Abstract. – Young-of-the-year pelagic juvenile rockfish (genus *Sebastes*) were collected during annual surveys in the spring and early summer, 1983–88, off the central California coast. Growth rates and back-calculated birthdate distributions of five species (shortbelly rockfish *S. jordani*, bocaccio *S. paucispinis*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus*) were estimated from daily otolith increments.

Interspecific variation in growth rates was evident, with bocaccio exhibiting the fastest growth (0.56–0.97 mm/day) and yellowtail rockfish growing slowest (0.19–0.46 mm/day). Growth rates of all species varied among years. Comparisons of annual growth performance, measured by predicting standard length at a selected standard age, revealed strong positive interannual covariation among the five species studied; in general, growth was relatively good in 1987 and was poor in 1985.

Back-calculated birthdate distributions also revealed strong positive interannual covariation among these species; most distributions were unimodal. The years 1985 and 1988 were characterized by distributions that were centered early in the year; whereas in 1986 (and possibly in 1983) these distributions occurred later.

Interannual Variation in Growth Rates and Back-Calculated Birthdate Distributions of Pelagic Juvenile Rockfishes (*Sebastes* spp.) off the Central California Coast

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Understanding recruitment fluctuations and the interplay of factors affecting the establishment of year-class strength is the single most challenging issue in fisheries today (Rothschild 1986). In particular, rockfishes of the genus *Sebastes* are known to exhibit large fluctuations in recruitment (Leaman and Beamish 1984), wherein a single dominant year-class can sustain a fishery for a number of years. Rockfishes are an important component of the west coast groundfish fishery, with combined 1988 landings of 35,000 MT (PFMC 1989). Historically, rockfish stock assessments have relied almost exclusively on catch-at-age data (e.g., Hightower and Lenarz 1989); such analyses do not perform well in the absence of auxiliary information (e.g., an index of pre-recruit abundance). Knowledge of mechanisms affecting first-year survival could improve our ability to predict recruitment, which in turn could have major implications to the management of this group (Deriso et al. 1985, Methot 1989, but see Walters 1989).

In some situations starvation and food limitation have been shown to control larval abundance (Lasker 1981), although predation is believed to be important in others (reviewed in Sissenwine 1984, Bailey and Houde 1989). In either case, if mortality decreases with increasing size (Miller et al. 1988), larval and pelagic juvenile growth rates can have a major impact on survivorship during the first year of life. This is because fast-growing fish are exposed to high mortality rates for shorter periods of time (Houde 1987).

As part of an ongoing study to monitor annual fluctuations in the abundance of young-of-the-year pelagic juvenile rockfishes inhabiting the coastal waters off central California, the growth of five species (shortbelly rockfish *S. jordani*, bocaccio *S. paucispinis*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus*) was assessed through the study of otolith daily-increment microstructure formed during the pelagic larval and juvenile life stages (Jones 1986). Intraspecific differences in growth performance over the period 1983–88 were then examined statistically and trends were compared among species.

Birthdate frequency distributions of the fish that survived from birth to the time of sampling were back-calculated from aged subsamples, length measurements, and known dates of capture (Bolz and Lough 1983). These projected distributions were compared intraspecifically among years to evaluate whether the preponderance of juvenile survivors

came from larvae that were extruded early or late in the season. Birthdate distributions were also compared among species to reveal the extent of interspecific covariation in annual survivorship.

Methods

Midwater trawl collections

Annual 30-day cruises aboard NOAA's R/V *David Starr Jordan* began in 1983 and were conducted during late spring (May–June), a time when most pelagic-stage juvenile rockfishes are identifiable to species, but prior to their settling to nearshore and benthic habitats. The sampling gear used was a midwater trawl with a 26 m headrope and 169 m² net opening, equipped with a 0.945 cm (3/8") inner liner. A standard haul consisted of a 15-min nighttime tow at a depth of 30 m covering a distance of roughly 1 km. Additional tows were made at other depths (i.e., 10 and 100 m) as time and bottom topography permitted.

