warm and cold currents bathing the Bight (from Cowen 1985).

southeast. Typically, it bathes the westernmost northern Channel Islands (San Miguel and Santa Rosa) and some spills into the Santa Barbara Channel, slowly warming as it travels. Much of the California Current continues to flow southeastward, past San Nicolas Island, and is eventually entrained in a warm counter-clockwise eddy (Southern California Eddy) within the southern California Bight. Waters influenced by this eddy, such as most along the mainland, and around Santa Catalina, San Clemente, Santa Barbara, Anacapa, and Santa Cruz Islands, are warmer than offshore waters of the California Current.

Because of these temperature differences, the Bight forms an ecotone between two faunal provinces, a warm-temperate Californian Province to the south and a cold-temperate Oregonian Province in the northern part (Seapy and Littler 1980). This melding of provinces can be readily seen over a short distance along the Northern Channel Islands, where warm-temperate species predominate in the eastern part of the chain and cooler-water forms characterize the more westerly islands (Seapy and Littler 1980; Love et al. 1985).

### Collection Procedures

Rockfishes for age, weight, and reproduction studies were

collected in a variety of ways, between June 1980 and February 1987. Almost all specimens of the dwarf species *Sebastes semicinctus* and *S. dalli* (as well as small *S. elongatus*, *S. hopkinsi*, *S. rosenblatti*, and *S. saxicola*) were collected by 7.6 m otter trawl (the body having a 3½ cm stretch mesh, the cod-end inner liner having a 1 cm stretch mesh), between Dana Pt. and Santa Barbara, California. All other specimens were collected by hook and line from throughout the Bight, or were sampled from commercial catches, primarily in the northern half of the Bight. We made an effort to collect as wide a size range, over as long a time period as we could. For each fish sampled, the sex and total length (cm) were determined and otoliths of appropriate species obtained. Most fish were weighed (g), though in commercial samples this was not always possible.

### General Information on the Species

We were interested in establishing what, if any, relationships existed between life history aspects (such as length-weight relations, fecundity, and spawning season) and aspects of species' biology (such as maximum size, habitat depth, and degree of substrata association). We used Eschmeyer et al. (1983) for information on maximum fish size and our own

data (this paper) for depth preferences. We categorized each species as benthic, midwater, or transitional (found from near or on the sea floor to at least several m above), based on our observations of *in situ* photographs and films (Sources: Cross<sup>1</sup> and Parr<sup>2</sup>) and on the depth above the substrata at which the species are usually taken by hook and line and nets. Table 2 lists maximum length, peak abundance depth, and substrata association category for each species.

## Depth Distribution

The rugged substrata over which most of these species live have made it difficult to characterize their depth characteristics. The relatively deep water inhabited has ruled out direct diver observation and the rough terrain makes trawling studies inaccurate. To distinguish the depth characteristics preferences of 15 of the 19 species, we utilized the California Department of Fish and Game commercial passenger fishing vessel creel census (conducted from April 1975 to December 1978). In that study (in which Love participated), a sampler was randomly assigned to a hook and line sport-fishing vessel operating within the southern California Bight. All fish caught by passengers (whether retained or returned to the water) were identified and measured (TL). Also noted were the number of anglers aboard the vessels, hours fished, and location and depth of fishing effort (see Love et al. 1985 for a more complete description of this study).

We stratified the catch data for 15 species by depth (30 m to 269 m intervals) using all data from throughout the Bight and measured each species' abundance by catch per unit effort, defined as number of fish taken per angler hours (where angler hours = number of anglers × number of hours fished). Fishes were assumed to be on or near the bottom and depth was ascertained from an on-board echo sounder.

Small juvenile rockfishes were not well sampled, as their small mouths prevented their capture in proportion to their numbers. While mouth size increases rapidly in most of these species, removing some of this bias, three dwarf species (*Sebastes dalli*, *S. saxicola*, and *S. semicinctus*) were rarely taken by hook and line. As all three are abundant over soft substrata, we utilized trawl data to delineate capture depths of smaller *S. saxicola* and *S. semicinctus*, and hook and line data for larger individuals. Only trawl data were used for *S. dalli*. Data were collected between 1976 and 1986 throughout the southern California Bight, in waters from 6 to 270 m deep, using an 8.6 m trawl.

## Age Determination

We determined age-length relationships for seven species (*Sebastes constellatus*, *S. elongatus*, *S. hopkinsi*, *S. ovalis*,

*S. rosenblatti*, *S. saxicola*, and *S. semicinctus*). Six species had not been previously aged, while the growth rate of the other (*S. saxicola*) had been examined only from northern California specimens.

We used sagittae for our analysis. These were removed from each specimen, cleaned and stored in coin envelopes. Because we experienced difficulties in reading broken and burned otoliths, we read otolith cross sections of five species (*S. constellatus*, *S. elongatus*, *S. ovalis*, *S. rosenblatti*, *S. saxicola*). Otoliths from these species were placed on wood blocks and embedded in clear epoxy (Ciba 825 and Ciba 6010 resin). Each block with its otolith was placed on a Buehler Isomet low-speed saw and an 0.05-cm wafer was cut from it, using two diamond-edge blades separated by a stainless steel shim. Before reading, the wafers were slightly burned over an alcohol lamp. The wafers were then placed in a water-filled, black-bottomed watch glass and examined under a dissecting microscope. All wafers were read twice, about 7 months apart, by Love. When readings did not agree, the otoliths were read again. The value of two coincident readings was accepted as the best estimate of age.

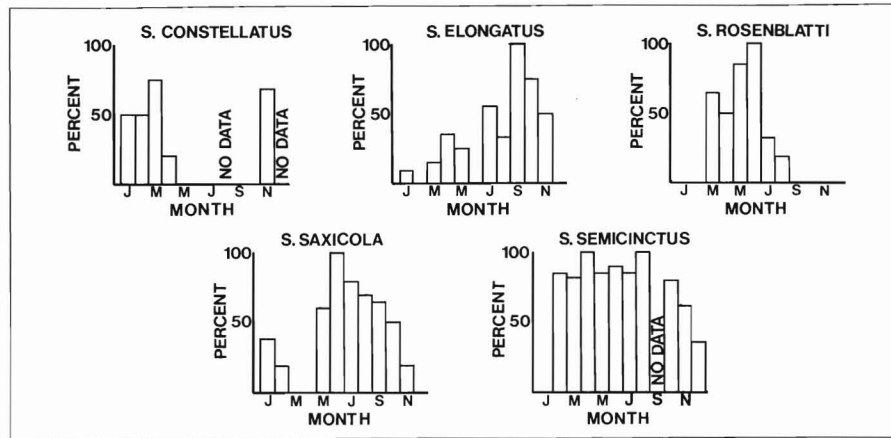
Two small species (*S. hopkinsi* and *S. semicinctus*) were aged from observations of whole otolith surfaces. Beamish (1979) showed that surface ageing of older Pacific ocean perch, *S. alutus*, gave spuriously low counts, as older fishes produced annuli that grew toward the center of the otolith—bands not visible on sagittae surfaces. We compared surface and section ages in these species and found excellent agreement in fish of all lengths.

There are also no published accounts of *S. rufus* and *S. melanostomus* growth rates. We examined these species using whole, sectioned, and broken-burned sagittae and found it very difficult to separate annuli from numerous confounding checks. Because of this, we did not continue ageing these species.

Many fish species lay down annually an opaque and a translucent zone in the otoliths. There is evidence that seasonal variations in calcium deposition are responsible for this zonation. By calculating the percentage of fish with opaque margins occurring on sagittae taken during each month of the year, we attempted to validate that sagittae bands were formed annually for the seven species. It was reasonable to assume that band deposition was seasonal if the bands were present during one part of the year. We found this technique worked well for fish to about 6 years of age, at which point the rings became too narrow for accurate assessment. Five species showed seasonal deposition of opaque rings (Fig. 2), though these patterns may be difficult to see in *S. constellatus* and *S. semicinctus*. In no month for which we have data, was ring deposition in *S. constellatus* greater than 75%. We saw opaque margins in some fish from November through April (with no data in December). From May to October no opaque deposition occurred. Opaque rings were found throughout most of the year in *S. semicinctus*, though less than 50% had them in December and none showed them in

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**Figure 2.**  
Seasonal deposition of opaque rings in otoliths of five *Sebastes* species from the southern California Bight.

January. These rings were particularly wide, indicating that opaque rings were laid down for most of the year. As opaque rings are associated with periods of rapid growth, it may be that this dwarf species exhibits considerable growth throughout most of the year. Two species, *S. hopkinsi* and *S. ovalis*, were not examined, as too few young fish were available.

### Maturation and Reproduction

We estimated length at first maturity by classifying gonads as immature or mature, based on criteria given in Westrheim (1975), Gunderson (1977), and Love and Westphal (1981). As noted in Love and Westphal for olive rockfish (*Sebastes serranoides*), it was difficult to distinguish between pre-reproductive and mature resting-stage females during each species' nonreproductive season, because females exhibit small, light orange or pinkish ovaries at both stages. Owing to this possible confusion in the analysis, we did not use females captured during the nonreproductive period. Age at first maturity was determined for the seven species aged. A gonadosomatic index [(gonad weight/(total body weight) × 100)] was computed from frozen specimens to quantify changes in gonad size with season. Gonad conditions (immature, vitellogenesis, fertilized, eyed, spawned, and resting—Wyllie Echeverria 1987) were determined for all females.

We computed condition factor as

$$100 \times \frac{(W - GW)}{L^3} \quad (1)$$

where  $W$  = body weight (g),  $GW$  = gonad weight (g), and  $L$  = total length (cm), of mature rockfish. Condition factor was computed using body weight with gonad weight sub-

tracted, so as to minimize the effects of seasonal changes in gonad size. We compared these values between seasons (reproductive and nonreproductive) within sexes and between sexes, using the Mann-Whitney U-Test (Sokal and Rohlf 1969).

We determined egg production of all species in our study, counting subsamples of unfertilized eggs, referable to gonad stage 3 in Wyllie Echeverria (1987). Because most of these species are batch spawners, we used several methods to insure that all fish from which ovaries were taken had not spawned that season. First, we tried to use only those females taken early in the reproductive season before eyed larvae were observed in ovaries (but also late enough in the season so that eggs would be large and easily counted). We also used only those fish with orange (or in *S. entomelas*, with white) ovaries, without any larvae present. After the first spawning of the year, the ovaries of batch spawners take on a reddish tone and usually contain residual unspawned larvae.

Eggs were excised from the ovarian membrane and placed in Gilson's solution (equal parts concentrated glacial acetic acid, chloroform, and 60% ethanol) for about 2 months and shaken periodically to loosen them from ovarian tissue. Before counting, the ovaries were repeatedly washed and the egg masses broken up to remove remaining connective tissue. The resulting eggs were weighed; the subsamples were removed and also weighed. Eggs in each subsample were counted and the mean number per weight calculated for each subsample. Egg production was estimated by the calculation

$$F = \frac{TW \times SN}{SW} \quad (2)$$

where  $F$  = fecundity,  $TW$  = total weight of gonads,  $SN$  = mean subsample egg number, and  $SW$  = subsample weight.



## Results and Discussion

### Depth Distribution

With the exception of *S. dalli*, *S. hopkinsi*, and *S. melanostomus*, all species we examined were caught in all depths sampled. However, the species tended to be most abundant over specific depth ranges and there was very broad overlap in abundance among species. We characterized these peak abundance depth patterns as either shallow (60–149 m) or deep (150–239+ m).

Species are listed by depth preferences, from shallowest to deepest as indicated in Figure 3.

#### Shallow

***Sebastes dalli***—Calico rockfish were most abundant in 61–89 m. We saw little relationship between fish length and depth, though largest fish were taken in deepest water.

***Sebastes hopkinsi***—Squarespot rockfish abundance peaked in 60–119 m. Smaller fishes were found in the shallower parts of the species' depth range. Our observations from occasional scuba and trawl samples indicated that this species recruits in 30 m or more of water. This species was always found above the substrata, over high relief.

***Sebastes constellatus***—The starry rockfish was another species limited to hard, usually high relief. The species was most abundant in 60–149 m, though it remained fairly common down to the 269 m sampling limit. Smaller fishes (primarily juveniles) were found between 30 and 89 m.

***Sebastes semicinctus***—In both trawl and hook and line samples, halfbanded rockfish were most abundant in about 90–149 m. In hook and line samples, fish were taken down to 210–239 m. There was no apparent difference in the length–depth relationship. This conforms to our observations from trawls that recruitment and the subsequent juvenile period occur at depths preferred by adults. This species forms large, motile midwater aggregations (as much as 30 m thick), over both soft and hard substrata—most commonly on bank edges.

***Sebastes chlorostictus***—The greenspotted rockfish was most commonly taken in 90–209 m. Small fish (primarily juveniles) were taken between 30 and 89 m. We captured all of this species over high relief.

***Sebastes flavidus***—Yellowtail rockfish were most commonly taken in 60–149 m. Juveniles were taken in the 30–129 m interval, while adults were first encountered in 120 m. Catches of these midwater dwellers were limited to rocky reefs and oil platforms.

***Sebastes rosaceus***—Rosy rockfish, a small, benthic, hard substrate dweller, was most abundant in 60–119 m. Though small juveniles are rarely taken by trawl or hook and line, we occasionally observed young-of-the-year captured between 30 and 59 m.

***Sebastes ovalis***—The speckled rockfish is a midwater aggregating species, limited to waters over high relief reefs.

It was most abundant between 90 and 149 m. Most juveniles were taken in 30–89 m, occasionally down to 119 m. We found occasional adults in waters as shallow as 80 m.

#### Deep

***Sebastes entomelas***—The widow rockfish was abundant from 90 to at least 239 m. Juveniles were taken from 30 to 149 m, most commonly in 60–119 m. In the southern California Bight, juveniles and adults form large midwater aggregations, usually associated with high relief, but occasionally occurring over hard or even soft flat substrata. At times, juveniles are particularly abundant around the oil platforms off Santa Barbara.

***Sebastes elongatus***—Greenspotted rockfish were most abundant in the deepest parts of the depths sampled, starting in 60 m. This species was found associated with high and low relief, over both hard and soft substrata. Though juveniles were taken in all depth intervals, our trawling studies indicate that recruitment occurs in the shallower depths, primarily 30–89 m.

***Sebastes ensifer***—The swordspine rockfish is a bottom-oriented species, inhabiting high relief or hard flat substrata. It was most abundant at the deepest depths sampled. Smaller individuals were usually found in shallower waters, though adults inhabit even the shallowest parts of the species' range.

***Sebastes goodei***—The chilipepper is a relatively deep dwelling midwater aggregating species, which in our survey was abundant from about 150–239+ m. We found it primarily over high relief and along dropoffs, but also occasionally over flat, hard substrata. Juveniles occurred in the shallowest part of the species depth range, primarily at 30–50 m, but a few were also taken in 60–89 m. We took a rare adult in water as shallow as 40 m, though they were more abundant below 60 m.

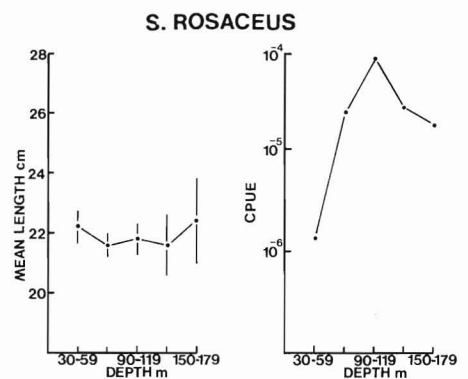
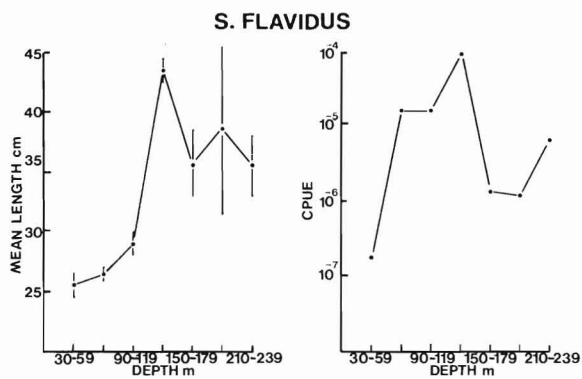
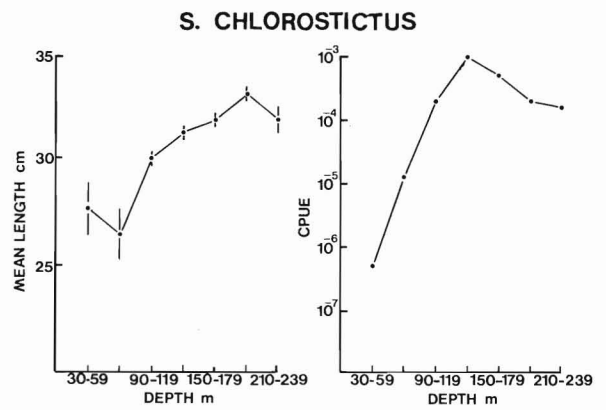
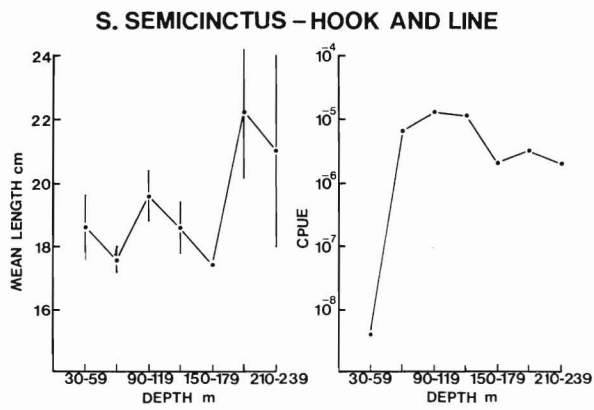
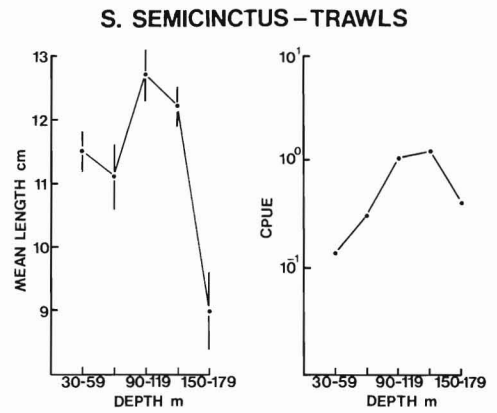
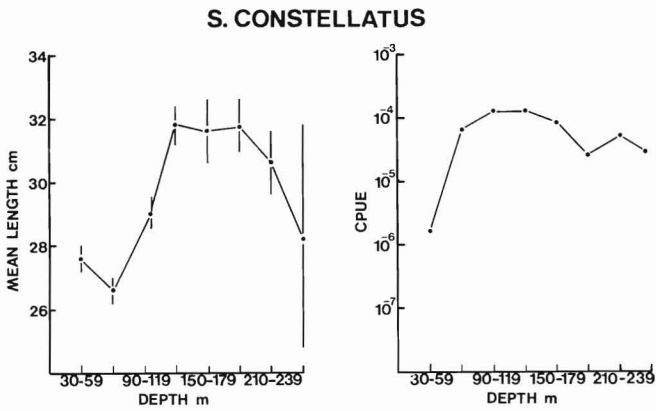
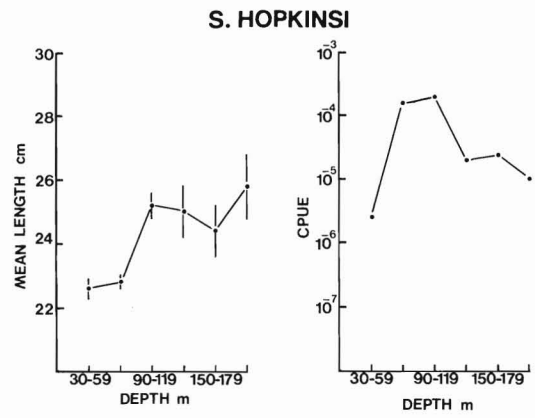
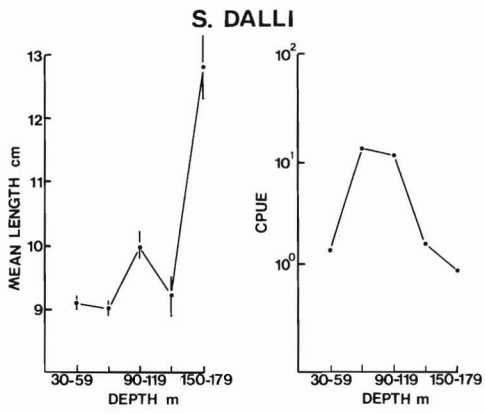
***Sebastes levis***—The cow rockfish is a solitary or occasionally aggregating species, usually restricted to near or slightly above the substrata, over high relief. Though *S. levis* were found over a wide depth range, they were most abundant in the deepest sampling depths. Juveniles were found from 30 to 149 m, depths where adults were rarely taken. Adults were abundant in 150 m and deeper.