From 1983 to 1985, the survey was designed to sample from nearshore waters out to a distance of 55 km (30 nmi) along transects located at 31 km intervals perpendicular to the coast. Sampling began at Pt. Sur (36°18′N) and continued northward until completion of the cruise. In 1986, the sampling design was modified to permit three "sweeps" through a study area bounded by Cypress Pt. (36°35′N) and Pt. Reyes (38°10′N) (Table 1). Four additional cruises were conducted in April of 1985–88. These cruises ranged from 5 to 10 days in length and were limited to the Gulf of the Farallones (1985–86), or covered one complete sweep of the study area (1987–88). Trawls were conducted at 5–7 stations per night along 7 transects during a sweep. Wyllie Echeverria et al. (1990) discuss the survey methodology in greater detail.

As many as 24 species of pelagic-stage juvenile rockfish were collected during a single cruise. All specimens were tentatively identified and frozen at sea. On rare occasions catches were subsampled when they were too large to enumerate. After 1987, length compositions of large trawl catches were based upon expansion from measured subsamples of each species.

Otolith preparation and analysis

In the laboratory, species identifications were confirmed and fish were measured to the nearest 1.0 mm standard length (SL). For this study, the most important species were selected for age determination. A subsample of juveniles, measured to the nearest 0.1 mm, was selected for daily age analysis based on the size range encountered on each cruise. Specimens were

Table 1

Summary of sampling dates for juvenile rockfish cruises. Asterisks indicate trawls limited to Gulf of the Farallones.

Year	Sweep	Dates	Stations
1983	1	8–24 June	18
1984	1	12–27 June	25
1985	1*	10–16 April	18
	2	31 May–30 June	37
1986	1*	13–22 April	30
	2	3–11 June	33
	3	11–18 June	28
	4	20–25 June	28
1987	1	10–20 April	34
	2	23 May–1 June	33
	3	2–12 June	34
	4	12–21 June	33
1988	1	16–22 April	28
	2	22–31 May	33
	3	2–9 June	33
	4	11–18 June	31

selected at 0.5 mm intervals from the smallest to largest. The sagittal otoliths were removed, cleaned, and adhered concave (lateral)-side-down onto glass microslides using clear nail polish. To reveal the inner microstructure, otoliths were ground with wet 300–600 grit sandpaper and etched with HCl (Brothers et al. 1976).

A compound microscope with 40 and 100× objectives was used during otolith examination. Immersion oil was applied to the otolith, which was illuminated with polarized light. A closed circuit television camera was mounted on top of the microscope and the image was relayed to a video monitor. A digitizer with a precision of 0.13 μm was interfaced with the monitor and a microcomputer to accurately measure and record daily increments (e.g., McGowan et al. 1987). In combination, the equipment yielded an 800–2000× on-screen magnification range.

A computer program assisted in recording the distance from the nucleus to each increment, measured along the growth axis running from the focus to the postrostral margin. On occasion the periodic bipartite microstructure of daily increments was difficult to resolve within short (~50 μm) segments of the otolith. In these cases their number and width were interpolated by averaging the widths of the rings immediately preceding and following that segment, and dividing the mean into the segment length. Usually such averaging involved only about 10% of the total increments observed. In most cases (~80%), only one otolith was used unless it was damaged or destroyed

during preparation. Otoliths were read only once due to the destructive nature of the preparation method.

A photomicrograph of a shortbelly rockfish otolith (Fig. 1) shows increments that we interpreted to be produced daily. A dark ring followed by narrow, closely spaced rings was used as the starting point for enumeration of increments. The time of first increment formation is species-specific. Cases are known where fish larvae form the first increment at hatch, yolksac absorption, first feeding, or at other times (Jones 1986). Penney and Evans (1985), in their study of larval redfish (*Sebastes* spp.) off Newfoundland, noted a "heavy ring composed of a wide, translucent band followed by a prominent, high-contrast dark band" which they used as the first increment for age determination. Since all pre-extrusion larvae lacked the dark band and all planktonic larvae possessed it (some as young as 1 day), they assumed that it formed at the time of extrusion. Structurally, their extrusion check was quite similar to the marks seen in this study (Fig. 1). They, like us, also observed a number of thin, weakly expressed "pre-extrusion rings" laid down prior to the first increment (see also Campana et al. 1987). There are instances in which small (~4.8–5.0 mm) field-caught planktonic larvae of shortbelly rockfish lack the conspicuous first increment (T. Laidig, SWFC Tiburon Lab., pers. commun.). Faced with this uncertainty, we conclude that the first increment used in our counts forms some time between extrusion and first feeding. The distance of this first ring from the center of the focus varied among species (i.e., 12–17 μm), but was consistent within a species. The first few increments laid down after this early check ring typically were about 0.5 μm in width and they increased in size thereafter.