***Sebastes miniatus***—Vermilion rockfish are usually found aggregating near or slightly above the bottom, often over high relief. In the southern California Bight, it was most abundant from 60 to at least 239 m, with two apparent peaks at 90–149 and 210–239+ m. Fishes from 90 to 149 m were primarily juveniles and small adults, while large adults made

### Figure 3.

Depth distribution of 18 *Sebastes* species from the southern California Bight, based on sampling techniques described under Depth Preference in Methods Section. The species are listed by characteristic depth—shallowest to deepest. Not figured is *S. melanostomus*, which was poorly sampled.





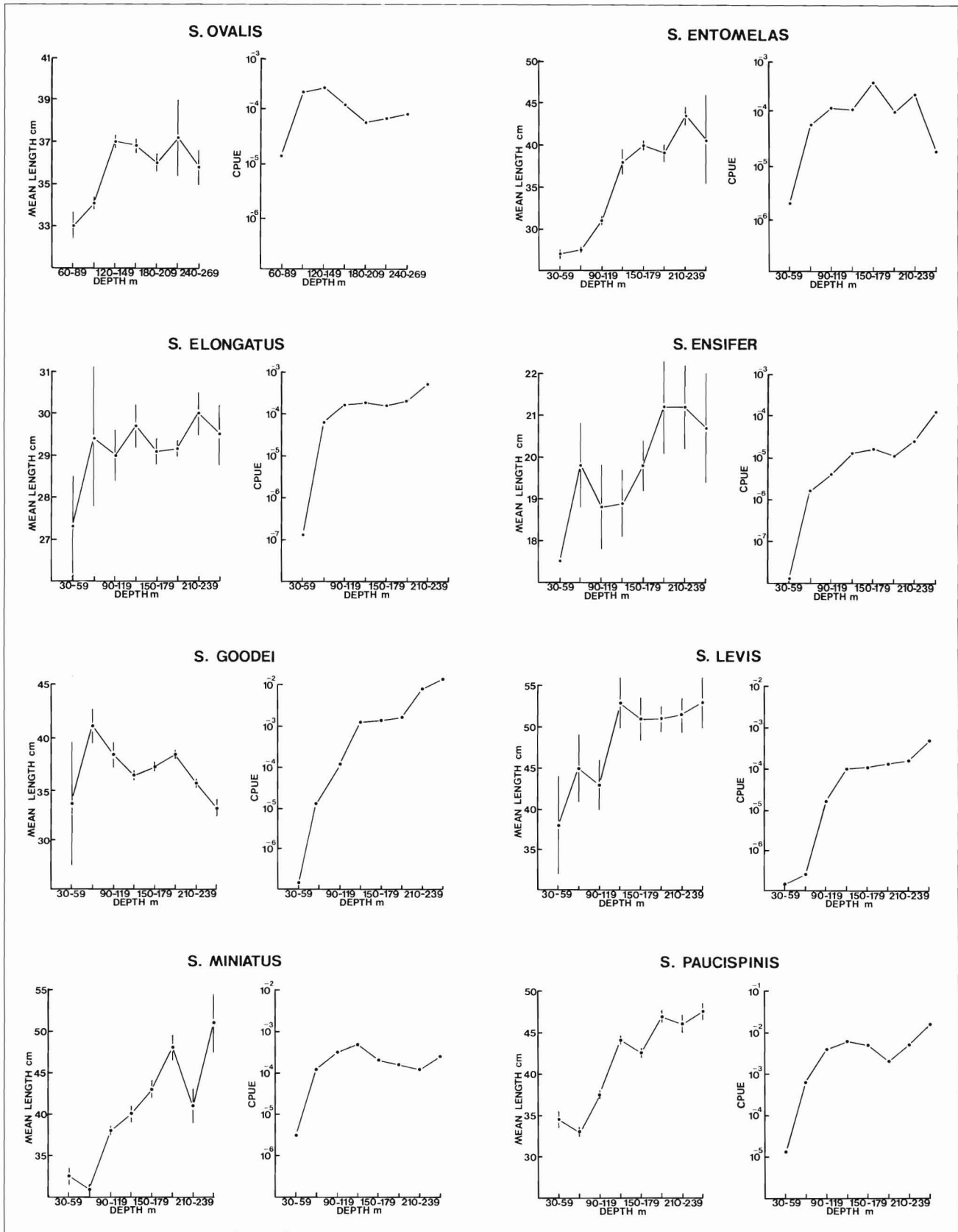


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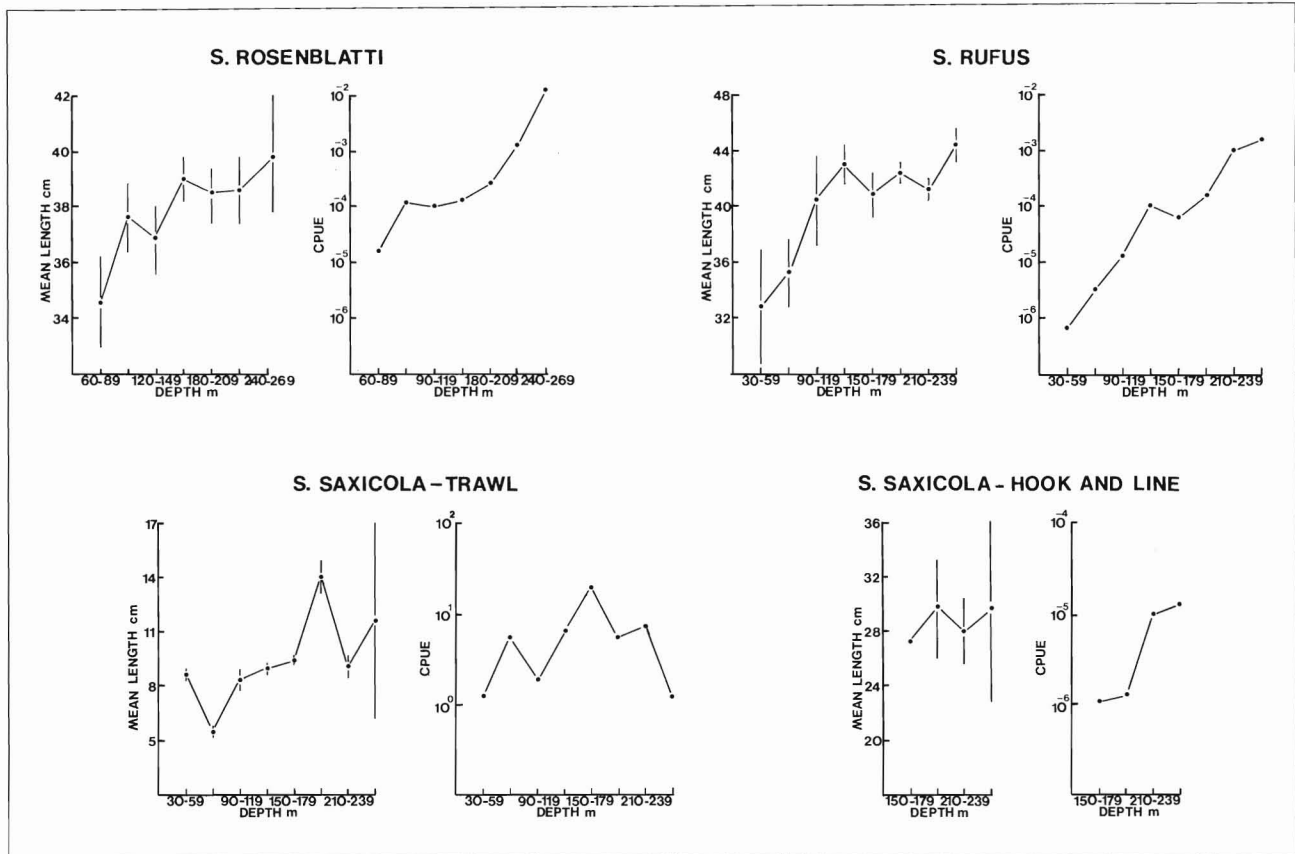


Figure 3.—Continued.

up the catch from the deeper intervals. We found newly settled *S. miniatus* recruiting in waters between 5 and 30 m.

***Sebastes paucispinis***—The bocaccio is a wide-ranging species, found from near bottom to as much as 50 m above the substrata, over a variety of substrata. The species was commonly taken from 90 to 239+ m, with fish size generally increasing with depth. Juveniles comprised most of the catch in 30–120 m and were occasionally taken to about 200 m. Adults were rare in waters less than 80 m. However, in the past we have noted mature *S. paucispinis* in depths as shallow as 20 m, where the water is unusually cold (as around San Miguel Island and at the head of Redondo Canyon). Juveniles recruit in the southern California Bight in 10–30 m.

***Sebastes rosenblatti***—The greenblotched rockfish is a substrate-oriented species, whose adults are found over hard bottom of either high or low relief. They were most commonly taken in the deeper parts of our sampling depths. Juveniles were rarely taken by hook and line. However, they were taken in our trawls in 70–120 m. As our trawls sample soft substrata, it appears juveniles are found on either hard or soft bottoms.

***Sebastes rufus***—The bank rockfish is a midwater, aggregating species, found over high relief, or on bank edges. It is primarily a deep-water species, and is rare in waters less

than 180 m. Juveniles are rarely taken in the sportfishery, but observations of commercial catches indicate juveniles occupy the shallower part of the species' range.

***Sebastes saxicola***—We present both sportfishing and trawl data for stripetail rockfish, as hook and line did not capture small fishes and large adults tended to avoid our trawls.

This is a small, motile midwater species, found over a variety of substrata. Juveniles and small adults were most abundant between 120 and 179 m. Larger adults were most abundant in the deepest part of the sportfishing sampling depths.

***Sebastes melanostomus***—We have no sportfishing or trawl data on blackgill rockfish, as it inhabits water deeper than that usually fished by sportfishing vessels and its preferred rocky habitat makes trawls unusable. However, based on commercial catches, it appears that adult *S. melanostomus* are taken in waters as shallow as 280 m, peaking in about 440–520 m. We took a few juveniles in 200 m.

Our results are similar to the limited data available from other southern California Bight studies. Lissner and Dorsey (1986) reported on submersible observations of *S. constellatus*, *S. hopkinsi*, and *S. rosaceus* abundance off the Cortes-Tanner Ridge and found almost identical abundance patterns.

Chen's (1971) data on bathymetric distribution of *S. constellatus*, *S. rosaceus*, *S. ensifer*, *S. chlorostictus*, and *S. rosenblatti* depth distributions were similar to ours, as were southern California trawl catch data on *S. dalli*, *S. saxicola*, and *S. semicinctus* (Mearns et al. 1980).

For most of the rockfishes reported here, juveniles were generally found in waters shallower than adult depths. Though our hook and line data tended to exclude many juveniles, the pattern of younger fishes in shallower waters was true in almost all species. This was particularly true of the large, relatively motile, midwater forms, such as *Sebastes entomelas*, *S. flavidus*, *S. paucispinis*, and *S. rufus*. However, even fishes we believe to be relatively sedentary, such as *S. chlorostictus* and *S. constellatus*, exhibited similar patterns. Perhaps the juvenile stages of these benthic species are more likely to move about (into deeper waters) than adults. This trend did not occur in all species. In a minority (i.e., *S. goodei*, *S. rosaceus*, *S. semicinctus*, and perhaps *S. elongatus* and *S. ensifer*) juveniles were commonly taken at the same depths as adults.

As we have noted in an earlier paper (Love et al. 1985), some rockfish species exhibit "isothermic submergence" (Briggs 1974) in the southern California Bight, seeking deeper, cooler waters in the warmer parts of their ranges. Love et al. found that even within the relatively compact Northern Channel Island chain, five species (*S. caurinus*, *S. miniatus*, *S. mystinus*, *S. paucispinis*, and *S. serranoides*) were more abundant in shallower water about the colder western islands. Moreover, mean lengths of these rockfishes increased in the shallow waters of the western islands—because only eurythermic<sup>3</sup> juveniles tolerated the warm inshore waters of the eastern part of the chain.

Isothermic submergence also occurs along the mainland. In a study at Diablo Canyon, about 75 km north of Pt. Conception, Burge and Schultz (1973) found adult *S. miniatus* in 7 m and juvenile *S. entomelas*, *S. goodei*, and *S. paucispinis* in 8–20 m, shallower than these fishes occur in the southern California Bight. This pattern is even more apparent from Oregon northwards because mature *S. entomelas*, *S. flavidus*, and *S. paucispinis* are abundant in shallower waters (Carlson and Haight 1972; Carlson and Barr 1977; Rosenthal et al. 1982; Nagtegaal 1983).

Within the southern California Bight, there are interspecific differences in species abundances. Based on our observations, southern, warmer-water dwelling species, such as *S. lentiginosus*, *S. simulator*, and *S. umbrosus*, become less abundant or do not occur in the northern part of the Bight. Northern, cold-water species such as *S. caurinus*, *S. flavidus*, and *S. ruberrimus*, reverse the pattern.

Southerly limits may be closely linked to water temperature. While southern species could, in theory, seek warmer

conditions in very shallow northern waters (inshore of usual depths), other constraints, such as behavior, body coloration and pattern etc. might prevent them from competing with inshore species. On the other hand, in the southern California Bight, water temperatures suitable for northern species do exist well within the species' depth range. Instead, these waters tend to be occupied by species equally abundant throughout California. Thus, the decline in abundances of northerly species seen in the central and southern Bight might more likely be caused by recruitment limitation due to variable transport of larvae in water currents (Love and Larson 1978; Cowen 1985). It is also possible that conditions for adults may be favorable, while those for recruiting juveniles are not.

Rockfish recruitment fluctuates in the shallow waters (3–25 m) of the Bight (Stephens et al. 1984). During the 1960's and early 1970's, two cold-preferring species, the blue rockfish (*S. mystinus*) and the olive rockfish (*S. serranoides*), were important constituents of the nearshore fauna of King Harbor and Palos Verdes, in the center of the Bight. Recruitment declined in the mid and late 1970's, ceasing in the early 1980's. This occurred with a general weakening of the California Current and a strengthening of warm water flow from Mexico.

## Age and Growth

Lengths at ages were estimated by direct observation of otolith annuli and by using the von Bertalanffy growth model:

$$L_t = L_\infty [1 - \exp - k(t - t_0)], \quad (3)$$

where  $L_t$  = length at time  $t$ ;

$L_\infty$  = theoretical maximum length;

$k$  = slope of curve expressing the rate of approach to  $L$ ; and

$t_0$  = theoretical age at which  $L_t = 0$

were fitted to observed age-length data (Tomlinson and Abramson 1961).

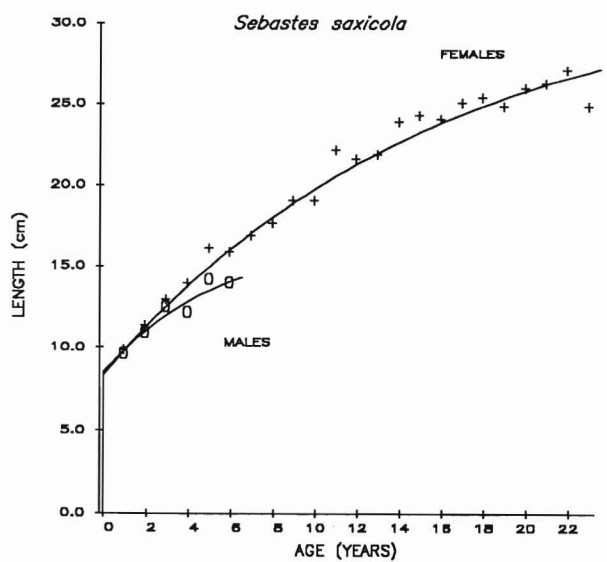
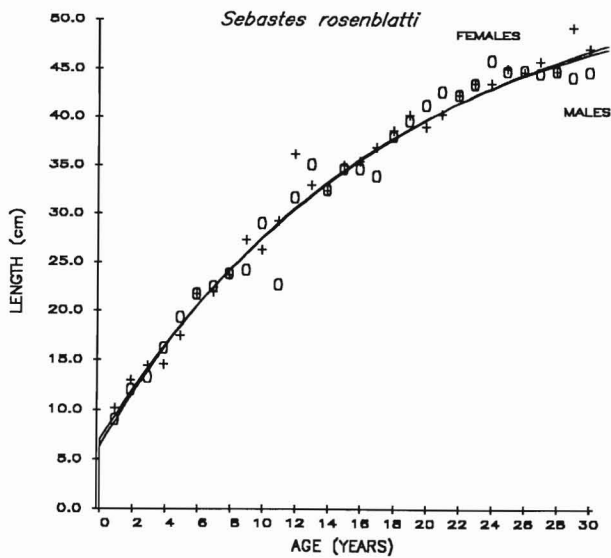
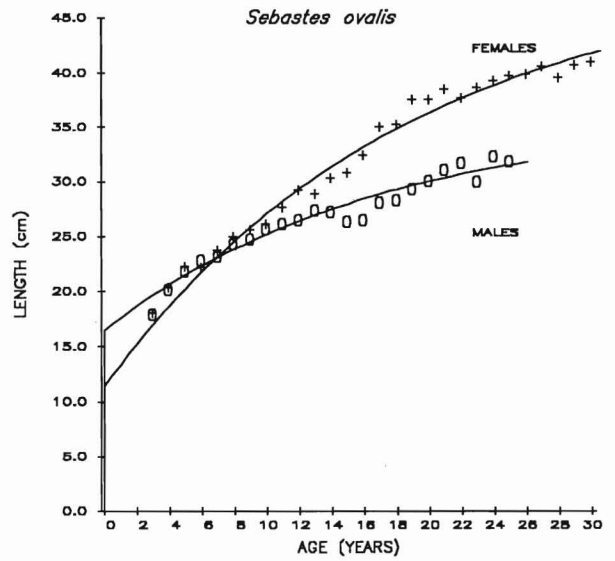
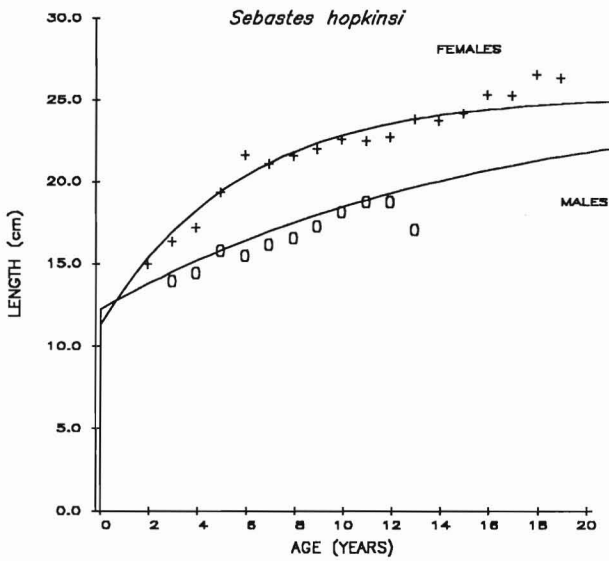
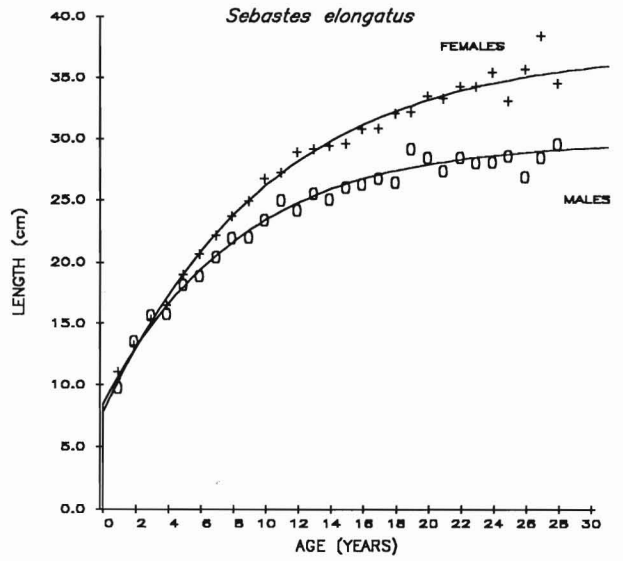
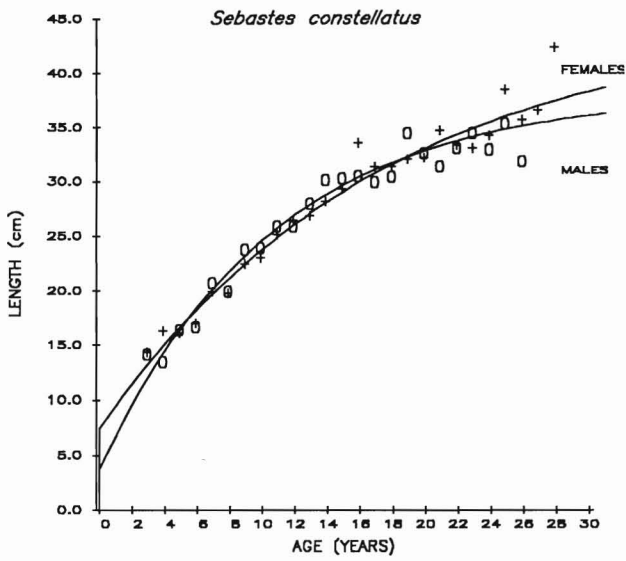
Von Bertalanffy growth curves are shown for *S. constellatus*, *S. elongatus*, *S. hopkinsi*, *S. ovalis*, *S. rosenblatti*, *S. saxicola*, and *S. semicinctus* (Fig. 4). Parameters of these curves are listed for these species, by sex, in Table 3. Also figured are mean lengths at age for each species.

Five of seven species showed differences in growth rate between sexes. In male and female *S. elongatus*, *S. hopkinsi*, *S. saxicola*, and *S. semicinctus*, growth rates were similar

**Figure 4.**

Von Bertalanffy growth curves of female and male *Sebastes constellatus*, *S. elongatus*, *S. hopkinsi*, *S. ovalis*, *S. rosenblatti*, *S. saxatilis*, and *S. semicinctus* taken from the southern California Bight. Also included are mean lengths at age computed from direct observations of otolith annuli.

<sup>3</sup>We believe juvenile rockfishes of these species are eurythermic rather than stenothermic to warm water, because they are found over a wide temperature range in southern and central California waters.



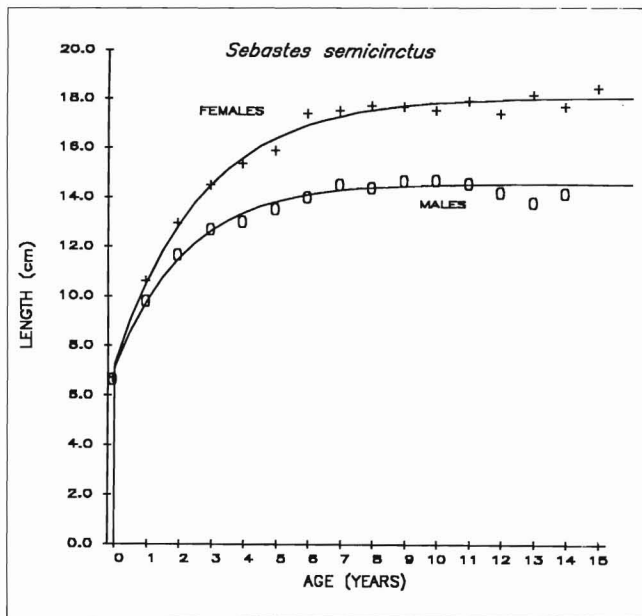


Figure 4.—Continued.

during the early years, with females later outgrowing males, reaching a larger maximum size. We caught very few male *S. saxicola* older than 6 years and the few we did take were comparatively old (28 years for a 17.0 cm individual). Juvenile *S. ovalis* males appeared to grow more quickly than females, with females outstripping males after maturation. However, relatively few juvenile *S. ovalis* were captured and this phenomenon may be a sampling artifact.

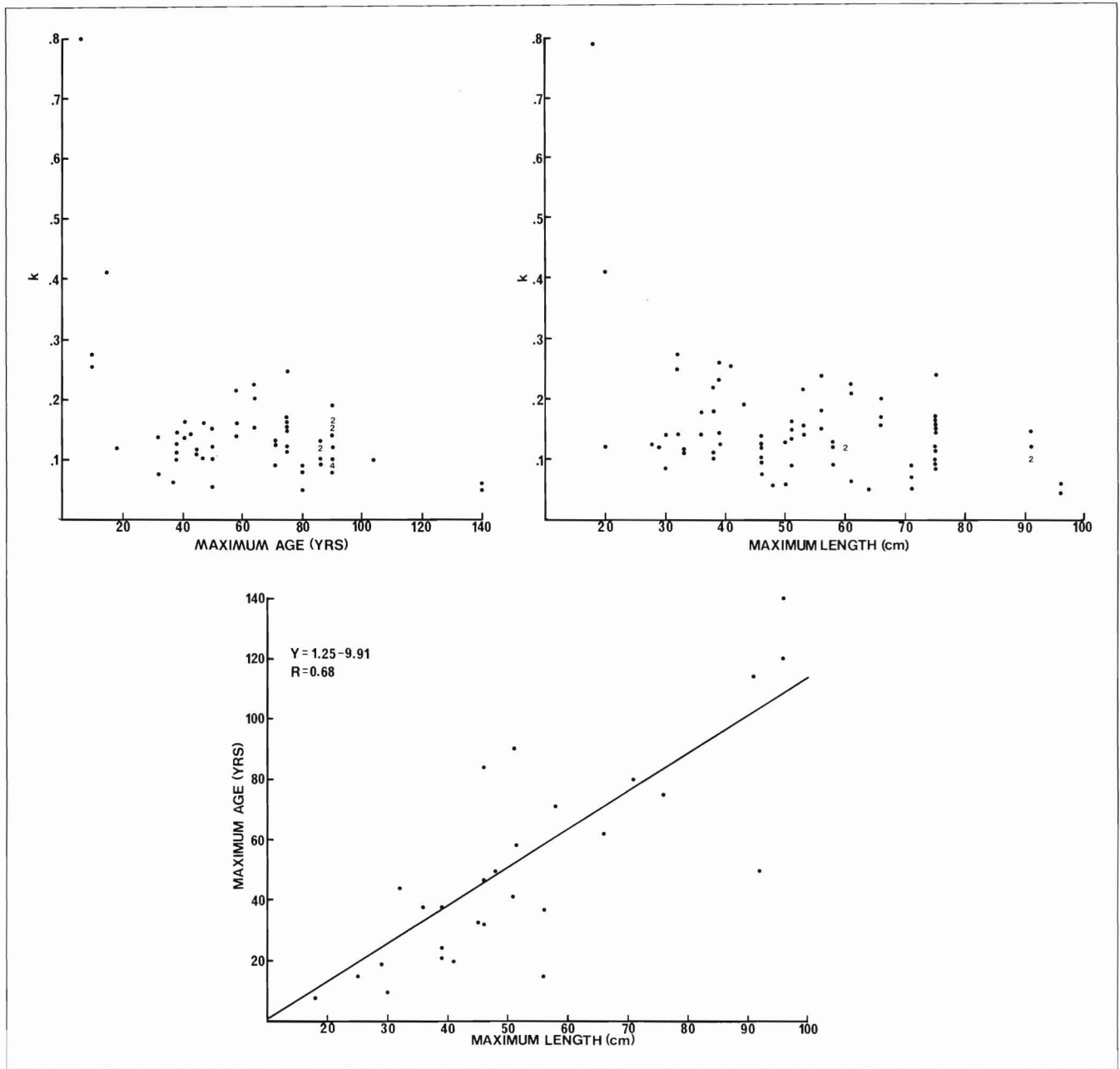
Maximum ages found for each species and sex are listed in Table 3. Oldest fishes were *S. rosenblatti*, with both males and females aged to 50 years. Dwarf species (*S. hopkinsi* and *S. semicinctus*) exhibited the shortest life spans. We plotted maximum observed lengths against maximum recorded age for all *Sebastes* species of the northeast Pacific for which ages had been assigned (data from Moulton 1975, Lenarz 1987; Bennett et al. 1982; Chilton and Beamish 1982; O'Connell and Funk 1986; present paper, Fig. 5). Though it is unlikely that maximum ages have been determined for some species and there is a tendency for rockfishes to be longer lived in the north, we believe there is sufficient data to show a trend within the genus, in which life span is positively correlated with maximum size.

The term  $k$ , the rate at which a species reaches maximum length, varied between species and sex. In general, males exhibited higher  $k$ 's (reached maximum size more rapidly) than females. Overall, *Sebastes semicinctus* values were highest, and *S. rosenblatti* and *S. ovalis* lowest. Among northeast Pacific *Sebastes*, it appears that several of the smallest and shortest-lived species exhibited the highest  $k$ 's (Fig. 5; data and references listed in Table 4), while the largest, longest-lived species had very low ones. However, there was no pattern to the species in between these extremes. Beverton and Holt (1960), comparing a broad range of taxa, discussed a widespread pattern among fish, in which maximum length ( $L$ ) is inversely correlated with  $k$ . While this may be true for very small and very large species within the genus *Sebastes*, it does not seem to hold for the majority of rockfishes.

In general, *Sebastes* grow more slowly than species of most other taxa. Beverton and Holt, surveying growth data from

**Table 3.**  
Parameters of the von Bertalanffy equation for *Sebastes constellatus*, *S. elongatus*, *S. hopkinsi*, *S. ovalis*, *S. rosenblatti*, *S. saxicola*, and *S. semicinctus* from southern California.

Species	Sex	$L_{\infty}$	SE	$k$	SE	$t_0$	SE	Max. obs. age (yr)
<i>constellatus</i>	male	38.06	1.68	0.094	0.014	-1.065	0.712	32
	female	45.00	2.87	0.087	0.009	-3.107	0.822	28
<i>elongatus</i>	male	29.65	0.55	0.121	0.009	-2.732	0.334	37
	female	37.26	0.66	0.098	0.006	-2.360	0.288	28
<i>hopkinsi</i>	male	24.71	10.77	0.063	0.082	-10.329	8.655	13
	female	25.25	0.43	0.176	0.021	-3.358	0.708	19
<i>ovalis</i>	male	35.86	2.60	0.060	0.018	-10.247	3.160	30
	female	49.99	2.08	0.053	0.007	-4.936	1.031	37
<i>rosenblatti</i>	male	56.11	1.77	0.058	0.004	-2.103	0.230	50
	female	57.99	2.58	0.053	0.006	-2.468	0.429	50
<i>saxicola</i>	male	17.38	5.81	0.186	0.194	-3.782	2.526	28
	female	33.05	1.68	0.064	0.007	-4.634	0.433	38
<i>semicinctus</i>	male	14.62	0.15	0.452	0.037	-1.458	0.182	14
	female	18.14	0.22	0.370	0.030	-1.368	0.176	15



**Figure 5.**

The relationship of the von Bertalanffy factor  $k$ , describing the rate to asymmetric growth against maximum age and maximum length of *Sebastes* species from the northeast Pacific. (Data from references listed in Table 5.) Also figured is the relationship of maximum age to mean length of *Sebastes* species from the northeast Pacific.

species in 23 fish families, found that most had  $k$  values between 0.3 and 1.0. By comparison, most rockfish have  $k$ 's between 0.1 and 0.3. Some, such as *S. aleutianus* (0.048) have values among the lowest recorded for any fish species. On the other hand, the growth rate of *S. emphaeus* is in the higher range found in fishes, in keeping with the widespread phenomenon that small species quickly reach maximum lengths.

Growth rates of *S. elongatus* and *S. saxicola* have been examined previously—*S. elongatus* off British Columbia (Westheim and Harling 1975) and *S. saxicola* off central and northern California (Phillips 1964). In Figure 6, we compare our growth data with theirs. Male *S. elongatus* from California appeared to grow faster, while females grew more slowly. However, the species as a whole seem to show similar growth rates between the two areas. *Sebastes saxicola*

**Table 4.**  
**Maximum length, von Bertalanffy *k* values by sex and mean *k* for rockfishes of the northeast Pacific.**

Species	Maximum length (cm)	Sex	<i>k</i>	Mean <i>k</i>	Source	Species	Maximum length (cm)	Sex	<i>k</i>	Mean <i>k</i>	Source
<i>aleutianus</i>	96	M	0.066	0.063	Westrheim and Harling 1975	<i>entomelas</i> — continued		M	0.150	0.158	Lenarz 1987
		F	0.059					F	0.165		
		M	0.053	0.048	Nelson and Quinn 1981	<i>flavidus</i>	66			0.173 <sup>b</sup>	Phillips 1964
		F	0.043							0.190 <sup>b</sup>	Moulton 1977
<i>alutus</i>	51	M	0.097	0.088	Archibald et al. 1981			M	0.153	0.155	Archibald 1981
		F	0.078					F	0.157		
		M	0.172	0.150	Archibald et al. 1981			M	0.247	0.202	Lea et al. <sup>a</sup>
		F	0.132					F	0.157		
<i>atrovirens</i>	42	M	0.255	0.255	Lea et al. <sup>a</sup>	<i>goodei</i>	56			0.182 <sup>b</sup>	Phillips 1964
		F	0.255							0.240	Wilkins 1980
<i>babcocki</i>	64	M	0.062	0.055	Westrheim and Harling 1975	<i>helvomaculatus</i>	30	M	0.092	0.085	Westrheim and Harling 1975
		F	0.047					F	0.079		
<i>brevispinis</i>	71	M	0.088	0.078	Archibald et al. 1981	<i>hopkinsi</i>	29	M	0.060	0.120	Present paper
		F	0.068					F	0.180		
		M	0.101	0.085	Archibald et al. 1981	<i>jordani</i>	32			0.275 <sup>b</sup>	Phillips 1964
		F	0.069							0.254	Lenarz 1980
		M	0.060	0.051	Archibald et al. 1981			M	0.298	0.254	
		F	0.042					F	0.211		
<i>carnatus</i>	39	M	0.275	0.264	Lea et al. <sup>a</sup>	<i>maliger</i>	61			0.068 <sup>b</sup>	Moulton 1977
		F	0.253							0.121 <sup>b</sup>	Moulton 1977
<i>caurinus</i>	57			0.183 <sup>b</sup>	Moulton 1981	<i>melanops</i>	60	M	0.230	0.205	Six and Horton 1977
		M	0.193		Lea et al. <sup>a</sup>			F	0.180		
		F	0.166	0.180	Lea et al. <sup>a</sup>			M	0.137	0.125	Lea et al. <sup>a</sup>
								F	0.113		
<i>chlorostictus</i>	50			0.058 <sup>b</sup>	Chen 1971	<i>miniatus</i>	76			0.098 <sup>b</sup>	Phillips 1964
		M	0.136	0.134	Lea et al. <sup>a</sup>					0.178	Lea et al. <sup>a</sup>
		F	0.131			<i>nebulosus</i>	43	M	0.191	0.190	Lea et al. <sup>a</sup>
								F	0.188		
<i>chrysomelas</i>	39	M	0.241		Lea et al. <sup>a</sup>	<i>ovalis</i>	56	M	0.060	0.057	Present paper
		F	0.213	0.227				F	0.053		
<i>constellatus</i>	46	M	0.094	0.090	Present paper	<i>paucispinis</i>	91			0.148 <sup>b</sup>	Phillips 1964
		F	0.087							0.100	Westrheim and Harling 1975
		M	0.121	0.137	Lea et al. <sup>a</sup>			M	0.130	0.12	Wilkins 1980
		F	0.152					F	0.110		
<i>crameri</i>	76			0.160 <sup>b</sup>	Phillips 1964	<i>pinniger</i>	76			0.122 <sup>b</sup>	Phillips 1964
		M	0.120	0.107	Westrheim and Harling 1975					0.168	Six and Horton 1977
		F	0.094					M	0.160	0.155	Westrheim and Harling 1975
								F	0.150		
<i>dalli</i>	25			0.122 <sup>b</sup>	Chen 1971			M	0.178	0.148	Boehlert and Kappenmann 1980
								F	0.118		
<i>diploproa</i>	46	M	0.140	0.120	Westrheim and Harling 1980			M	0.114	0.162	Archibald et al. 1981
		F	0.100					F	0.209		
		M	0.117	0.104	Boehlert and Kappenmann 1980			M	0.137	0.116	Archibald et al. 1981
		F	0.091					F	0.095		
		M	0.129	0.127	Boehlert and Kappenmann 1980			M	0.261	0.246	Lea et al. <sup>a</sup>
		F	0.125					F	0.230		
		M	0.105	0.095	Boehlert and Kappenmann 1980	<i>polyspinis</i>	38			0.180 <sup>b</sup>	Westrheim and Tsyuki 1971
		F	0.084							0.220	Westrheim and Harling 1975
<i>elongatus</i>	38	M	0.077	0.099	Westrheim and Harling 1975						
		F	0.120								
		M	0.120	0.110	Present paper						
		F	0.100								
<i>emphaeus</i>	18			0.789 <sup>b</sup>	Moulton 1977						
<i>ensifer</i>	30			0.141 <sup>b</sup>	Chen 1971						
<i>entomelas</i>	53			0.215 <sup>b</sup>	Phillips 1964						
		M	0.130	0.140	Westrheim and Harling 1975						
		F	0.150								



Table 4.—Continued.

Species	Maximum length (cm)	Sex	k	Mean k	Source	Species	Maximum length (cm)	Sex	k	Mean k	Source
<i>proriger</i>	51	M	0.120	0.135	Westrheim and Harling 1975	<i>ruberrimus</i>	91	M	0.089	0.102	Lea et al. <sup>a</sup>
		F	0.150					F	0.115		
<i>rastrelliger</i>	56	M	0.178	0.163	Archibald et al. 1981	<i>saxicola</i>	39			0.147 <sup>b</sup>	Phillips 1964 Present paper
		F	0.148					M	0.190		
<i>reedi</i>	58	M	0.170	0.154	Lea et al. <sup>a</sup>	<i>semicinctus</i>	25	M	0.450	0.410	Present paper
		F	0.138					F	0.370		
<i>rosaceus</i>	36	M	0.082	0.092	Westrheim and Harling 1975	<i>serranooides</i>	61	M	0.270	0.225	Love 1981
		F	0.110					F	0.180		
		M	0.125		0.125	Archibald et al. 1981	M	0.261	0.214	Lea et al. <sup>a</sup>	
		F	0.124				F	0.167			
<i>rosenblatti</i>	48	M	0.132	0.133	Archibald et al. 1981	<i>umbrosus</i>	27	M	0.109	0.123	Chen 1971
		F	0.133					F	0.137		
<i>rosaceus</i>	36	M	0.156	0.140	Westrheim and Harling 1975	<i>variegatus</i>	32	M	0.200	0.140	Westrheim and Harling 1975
		F	0.124					F	0.160		
<i>rosenblatti</i>	48	M	0.060	0.55	Present paper	<i>zacentrus</i>	33	M	0.160	0.110	Westrheim and Harling 1975
		F	0.050					F	0.060		
		M	0.100					0.134	Archibald et al. 1981		
		F	0.134								

<sup>a</sup>Lea, R., R. McAllister and D. VenTresca. Biological aspects of nearshore fishes of the genus *Sebastes* with notes on ecologically related species. Calif. Fish Game, Fish Bull. In prep.

<sup>b</sup>Data from both sexes combined in original paper.

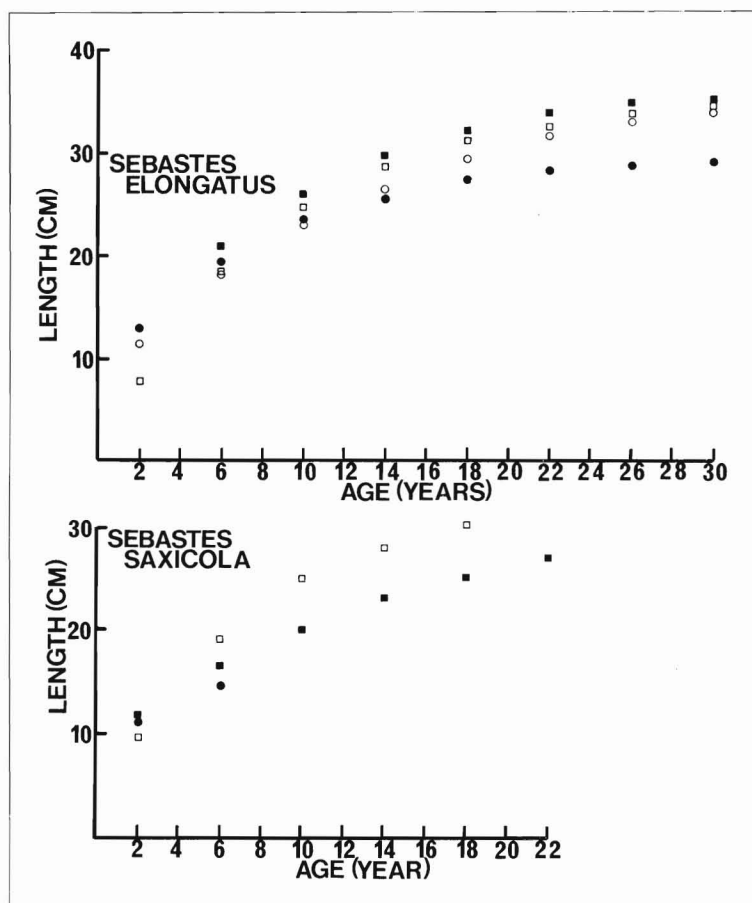


Figure 6.

A comparison of von Bertalanffy growth curves between *Sebastes elongatus* from the southern California Bight and British Columbia (from Westrheim and Harling 1975) and *S. saxicola* from the southern California Bight and central-northern California (Phillips 1964). For *S. elongatus*, ● = males and ■ = females from the southern California Bight; ○ = males and □ = females from British Columbia. For *S. saxicola*, ● = males and ■ = females from the southern California Bight and □ = both sexes combined from central-northern California.

grew faster off northern and central California, than off the southern California Bight.

It is probable that these studies are not strictly comparable. Phillips aged fishes with scales, and therefore may have underestimated age (particularly in older fish) and hence have overestimated size at age (Lenarz 1987). However, differences in *S. saxicola* growth rates appear early in this species' life and it is unlikely that these differences are due to age underestimation of young fish. Though Westrheim and Harling used otoliths, they did not use sectioned or broken pieces. Thus, their age data, from larger, older individuals, are underestimated. However, the growth asymptote occurred at an age where underestimation is less likely to occur.

Thus, of the six *Sebastes* species for which data are available and where comparisons have been made (*S. elongatus* and *S. saxicola*, plus *S. diploproa* and *S. pinniger*—Boehlert and Kappenmann 1980; *S. serranoides*—Love 1980; *S. entomelas*—Lenarz 1987), three (*S. diploproa*, *S. saxicola*, and *S. serranoides*) exhibit geographic variations in growth rates (though *S. entomelas*, based on unpublished observations, may also show variability between Morro Bay and California north of Morro Bay<sup>4</sup>).

### Length-Weight Relationships

For all species, the relationship between total length and weight fits the relationship  $W = aL^b$ , where  $W$  = weight (g),  $L$  = total length (cm), and  $a$  and  $b$  are constants, with values determined by using  $\log_{10}$  transformations and by fitting the values to a straight line by least squares (Fig. 7). For almost all species the relationship between length and weight was identical between sexes. The exceptions were *Sebastes flavidus*, *S. ovalis*, *S. paucispinis*, *S. saxicola*, and *S. semicinctus*, where females were heavier than males (Table 5). To test whether this difference was caused by seasonal and/or gender-related factors, we subtracted gonad weight from body weight, generated the length-weight relationship for each sex, and tested these between sexes. Again, differences between sexes existed (Table 5).

We compared the calculated weights at 25 cm for 17 species (two did not grow to this length). In general, benthic rockfishes were heavier at length than were transitional or midwater species (Fig. 8). Most benthic species were thicker and deeper-bodied than midwater ones. One midwater species (*S. flavidus*) was quite heavy at 25 cm (250 g), compared to other midwater species. Similarly, the somewhat elongate, benthic *S. ensifer* (185 g) was much lighter than its sibling species (also benthic), *S. rosaceus* (281 g).

There does not appear to be geographic variability in the length-weight relationships of at least some species (*S. entomelas*, *S. flavidus*, *S. goodei*, *S. paucispinis*, and *S. saxicola*)

based on the limited data available (Phillips 1964; Moulton 1977).

### Condition Factor

We grouped data for each species, by sex, into two seasons to examine changes in condition factor. Guillemot et al. (1985), reporting on offshore rockfishes from central California, noted differences in fat storage between two periods, December–May and June–November. As we subtracted gonad weight from body weight in our condition factor analyses, it is probable that differences in condition factor primarily reflected changes in fat storage in our fishes. For this reason, we used these two periods in our analyses.

Males of 11 species and females of 13 showed significant differences in condition factor between the two periods (Table 6). Grouping all data by sex for each species, we found sexual differences in four species. In these species, two males and two females were more robust.

Guillemot et al. (1985) suggested that the fat cycling in the rockfishes they studied was linked to upwelling-derived seasonal variation in food availability. While we found no single factor which might predict the patterns seen (such as habitat, maximum size, etc.), seasonality did occur in almost all of the active, midwater species. Thus, it is possible that the variations we observed also reflected differences in food availability between upwelling and nonupwelling seasons. However, some species which may not depend on upwelling for increased food (such as the benthic feeding *S. chlorostictus*) also exhibited seasonality.

### Maturation and Reproduction

#### Multiple Broods

Multiple broods, in which a female spawns two or more times per season, were found in 12 species: *Sebastes chlorostictus*, *S. constellatus*, *S. elongatus*, *S. ensifer*, *S. goodei*, *S. hopkinsi*, *S. levis*, *S. ovalis*, *S. paucispinis*, *S. rosaceus*, *S. rosenblatti*, and *S. rufus*. We classified individuals as multiple brooders if the ovaries contained both eyed larvae and either fertilized or unfertilized eggs in large numbers. We were careful to exclude either females with a few eyed larvae retained from a previous spawning season or newly spent females containing retained larvae. Seven species (*S. dalli*, *S. entomelas*, *S. flavidus*, *S. melanostomus*, *S. miniatus*, *S. saxicola*, and *S. semicinctus*) produced only one brood per year. In the former group of species, multiple brooding was very common. In fact, we noted the phenomenon in all *S. paucispinis* over 55 cm, examined at the beginning of the spawning season. The smaller mature females of all species of multiple brooders were most likely to be single brooders. It appears that, among the multiple brooders, two broods a year was the norm. However, large *S. levis* and *S. paucispinis* may produce as many as three broods.

<sup>4</sup>W. Lenarz, National Marine Fisheries Service, Tiburon Laboratory, 3150 Paradise Dr., Tiburon, CA 94920, pers. commun.

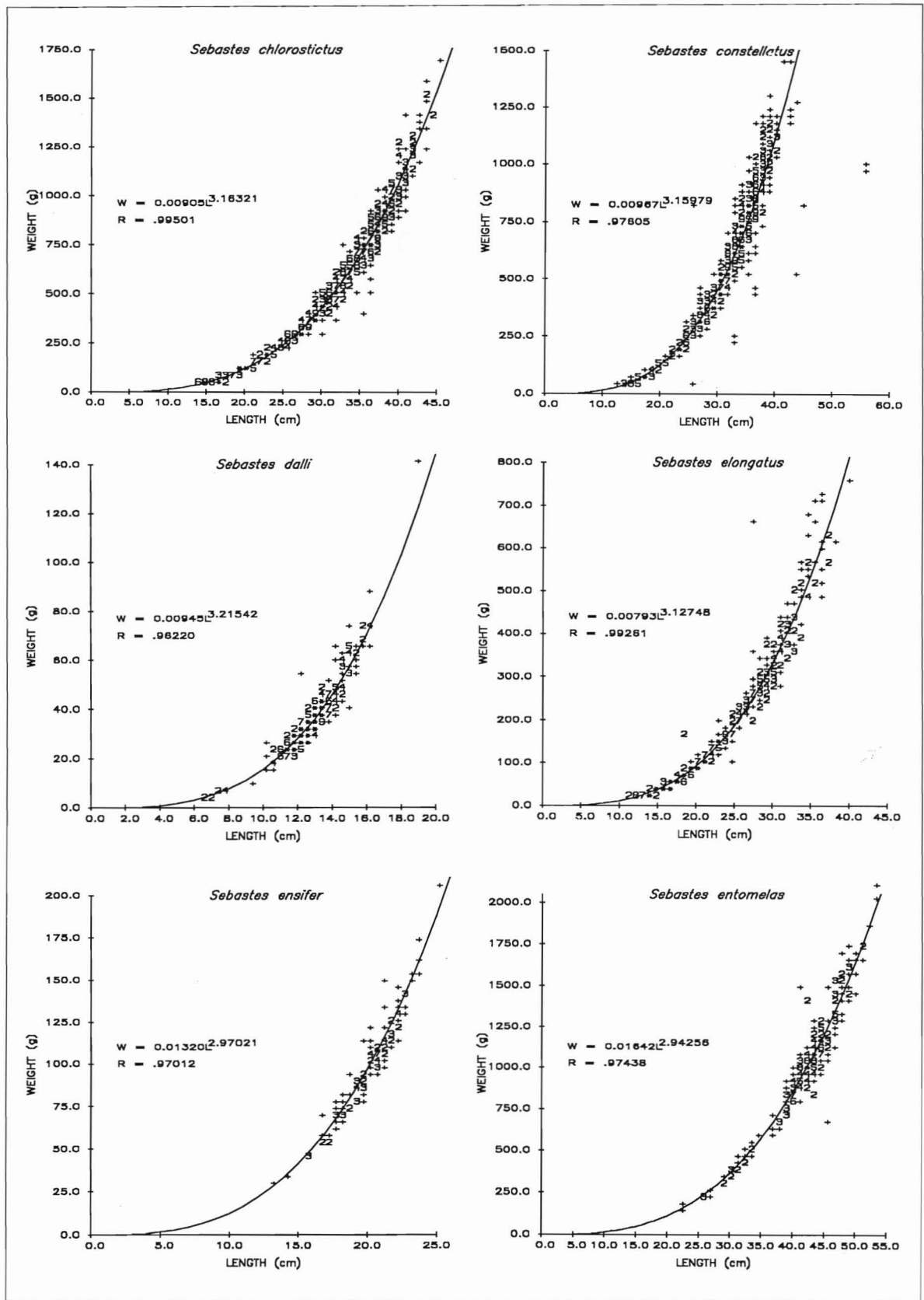


Figure 7.  
Length-weight relationships of 19 *Sebastes* species from the southern California Bight. Sexes are combined unless shown to be statistically different (see Table 6).

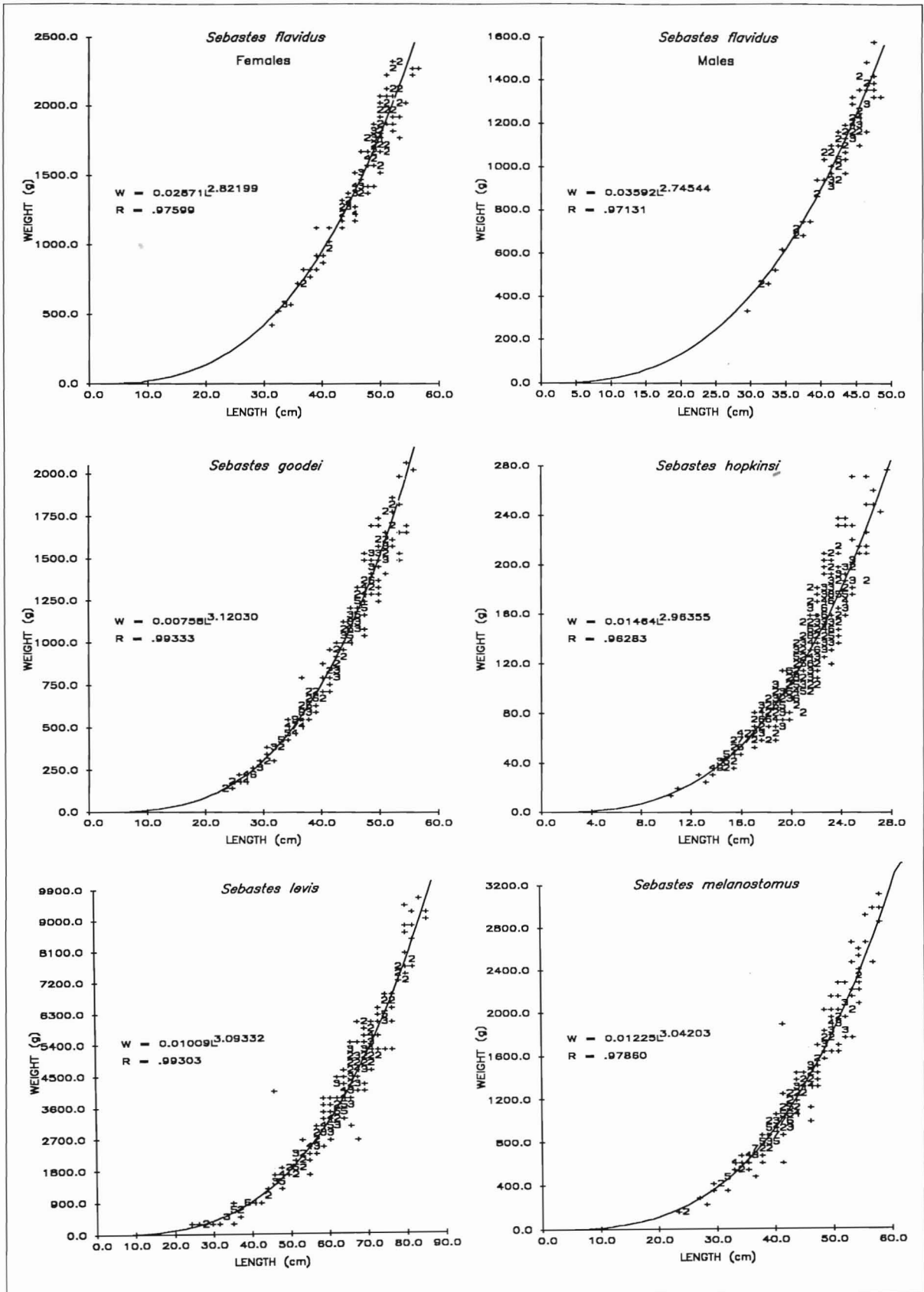


Figure 7.—Continued.

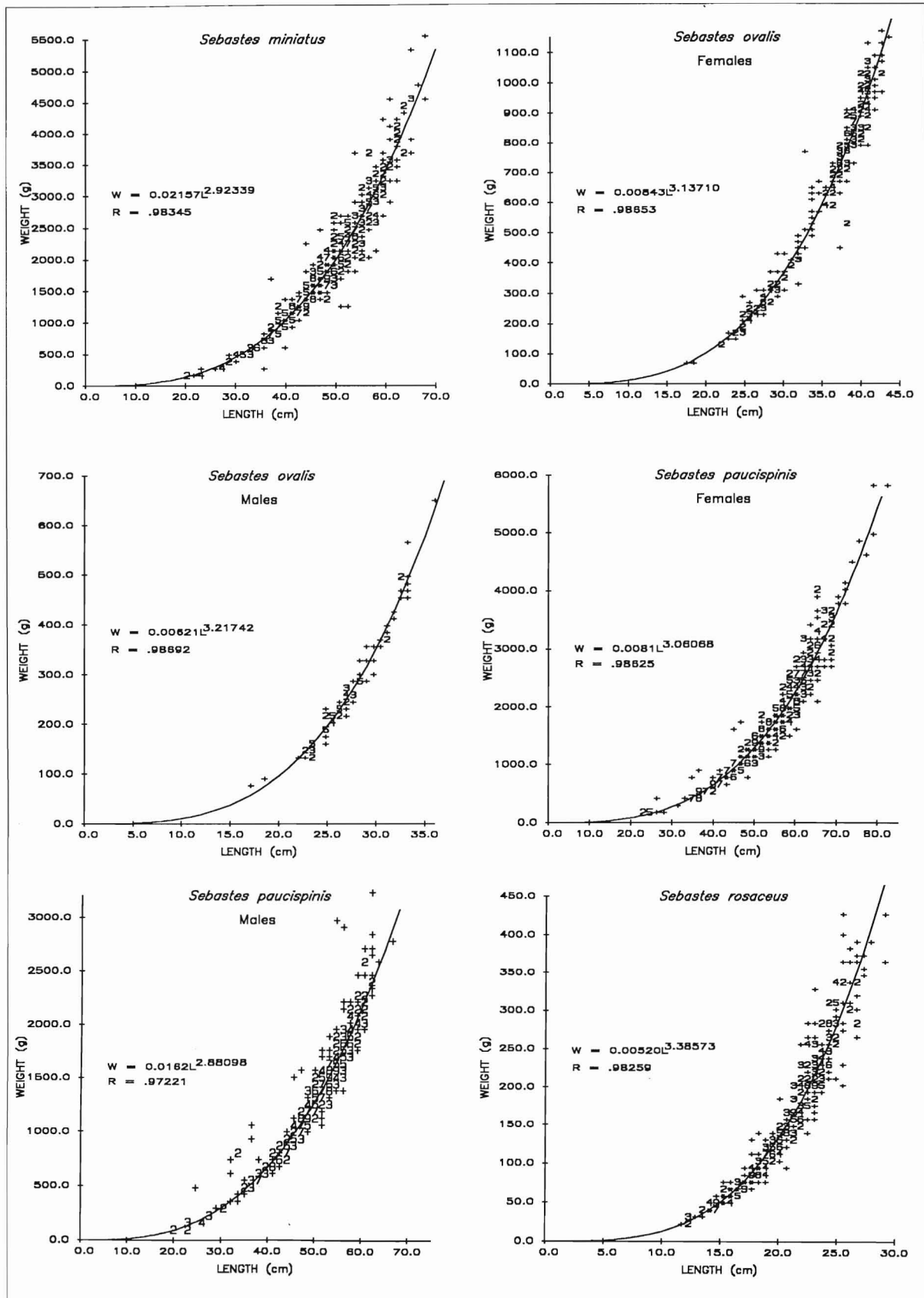


Figure 7.—Continued.

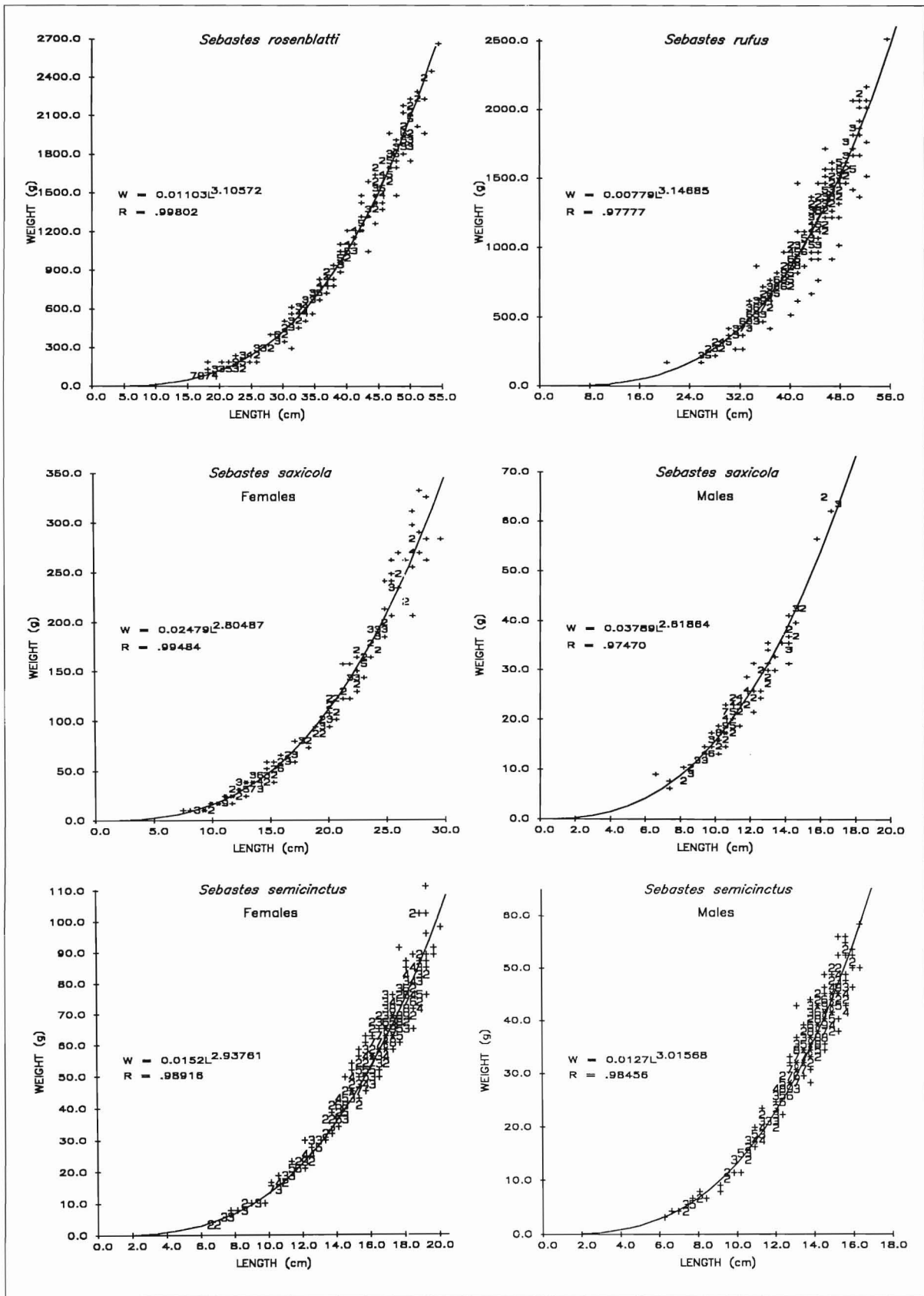
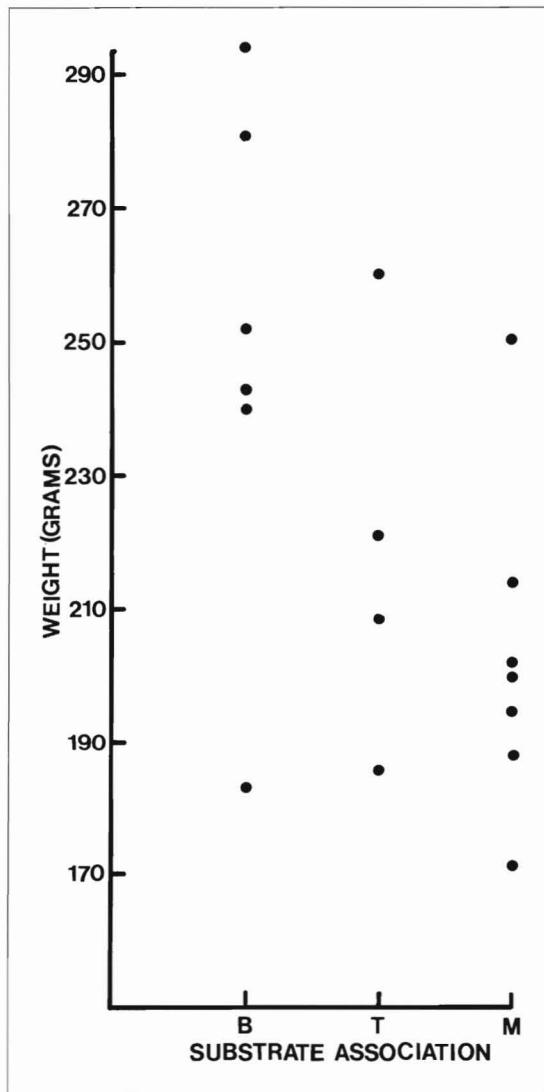


Figure 7.—Continued.

**Table 5.**  
Analysis of variance of length-weight data for five *Sebastes* species with significant male-female differences.

Species	ANOVA (gonads)		ANOVA (gonads subtracted)	
	F	P	F	P
<i>flavidus</i>	19.70	<0.0001	10.6	<0.001
<i>ovalis</i>	5.13	<0.006	180.0	<0.00001
<i>paucispinis</i>	17.89	<0.00004	18.8	<0.00003
<i>saxicola</i>	11.00	<0.00002	93.0	<0.00001
<i>semicinctus</i>	182.80	<0.0001	14.1	<0.0002



**Figure 8.**

Weights at 25 cm of 17 rockfish species. Not included are the dwarf species *S. hopkinsi* and *S. semicinctus*. Fishes figured by degree of substrate orientation, B = benthic, T = transitional, M = midwater.

**Table 6.**  
Condition factors of 19 rockfish species from the Southern California Bight. Significant differences at ( $P = 0.05$ ) marked with an asterisk.

Species	N	K	SD	t	P
<i>chlorostictus</i>					
Males					
Dec.-May	82	1.58	0.10	-3.26	0.0017*
June-Nov.	104	1.63	0.11		
Females					
Dec.-May	80	1.54	0.14	-3.12	0.0026*
June-Nov.	88	1.60	0.11		
All Seasons					
Males	186	1.61	0.10	2.83	0.0052*
Females	168	1.57	0.13		
<i>constellatus</i>					
Males					
Dec.-May	87	1.63	0.13	-1.63	0.1010
June-Nov.	70	1.66	0.17		
Females					
Dec.-May	110	1.65	0.14	0.72	0.4774
June-Nov.	55	1.63	0.21		
All Seasons					
Males	157	1.64	0.15	0.20	0.8242
Females	165	1.64	0.16		
<i>dalli</i>					
Males					
Dec.-May	81	1.55	0.15	-4.28	0.0001*
June-Nov.	153	1.64	0.14		
Females					
Dec.-May	150	1.54	0.16	-5.26	<0.0001*
June-Nov.	171	1.66	0.19		
All Seasons					
Males	234	1.61	0.15	0.31	0.7532
Females	321	1.61	0.18		
<i>elongatus</i>					
Males					
Dec.-May	52	1.14	0.10	-2.00	0.0489*
June-Nov.	50	1.22	0.30		
Females					
Dec.-May	105	1.17	0.12	-1.56	0.1160
June-Nov.	134	1.20	0.19		
All Seasons					
Males	102	1.18	0.22	-0.16	0.8490
Females	239	1.19	0.12		
<i>ensifer</i>					
Males					
Dec.-May	16	1.15	0.11	-1.97	0.0553
June-Nov.	17	1.22	0.12		
Females					
Dec.-May	19	1.19	0.09	0.09	0.8910
June-Nov.	63	1.19	0.10		
All Seasons					
Males	33	1.19	0.21	-0.07	0.9021
Females	82	1.19	0.20		
<i>entomelas</i>					
Males					
Dec.-May	22	1.27	0.11	-2.39	0.0174*
June-Nov.	111	1.33	0.13		
Females					
Dec.-May	70	1.24	0.10	-6.65	<0.001*
June-Nov.	85	1.36	0.12		

Table 6.—Continued.

Species	<i>N</i>	<i>K</i>	<i>SD</i>	<i>t</i>	<i>P</i>	Species	<i>N</i>	<i>K</i>	<i>SD</i>	<i>t</i>	<i>P</i>
<i>entomelas</i> —continued						<i>miniatus</i> —continued					
All Seasons						All Seasons					
Males	133	1.32	0.12	1.09	0.2781	Males	304	1.61	0.18	1.19	0.2327
Females	155	1.31	0.12			Females	333	1.59	0.20		
<i>flavidus</i>						<i>ovalis</i>					
Males						Males					
Dec.–May	55	1.37	0.12	-2.64	0.0094*	Dec.–May	46	1.28	0.14	-0.561	0.5829
June–Nov.	52	1.41	0.10			June–Nov.	52	1.29	0.13		
Females						Females					
Dec.–May	76	1.37	0.17	-1.31	0.1883	Dec.–May	139	1.33	0.10	-3.69	0.0005*
June–Nov.	89	1.41	0.25			June–Nov.	192	1.38	0.12		
All Seasons						All Seasons					
Males	107	1.39	0.20	-0.04	0.9238	Males	98	1.29	0.11	-6.00	<0.0001*
Females	165	1.39	0.21			Females	331	1.36	0.11		
<i>goodei</i>						<i>paucispinis</i>					
Males						Males					
Dec.–May	24	1.11	0.24	-2.23	0.0268*	Dec.–May	195	0.98	0.11	-4.04	0.0002*
June–Nov.	68	1.18	0.13			June–Nov.	189	1.04	0.18		
Females						Females					
Dec.–May	54	1.14	0.11	-5.09	<0.0001*	Dec.–May	310	0.98	0.10	-5.42	<0.0001*
June–Nov.	165	1.19	0.10			June–Nov.	317	1.03	0.11		
All Seasons						All Seasons					
Males	92	1.16	0.14	-1.44	0.1471	Males	384	1.01	0.15	-0.835	0.4087
Females	219	1.18	0.21			Females	627	1.00	0.10		
<i>hopkinsi</i>						<i>rosaceus</i>					
Males						Males					
Dec.–May	36	1.33	0.10	-0.31	0.7552	Dec.–May	129	1.62	0.13	2.00	0.0445*
June–Nov.	40	1.33	0.11			June–Nov.	59	1.58	0.14		
Females						Females					
Dec.–May	228	1.32	0.17	3.54	0.0008*	Dec.–May	124	1.61	0.14	-0.61	0.5521
June–Nov.	164	1.26	0.19			June–Nov.	69	1.62	0.16		
All Seasons						All Seasons					
Males	76	1.32	0.10	1.49	0.1337	Males	188	1.61	0.14	-0.58	0.5699
Females	392	1.30	0.18			Females	193	1.61	0.15		
<i>levis</i>						<i>rosenblatti</i>					
Males						Males					
Dec.–May	87	1.46	0.15	-1.60	0.1081	Dec.–May	83	1.59	0.15	-1.27	0.2016
June–Nov.	99	1.52	0.29			June–Nov.	71	1.62	0.16		
Females						Females					
Dec.–May	76	1.44	0.11	-1.76	0.0758	Dec.–May	93	1.59	0.10	-4.78	<0.0001*
June–Nov.	118	1.47	0.14			June–Nov.	97	1.64	0.11		
All Seasons						All Seasons					
Males	186	1.49	0.23	1.74	0.0784	Males	154	1.60	0.13	-1.44	0.1483
Females	194	1.46	0.13			Females	190	1.62	0.11		
<i>melanostomus</i>						<i>rufus</i>					
Males						Males					
Dec.–May	75	1.42	0.14	-1.32	0.1854	Dec.–May	80	1.32	0.11	-3.12	0.0025*
June–Nov.	63	1.40	0.12			June–Nov.	107	1.37	0.12		
Females						Females					
Dec.–May	83	1.44	0.12	0.37	0.7145	Dec.–May	115	1.33	0.13	-2.53	0.0116*
June–Nov.	37	1.45	0.22			June–Nov.	121	1.37	0.12		
All Seasons						All Seasons					
Males	138	1.41	0.11	-1.86	0.0754	Males	187	1.35	0.12	-0.19	0.8290
Females	120	1.44	0.16			Females	236	1.35	0.12		
<i>miniatus</i>						<i>saxicola</i>					
Males						Males					
Dec.–May	167	1.61	0.19	0.69	0.5004	Dec.–May	26	1.48	0.14	-2.10	0.0362*
June–Nov.	137	1.60	0.17			June–Nov.	68	1.55	0.14		
Females						Females					
Dec.–May	191	1.57	0.22	-2.28	0.0219*	Dec.–May	108	1.33	0.14	-7.94	<0.0001*
June–Nov.	142	1.62	0.15			June–Nov.	194	1.47	0.16		



**Table 6.—Continued.**

Species	N	K	SD	t	P
<i>saxicola</i> —continued					
All Seasons					
Males	134	1.36	0.15	-8.19	<0.0001*
Females	262	1.50	0.15		
<i>semicinctus</i>					
Males					
Dec.–May	408	1.30	0.10	-7.88	0.0001*
June–Nov.	171	1.37	0.10		
Females					
Dec.–May	390	1.20	0.11	-12.83	<0.0001*
June–Nov.	173	1.31	0.11		
All Seasons					
Males	579	1.32	0.10	13.86	<0.0001*
Females	563	1.23	0.10		

It is difficult to see any pattern in the occurrence of multiple broods within the genus *Sebastes*. There was little phylogenetic correlation (Table 7). For instance, while all members of the subgenus *Sebastomus* (*S. chlorostictus*, *S. rosaceus*, etc.) were multiple brooders, other species groups (such as *S. dalli*, *S. elongatus*, *S. saxicola*, *S. semicinctus*; and *S. entomelas*, *S. flavidus*, *S. hopkinsi*, *S. ovalis*, *S. rufus*) included both single and multiple brooders.

Species maximum length did not seem to be a good predictor of multiple brooding. Though some large species, such as *S. levis* and *S. paucispinis* were multiple brooders, others (*S. melanostomus*, *S. miniatus*) were not. Conversely, though the dwarf species *S. hopkinsi* was a multiple brooder, *S. dalli* and *S. semicinctus* were not. Similarly, there was no obvious relationship with preferred depth, northern and southern affinities, or food habits.

Thus, the phenomenon of multiple brooding in northeast Pacific rockfishes is quite intriguing. Both Moser (1967a) and MacGregor (1970), reporting on research from southern California, noted multiple spawning in many of the same species (*Sebastes chlorostictus*, *S. constellatus*, *S. goodei*, *S. levis*, *S. ovalis*, *S. paucispinis*, *S. rosaceus*, and *S. rosenblatti*). Conversely, Wylie Echeverria (1987), working on most of these species off central California, found only one individual (an *S. paucispinis*) with more than one brood. Further north, Leaman<sup>5</sup> found no multiple brooding in British Columbia rockfishes.

What might account for this discrepancy? A genetic component might be involved. Rockfish larvae are pelagic and the pelagic environment in the southern California Bight may be less predictable from year to year than that to the north (Boehlert and Kappenman 1980). There may have been selec-

<sup>5</sup>B. Leaman, Department of Fisheries and Oceans, Biological Sciences Branch, Biological Station, Nanaimo, British Columbia V9R 5K6, Canada, pers. commun.

**Table 7.**

**Occurrence of multiple brooding in *Sebastes* spp. off southern California. Listed by taxonomic order (Barsukov 1981).**

Species	Multiple brooding
<i>melanostomus</i>	no
<i>miniatus</i>	no
<i>levis</i>	yes
<i>rosaceus</i>	yes
<i>ensifer</i>	yes
<i>constellatus</i>	yes
<i>rosenblatti</i>	yes
<i>chlorostictus</i>	yes
<i>goodei</i>	yes
<i>paucispinis</i>	yes
<i>ovalis</i>	yes
<i>rufus</i>	yes
<i>hopkinsi</i>	yes
<i>entomelas</i>	no
<i>flavidus</i>	no
<i>elongatus</i>	yes
<i>semicinctus</i>	no
<i>dalli</i>	no
<i>saxicola</i>	no

tion for females which extend their spawning season through multiple brooding—thereby increasing the chances of larvae encountering optimal conditions.

However, this scenario seems unlikely for at least some species. For instance, tagging studies of *S. paucispinis* (Hartmann 1987) indicate that this species may travel extensively, from southern to central California. If this phenomenon were genetically programmed, we would expect to see some nominal amount of multiple brooding in *S. paucispinis* off central California. However, as noted before, this is an extremely rare occurrence. Moreover, we saw no evidence (in the form of discrete ova size classes) of additional egg production during the course of a spawning season. We believe all eggs to be spawned during a season are produced at the beginning of that season.

Hence, we believe a more reasonable hypothesis is that multiple brooding in offshore rockfishes in the southern California Bight is primarily a response to an environmental factor, most likely food availability before or during egg development.

Offshore rockfish prey primarily on such planktonic prey as euphausiids and pelagic tunicates as well as small fishes (e.g., juvenile rockfishes and hake, anchovies and lanternfish) and squid. Guillemot et al. (1985) discuss the possibility that relative to southern California, there is more food available in central California over a shorter time period, during the intense summer upwelling. In southern California, though prey

may not reach the peak abundances of further north, they may remain available for longer periods. If this is the case, then southern California rockfish may not find enough food during egg development to bring all eggs up to maturation simultaneously. Rather, they must continue feeding on less abundant, but still available prey, in order to bring up a second brood.

In an ongoing study, we have found no evidence of multiple brooding in the inshore rockfishes (*Sebastes atrovirens*, *S. carnatus*, *S. chrysomelas*, and *S. rastrelliger*) of the southern California Bight, fishes living in water less than about 30 m. These species feed primarily on substrate-oriented invertebrates, prey not as susceptible to seasonal availability as the more patchy, more upwelling-linked prey of deeper water species. This reinforces the possibility that multiple brooding is a response to insufficient food during egg maturation.

### Gonadosomatic Indices

Gonadosomatic indices (Fig. 9) were computed for all species. Peak gonad weights as percentages of body weights varied with season among species, paralleling insemination and parturition months. Maximum GSI's for females ranged from 25.54 (*Sebastes rosenblatti*) to 8.23 (*S. flavidus*) and minimums from 2.92 (*S. levis*) to 0.02 (*S. chlorostictus*) percent. Maximum male GSI's were less, ranging from 7.27 (*S. paucispinis*) to 0.60 (*S. ensifer*), with minimums from 0.18 (*S. semicinctus*) to 0.01 (many species) percent (Table 8). The length of time between peak testes and ovaries GSI's varied between species, from 2 to 6 months. Resting phases, where gonads were at their smallest, ranged from 3 to 7 months for both females and males. We found no relationship between any of these and such factors as species relationships, maximum sizes, adult depth preferences, and degree of substrate associations.

### Spawning Seasons

Spawning seasons (months of larval extrusion) varied widely among the 19 species. In general, most species spawned in late winter and early spring, though there was some spawning throughout the year (Table 9, Fig. 10). Fewest species (3) exhibited eyed larvae in August. Peak spawning months (defined as those in which the highest percentage of females carried eyed larvae) were also in late winter and spring (Fig. 10). No spawning peaks occurred in any species between June and October. Spawning season duration (Fig. 11) ranged from 2 (*Sebastes flavidus*) to 10 months (*S. paucispinis*). Within a species, larger females tended to begin spawning earlier in the season (e.g., *S. flavidus*, Table 10).

There were no apparent relationships between optimum habitat depth, maximum length, and midwater or benthic affinity (severally) and spawning season, length of spawning period, and peak spawning month. However, peak spawning periods do seem to be similar among closely-related species (Table 9). In particular, species in the *Sebastomus* subgenera

(*chlorostictus*, *constellatus*, *ensifer*, *rosaceus*, and *rosenblatti*) seem quite distinct, with most of their spawning occurring later in the year than almost any other group.

Comparing our data to Wyllie Echeverria (1987), we noted substantial differences in the onset and close of spawning seasons, spawning season length, and peak spawning periods between rockfishes in southern and central/northern California (Fig. 11). In almost all species (12 of 15), fishes in the southern California Bight had longer seasons (1 to 7 additional months) than did those in central/northern California, associated with multiple spawning in the south. Two species (*Sebastes entomelas* and *S. flavidus*) exhibited longer seasons off central/northern California, while *S. rufus* showed no difference.

Fishes tended to begin spawning earlier in the southern California Bight (12 of 15 species) with onset of parturition coinciding between areas in three species. In no case did the more northerly fishes begin to spawn earlier. Peak spawning months also tended to be earlier in the southern California Bight (9 of 15 species).

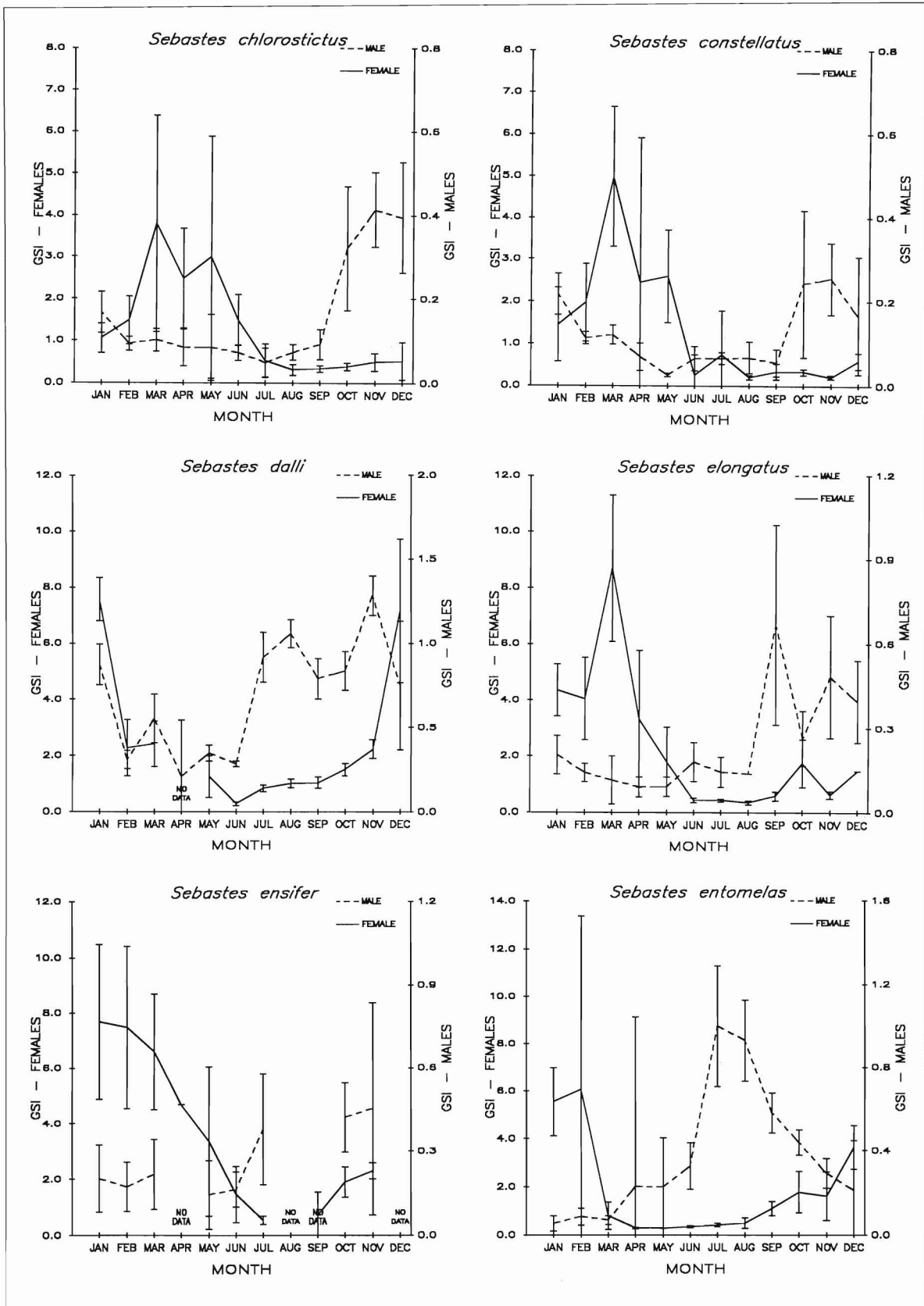
Males of most rockfish species also exhibited peak spermatogenesis earlier off southern California. Utilizing the peak months of male gonadosomatic indices (Fig. 9) to indicate peak spermatogenesis, we compared our data with those of Wyllie Echeverria (Table 11). Of the 13 species in common, 12 had earlier spermatogenesis peaks off southern California, while one (*S. levis*) peaked at either the same month or one month later.

Though the longer seasons in the southern California Bight may be due in part to multiple brooding, this cannot be the full explanation, as the single-brooding *S. melanostomus* and *S. miniatus* also exhibited considerably longer seasons off southern California.

Earlier spawning of southern California Bight rockfish may be due to earlier availability of upwelling-derived prey. Upwelling peaks off southern Baja California in February–March, reaching a maximum off Oregon during August–September. The timing of spawning and recruitment of at least one major rockfish prey, the euphausiid *Euphausia pacifica*, develops along the same northerly path (Brinton 1976). If the abundance of other prey, such as small fishes feeding on recruiting zooplankton, also increases with upwelling, food necessary for egg development may become available to southern California rockfishes earlier in the year, leading to earlier egg maturation.

### Length at 50% Maturity

To ascertain length at 50% maturity, we graphed the percentage of mature fish against length and noted the 50% length (tabulated in Table 12). We found between-sex differences in length at 50% maturity in seven (*Sebastes constellatus*, *S. flavidus*, *S. goodei*, *S. miniatus*, *S. paucispinis*, *S. rufus*, and *S. entomelas*) of the 17 species examined (Table 13). In all cases where differences existed, males matured at a smaller



**Figure 9.** Seasonal changes in the gonadosomatic indices (GSI = gonad weight as a percentage of total body weight) of female and male *Sebastes* from the southern California Bight.

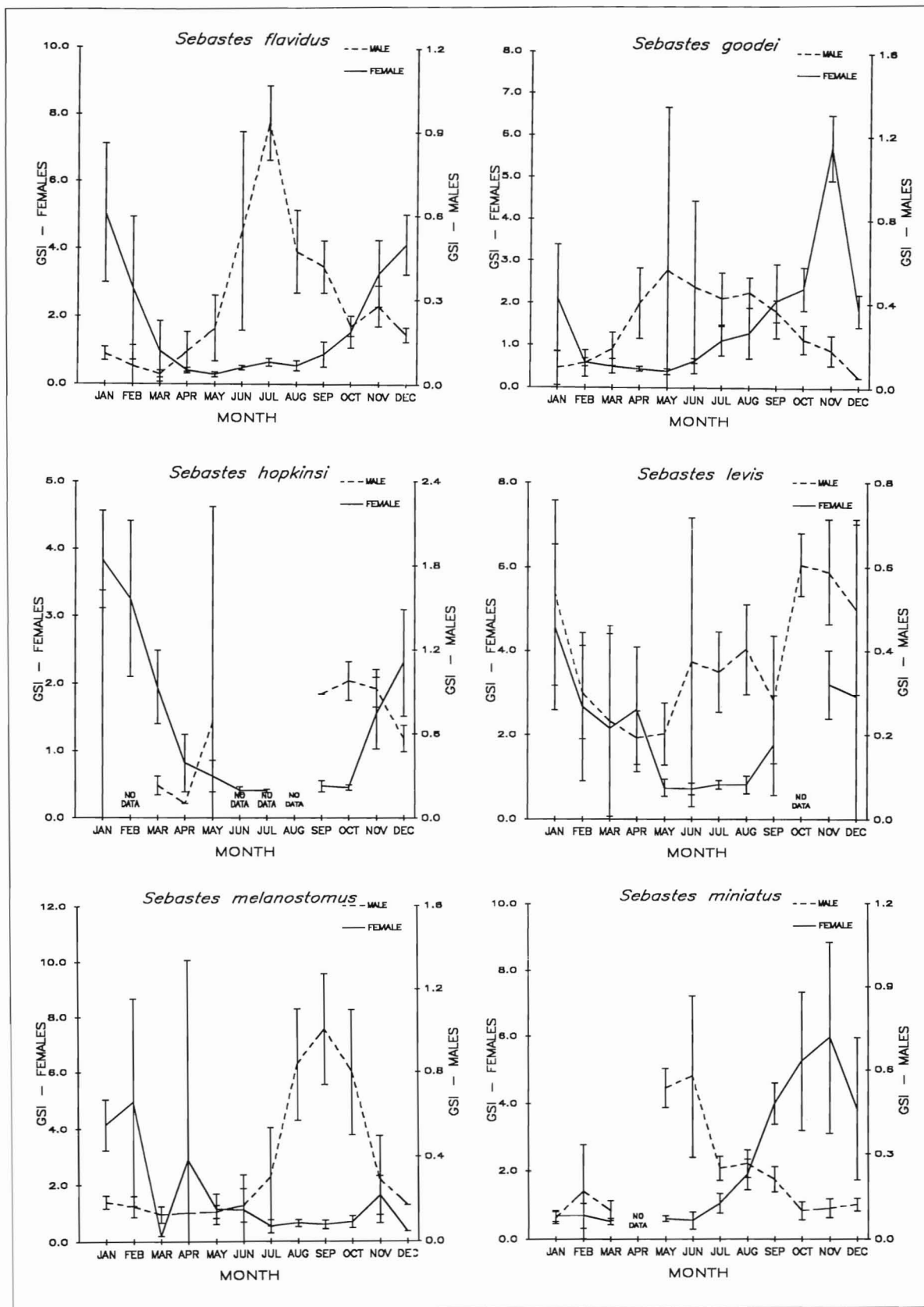


Figure 9.—Continued

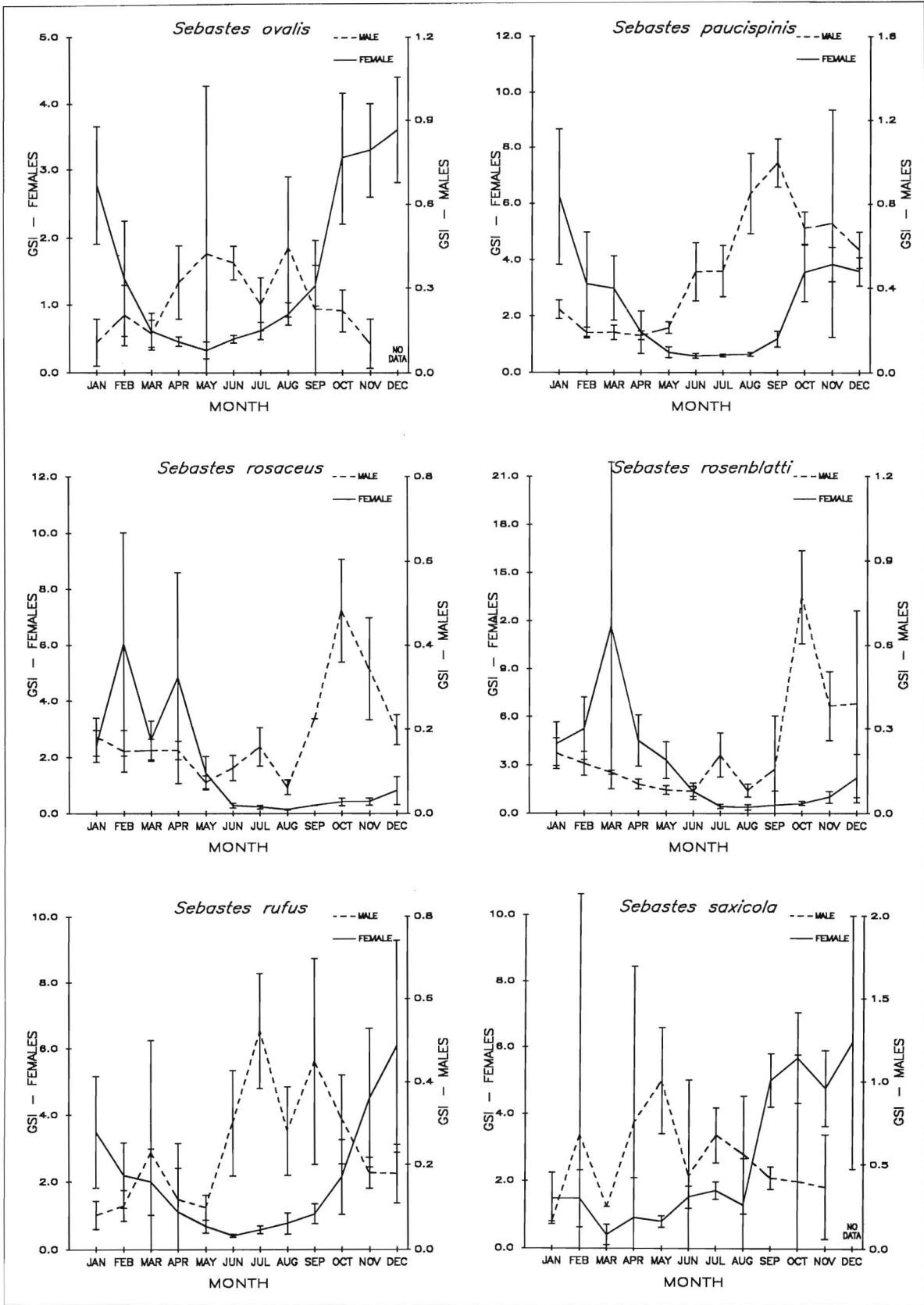


Figure 9.—Continued

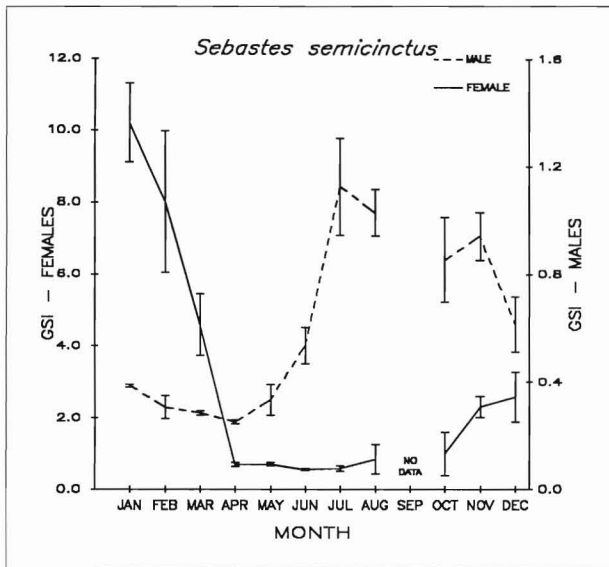


Figure 9.—Continued.

Table 9.

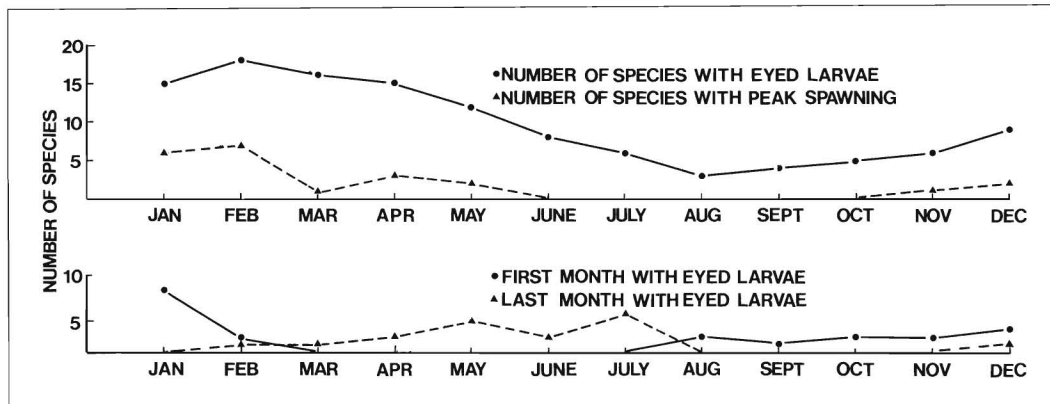
Peak spawning month(s) for *Sebastes* from the southern California Bight collected 1980–1987. Listed by taxonomic order (Barsukov 1981).

Species	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
<i>melanostomus</i>				x			
<i>miniatus</i>	x						
<i>levis</i>			x				
<i>rosaceus</i>							x
<i>ensifer</i>					x		
<i>constellatus</i>							x
<i>rosenblatti</i>						x	
<i>chlorostictus</i>						x	
<i>goodei</i>	x	x					
<i>paucispinus</i>			x				
<i>ovalis</i>			x	x			
<i>rufus</i>			x				
<i>hopkinsi</i>			x	x			
<i>entomelas</i>				x			
<i>flavidus</i>				x			
<i>elongatus</i>					x		
<i>semicinctus</i>				x			
<i>dalli</i>				x			
<i>saxicola</i>	x						

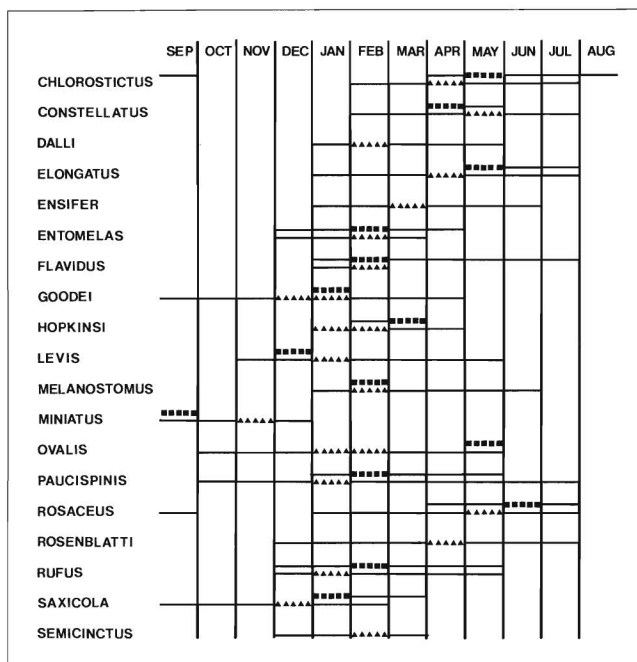
Table 8.

Maximum and minimum gonadosomatic indices of 19 rockfish species from southern California. The left data set under each sex refers to those months when there were developing gonads, the right set to the postreproductive period.

Species	Males		Females	
	Max.	Min.	Max.	Min.
<i>chlorostictus</i>	Sept.–June	Feb.–Aug.	Aug.–Nov.	Dec.–July
	0.95 0.01	0.29 0.02	1.79 0.02	10.69 0.02
<i>constellatus</i>	Oct.–Mar.	Apr.–Sept.	Jan.–July	Aug.–Dec.
	0.77 0.02	0.52 0.01	11.29 0.04	1.35 0.04
<i>dalli</i>	July–Feb.	Mar.–June	Nov.–May	June–Oct.
	2.06 0.21	1.03 0.13	16.02 0.22	3.40 0.20
<i>elongatus</i>	Sept.–Feb.	Mar.–Aug.	Dec.–May	June–May
	1.15 0.07	0.52 0.04	22.11 0.15	7.33 0.15
<i>ensifer</i>	June–Nov.	Dec.–May	Jan.–June	July–Dec.
	0.60 0.12	0.39 0.08	11.74 0.29	3.63 0.21
<i>entomelas</i>	June–Dec.	Jan.–May	Nov.–Mar.	Apr.–Oct.
	1.86 0.01	0.46 0.04	9.99 0.15	6.28 0.21
<i>flavidus</i>	June–Dec.	Jan.–May	Nov.–Feb.	Mar.–Oct.
	1.38 0.05	0.35 0.01	8.23 0.18	4.57 0.04
<i>goodei</i>	Apr.–Dec.	Nov.–Mar.	Sept.–Feb.	Mar.–Aug.
	0.74 0.10	0.30 0.04	11.18 0.39	5.35 0.17
<i>hopkinsi</i>	Mar.–May	Sept.–Dec.	Nov.–Mar.	Apr.–Oct.
	— —	— —	12.87 0.19	5.88 0.16
<i>levis</i>	June–Jan.	Feb.–May	Nov.–Apr.	May–Oct.
	1.09 0.02	1.09 0.03	11.43 0.15	3.02 2.92
<i>melanostomus</i>	July–Nov.	Dec.–June	Jan.–July	July–Dec.
	2.23 0.03	0.45 0.02	12.52 0.13	2.79 0.24
<i>miniatus</i>	May–Sept.	Oct.–Apr.	Aug.–Dec.	Jan.–July
	1.69 0.01	0.30 0.02	17.82 0.12	2.56 0.07
<i>ovalis</i>	Apr.–Oct.	Nov.–Mar.	Sept.–Mar.	Apr.–Aug.
	0.79 0.05	0.47 0.04	10.38 0.13	1.96 0.06
<i>paucispinus</i>	June–Jan.	Feb.–May	Oct.–Apr.	May–Sept.
	7.27 0.02	0.79 0.01	18.64 0.03	10.42 0.03
<i>rosaceus</i>	July–Dec.	Jan.–June	Dec.–May	June–Nov.
	1.09 0.03	0.71 0.03	20.19 0.04	1.21 0.05
<i>rosenblatti</i>	Sept.–Feb.	Mar.–Aug.	Jan.–June	July–Dec.
	1.23 0.02	0.43 0.01	25.54 0.07	4.67 0.14
<i>rufus</i>	June–De.	Jan.–May	Oct.–Mar.	Apr.–Sept.
	1.28 0.01	1.12 0.01	14.74 0.11	4.18 0.14
<i>saxicola</i>	Apr.–Oct.	Nov.–Mar.	Aug.–Dec.	Jan.–July
	3.23 0.16	1.06 0.16	16.73 0.27	10.96 0.25
<i>semicinctus</i>	May–Dec.	Jan.–Apr.	Nov.–Mar.	Apr.–Oct.
	1.82 0.21	0.87 0.18	24.81 0.11	8.13 0.18



**Figure 10.**  
A summary of spawning patterns of 19 *Sebastes* species from the southern California Bight.



**Figure 11.**  
Spawning months of 19 *Sebastes* species from the southern California Bight (from present study) and 15 species from central and northern California (Wyllie Echeverria 1987). ▲ represent peak spawning months in the southern California Bight, ■ = peak spawning off central and northern California.

**Table 10.**  
Percentages of female *Sebastes flavidus* in each gonad state, by total length, during January and February 1980-1987.

Month and total length (cm)	Vitello-genesis	Fertilized	Eyed	Spawnd	Resting
January					
30.6-40.5	100				
40.6-50.5	81	19			
50.6-60.5		29	43	29	
February					
30.6-40.5		33	67		
40.6-50.5	10		50	30	10
50.6-60.5				29	71

**Table 11.**  
A comparison of the principal months of spermatogenesis of 13 species of male rockfish between southern California (this paper) and central/northern California (Wyllie Echeverria 1987).

Species	Months of spermatogenesis		Month(s) Difference
	This paper	Wyllie Echeverria (1987)	
<i>chlorostictus</i>	Nov.	Feb.	3
<i>constellatus</i>	Nov.	Dec.	1
<i>entomelas</i>	July	Oct.	3
<i>flavidus</i>	July	Sept.	2
<i>goodei</i>	May	Oct.	5
<i>hopkinsi</i>	Oct.?	Dec.	2?
<i>levis</i>	Oct.	Sept.-Oct.	0 (-1)
<i>melanostomus</i>	Sept.	Nov.	2
<i>miniatus</i>	June	July	1
<i>ovalis</i>	Aug.	Nov.	3
<i>paucispinis</i>	Sept.	Oct.	1
<i>rosaceus</i>	Oct.	May	7
<i>rufus</i>	July	Nov.	4



**Table 12.**

Size at 1st, 50%, and 100% maturity of 19 *Sebastes* species taken from the southern California Bight.

Species	Male total length			Female total length		
	1st	50%	100%	1st	50%	100%
<i>chlorostictus</i>	20	22	28	15	22	32
<i>constellatus</i>	18	19	27	21	22	29
<i>dalli</i>	7	9	14	9	9	10
<i>elongatus</i>	15	18	26	16	19	25
<i>entomelas</i>	26	32	37	34	35	36
<i>flavidus</i>	31	32	37	33	36	38
<i>goodei</i>	27	28	33	28	30	32
<i>hopkinsi</i>	13	13	16	14	14	15
<i>levis</i>	34	44	48	42	43	52
<i>melanostomus</i>	33	34	38	31	34	38
<i>miniatus</i>	32	35	37	31	37	47
<i>ovalis</i>	23	24	29	24	25	32
<i>paucispinis</i>	35	35	42	36	36	44
<i>rosaceus</i>	14	15	19	12	15	18
<i>rosenblatti</i>	23	30	32	16	28	34
<i>rufus</i>	28	31	38	31	36	39
<i>saxicola</i>	9	10	16	9	10	17
<i>semicinctus</i>	10	11	15	10	11	14

length. Wyllie Echeverria (1987) also reported on maturity and length in rockfishes and also found some between-sex differences in maturation length. Unfortunately, our technique differed from hers and comparisons are inappropriate.

Thus, it appears that some species do show sexual dimorphism in length at 50% maturity. Wyllie Echeverria's results also indicated that difference was most often due to males maturing at a younger age. Using either our data or Wyllie Echeverria's, there appears to be no pattern to this phenomenon related to species habitat, behavior, or maximum size. However, some closely related species do show similar patterns (i.e., *S. goodei*-*S. paucispinis*, *S. chlorostictus*-*S. rosenblatti*, *S. saxicola*-*S. semicinctus*).

It is not clear why males of some species mature at an earlier length and/or age. Theories which seem appropriate to other fish families, such as high extrinsic male mortality, slow male growth rates before maturity or sperm competition and sperm storage (Warner and Harlan 1982; Stearns and Koella 1986) do not appear relevant to rockfishes.

### Fecundity

The relationships between egg production and body length of 16 *Sebastes* species are illustrated in Figure 12. Three species—*S. ensifer*, *S. melanostomus*, and *S. ovalis*—were not included in our analyses, as we did not have enough samples, over a representative female size range. Within all species, fecundity increased with increasing length and the relationship between egg number and body length best fit the equation  $F = aL^b$ . Minimum fecundities (from estimates of individual fish) ranged from 1,245 eggs in *S. saxicola* to

**Table 13.**

A between-sex comparison of length at 50% maturity in *Sebastes* taken off southern California (this study) and central/northern California (Wyllie Echeverria 1987). "Male < Female": males mature at a smaller length than females; "Male = Female": no size difference between sexes; "Male > Female": males mature at a longer length than females. Differences between studies are underlined.

Species	This study	Wyllie Echeverria (1987)
<i>chlorostictus</i>	Male = Female	Male = Female
<i>constellatus</i>	<u>Male &lt; Female</u>	<u>Male &gt; Female</u>
<i>dalli</i>	Male = Female	<sup>a</sup>
<i>elongatus</i>	Male = Female	Male = Female
<i>entomelas</i>	<u>Male &lt; Female</u>	<u>Male = Female</u>
<i>flavidus</i>	Male < Female	Male = Female
<i>goodei</i>	Male < Female	Male < Female
<i>hopkinsi</i>	<sup>b</sup>	<u>Male &lt; Female</u>
<i>levis</i>	Male = Female	Male = Female <sup>c</sup>
<i>melanostomus</i>	<u>Male = Female</u>	<u>Male &lt; Female</u>
<i>miniatus</i>	<u>Male &lt; Female</u>	<u>Male = Female</u>
<i>ovalis</i>	Male = Female	Male = Female
<i>paucispinis</i>	Male < Female	Male < Female
<i>rosaceus</i>	Male = Female	Male = Female
<i>rosenblatti</i>	Male = Female	<sup>a</sup>
<i>rufus</i>	<u>Male &lt; Female</u>	<u>Male = Female</u>
<i>saxicola</i>	Male = Female	Male = Female
<i>semicinctus</i>	Male = Female	<sup>a</sup>

<sup>a</sup>This species not reported upon in Wyllie Echeverria.

<sup>b</sup>No immature *S. hopkinsi* males examined in our study.

<sup>c</sup>Based on a limited sample size (n = 41).

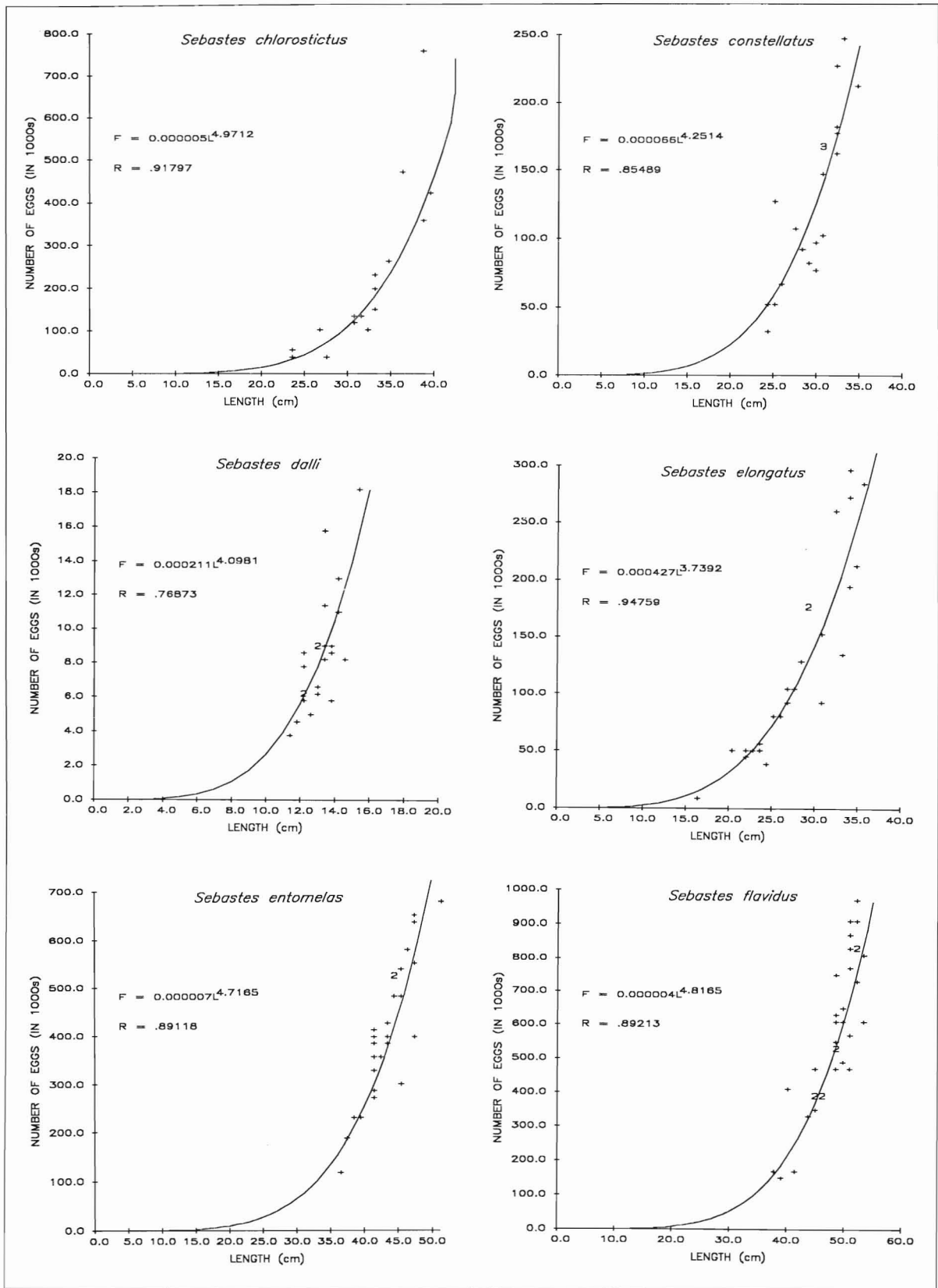
290,988 in *S. paucispinis*. Maximum numbers ranged from about 18,000 in *S. dalli* to about 2,680,000 in *S. levis* (Table 14).

We wished to ascertain whether, within the genus *Sebastes*, maximum egg production varied with maximum body length of the various species. We compared the species' maximum lengths with our estimated maximum fecundity (Fig. 13). It was apparent that a relationship does exist, again assuming the shape of a power curve.

The shape of these fecundity curves, that is how rapidly egg production increased with increasing body length, varied between species. There was no apparent correlation between the exponent *b*, a measure of rate increase, and such factors as species' maximum size, body shape, or habitat. There were some phylogenetic relationships (Fig. 14), though even some closely related species pairs (as proposed by Barsukov), such as *S. rufus*-*S. hopkinsi*, *S. miniatus*-*S. levis*, showed large differences in rates of increase.

We compared our egg production data for *S. entomelas*, *S. flavidus*, *S. goodei*, *S. miniatus*, *S. paucispinis*, and *S.*





**Figure 12.** Fecundity patterns of 16 *Sebastes* species from the southern California Bight. Not included are *S. ensifer*, *S. melanostomus*, and *S. ovalis* with too little data available.

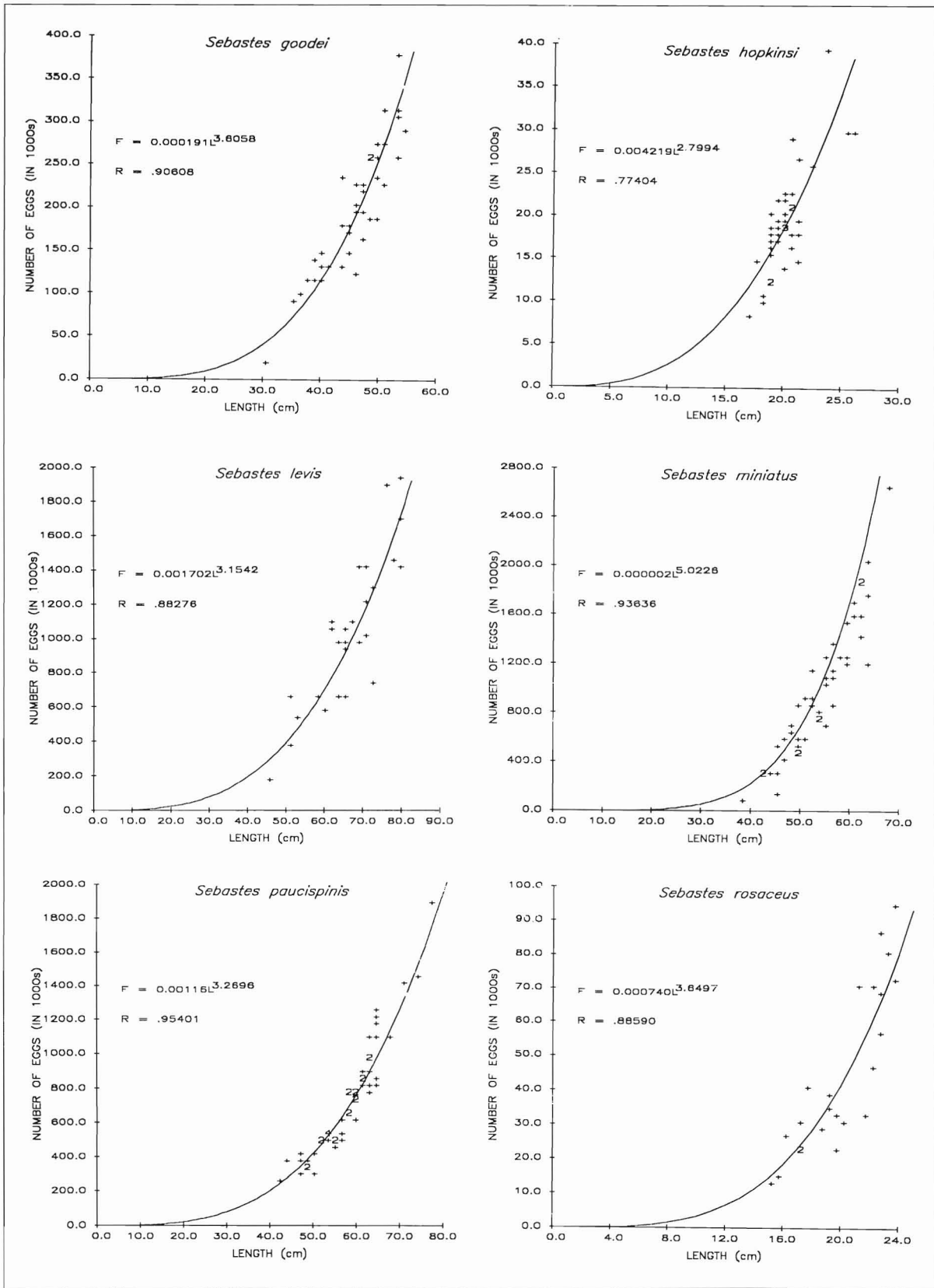


Figure 12.—Continued.

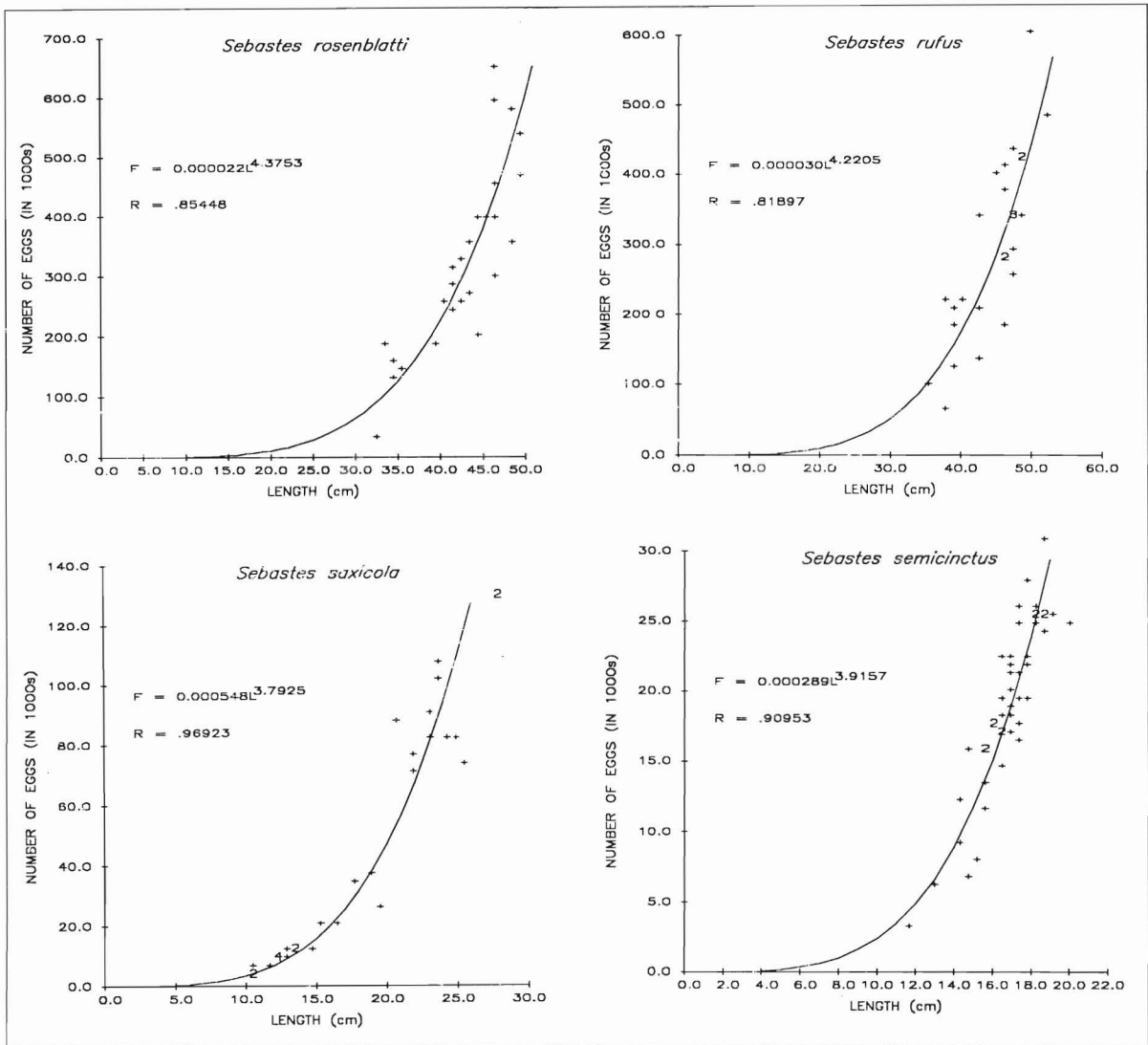


Figure 12.—Continued.

Table 14.

Maximum and minimum numbers of eggs found in 19 species of rockfish from the southern California Bight. *Sebastes ensifer*, *S. melanostomus*, and *S. ovalis* were not included in subsequent analyses, because the range of female sizes sampled was limited.

Species	N	Egg nos. (min.)	Length	Egg nos. (max.)	Length	Species	N	Egg no. (min.)	Length	Egg nos. (max.)	Length
<i>chlorostictus</i>	16	40,961	27.6	759,040	39.0	<i>melanostomus</i>	19	152,072	41.5	769,152	53.0
<i>constellatus</i>	21	32,674	24.0	227,573	32.6	<i>miniatus</i>	45	158,915	46.0	2,683,768	68.0
<i>dalli</i>	23	3,878	11.6	18,006	15.5	<i>ovalis</i>	26	61,217	33.1	160,320	39.3
<i>elongatus</i>	25	10,637	16.0	295,153	34.4	<i>paucispinis</i>	52	290,988	47.5	1,908,915	78.2
<i>ensifer</i>	19	17,018	20.0	38,403	23.0	<i>rosaceus</i>	23	12,601	15.2	95,267	23.5
<i>entomelas</i>	27	114,949	36.5	684,077	51.0	<i>rosenblatti</i>	26	30,600	32.5	655,050	46.7
<i>flavidus</i>	34	143,872	38.5	972,183	52.0	<i>rufus</i>	27	64,476	37.5	607,394	49.6
<i>goodei</i>	37	18,433	30.4	380,413	53.6	<i>saxicola</i>	33	1,245	9.5	131,382	28.0
<i>hopkinsi</i>	39	8,686	16.9	39,394	23.8	<i>semicinctus</i>	46	3,409	11.7	30,858	18.5
<i>levis</i>	27	180,840	45.5	1,925,004	80.0						

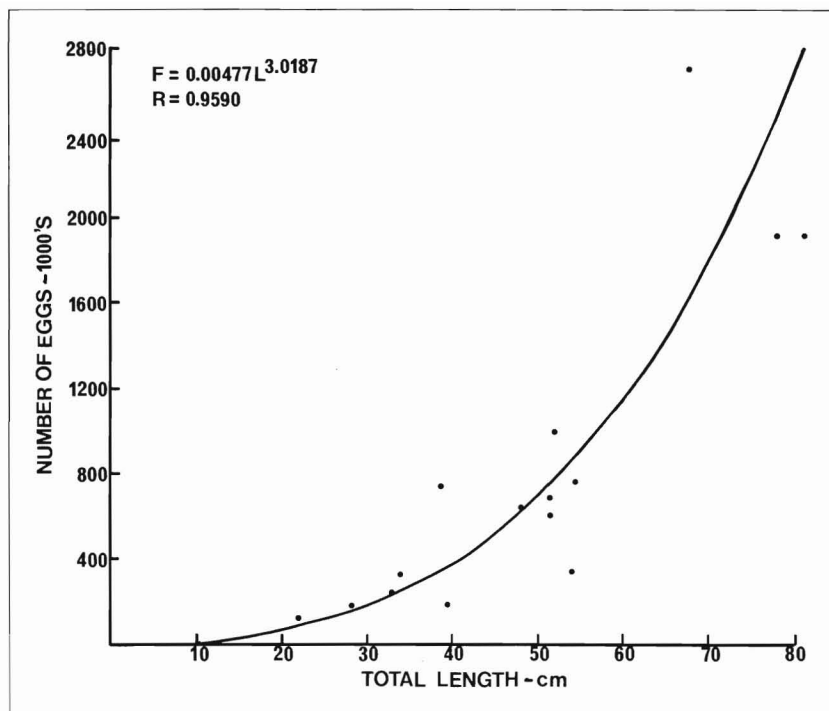


Figure 13.

The relationship between maximum egg numbers produced and maximum sizes for 16 *Sebastes* species from the southern California Bight.

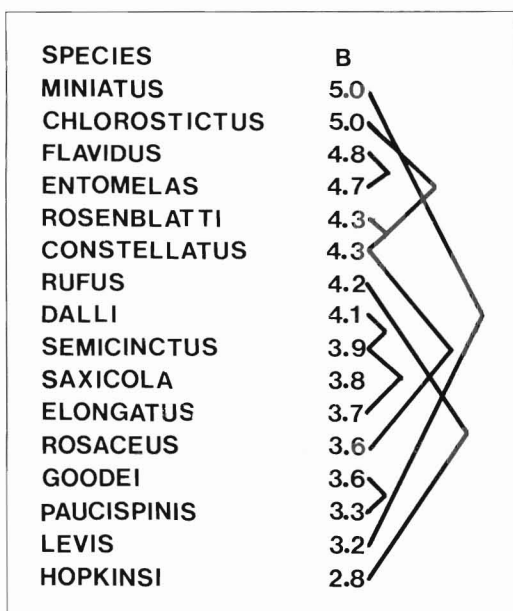


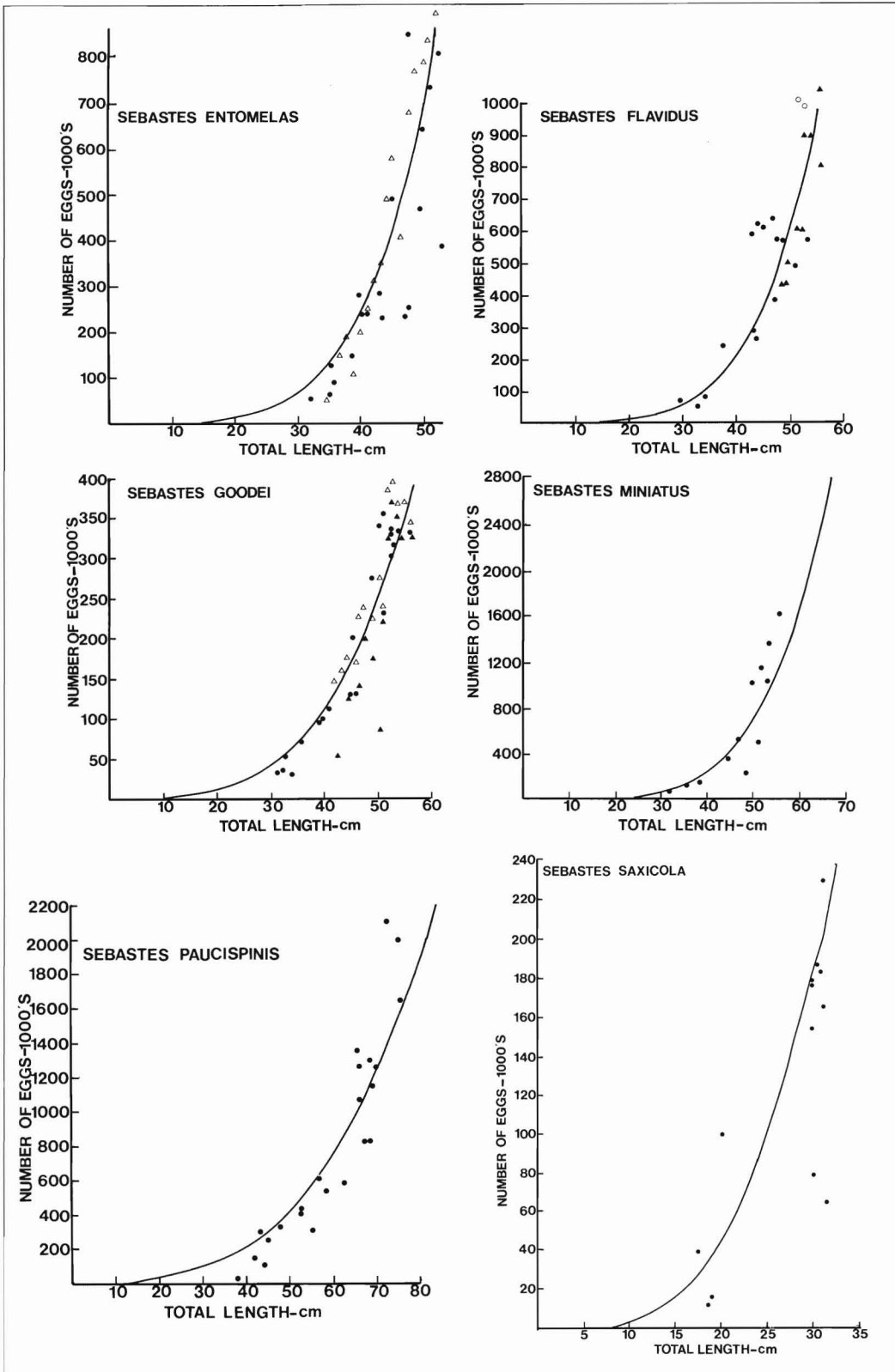
Figure 14.

The relationship between  $b$  (in the formula  $F = aL^b$  where  $F$  = fecundity and  $L$  = total length) among 16 *Sebastes* species. Closely related species pairs, from Barsukov (1981), are linked.

*saxicola* with results from other studies conducted from central California to Vancouver Island (Fig. 15), first converting the fork lengths of *S. entomelas*, *S. flavidus*, and *S. goodei* reported by Gunderson et al. (1980) and Boehlert et al. (1982) to total lengths, using the conversion factors of Echeverria and Lenarz (1984).

We saw few differences between our data and other studies on *S. flavidus*, *S. miniatus*, and *S. paucispinis*. However, our data implied greater egg production per body length off southern California than off central/northern California for *S. entomelas* (Phillips 1964), *S. goodei* (Gunderson et al. 1980), and *S. saxicola* (Phillips 1964).

These differences may be the result of methodological differences between studies. However, our egg numbers were not consistently higher when compared to other studies. That is, though our *S. entomelas* produced more eggs per body length than did those reported by Phillips, such was not the case for *S. miniatus*. Thus location may also play a role. Some evidence for geographical variation comes from Gunderson et al.'s observation that *S. goodei* from the Pt. Reyes area off California were less fecund than those from around Pt. Arena, about 96 km to the north. Boehlert et al. also noted that the *S. entomelas* off Oregon produced more eggs than those found in Phillips' study off central and northern California. Our results seem to fall in between the data of Gunderson et al. and Phillips for *S. goodei* and those of Boehlert et al. and Phillips for *S. entomelas*.



**Figure 15.**  
 A comparison of the fecundity of six *Sebastes* species with previous fecundity data. The six *Sebastes* species and their respective data are 1) *S. entomelas*: Phillips (1964)—central and northern California (●) and Boehlert et al. (1982)—Oregon (Δ); 2) *S. flavidus*: Phillips (1964)—central and northern California (●), Snytko and Borets (1972)—Oregon-Vancouver (○) and Gunderson et al. (1980)—central California-Oregon (▲); 3) *S. goodei*: Phillips (1964)—Central and northern California (●), Gunderson et al. (1980)—Pt. Reyes, northern California (▲) and Pt. Arena, northern California (Δ); 4) *S. miniatus*: Phillips (1964)—central and northern California (●); 5) *S. paucispinis*: Phillips (1964)—central and northern California (●); and 6) *S. saxicola*: Phillips (1964)—central and northern California (●).

## Summary

Those rockfish studied in the southern California Bight may be grouped by depth preference, a shallower group (most abundant from 60–149 m) and a deeper one (common from 150–239+ m). Juveniles of most species studied were most abundant in waters shallower than preferred adult depths. Scarcity of northern species in suitable southern habitats may be due to recruitment limitations reflecting variability in larval transport or unsuitable environmental parameters (such as temperature) for larvae.

Rockfishes are generally long-lived and slow growing, the exceptions being several dwarf species, which have short life spans and which quickly reach maximum lengths. Similarly, most species are relatively old and large at first maturity. Growth rate comparisons between conspecifics from the southern California Bight and more northerly areas yield mixed results. Of six species compared, three exhibit geographic variation in growth rate, with the northern group growing faster than the southern.

Many species in the southern California Bight are likely to spawn more than once per year (a rare occurrence to the north) and have longer parturition seasons with earlier onsets than do conspecifics to the north. Multiple spawnings per season may be the result of a less intense and temporally concentrated upwelling season in southern California, yielding less prey and preventing females from maturing all eggs simultaneously.

Fecundity varied widely between species, with the largest species producing the most eggs. Summarizing all species, there was a relationship, based on the power curve, between maximum length and maximum eggs produced. Some variation in fecundity was noted between some conspecifics from southern California and central-northern California.

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