Several lines of evidence indicate that the periodicity of otolith increments we counted was daily. For one, all back-calculated birthdate distributions fell within known annual parturition (spawning) seasons (Wyllie Echeverria 1987, MacGregor 1986). In addition, results from a separate study that sequentially sampled larval and juvenile shortbelly rockfish in 1989 showed that one increment was deposited each day from May to June (Laidig et al. In press). Lastly, Yoklavich and Boehlert (1987) validated the existence of daily growth increments in juvenile *S. melanops* using autoradiography to detect injected ^{45}Ca, as well as by tetracycline injection.
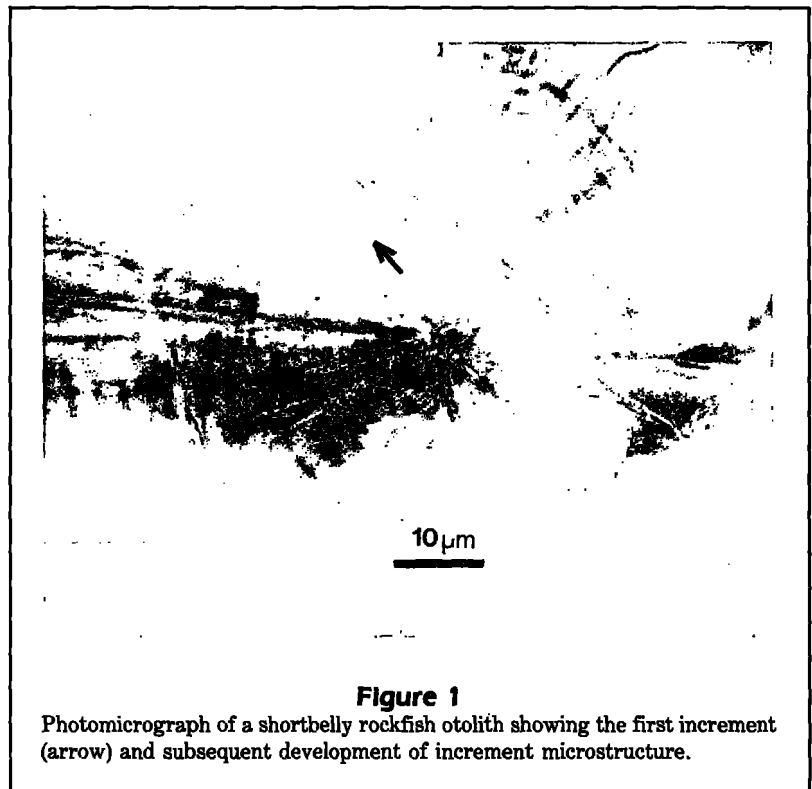

Figure 1
Photomicrograph of a shortbelly rockfish otolith showing the first increment (arrow) and subsequent development of increment microstructure.

Under the assumption that one increment was produced each day, growth rate was measured by regressing SL (mm) against estimated age (days). Analysis of covariance was used to test for differences in the relationship of SL and age within and among years. When differences were found, pairwise comparisons of class means were made using the least significant difference (LSD) test (Snedecor and Cochran 1967). This test maintains the comparisonwise error rate at $a = 0.05$, but, depending on the number of means compared, increases the experimentwise probability of committing a Type I error. In addition, indices of annual growth performance were obtained by predicting standard length at a selected standard age using regression statistics from each individual year. These were evaluated using principal component analysis (Green 1978) to reveal interdependency among the data. In this analysis, species were treated as variables, years comprised cases, and components were computed from the correlation matrix.

Back-calculated birthdate distributions of the fish that survived until the time of sampling were obtained by: (1) linearly regressing age on SL using the subsample of aged fish, (2) using the regression equation obtained to estimate the age of fish sampled during May–June cruises only, (3) back-calculating to the calendar date of first increment formation by differ-

ence (calendar date of capture minus age in days), and (4) aggregating the data into frequency distributions. Although with this approach some lengths were excluded, data from April cruises were not used due to the sporadic sampling (temporally and spatially) that occurred. Back-calculated birthdate distributions were compared within and among years, as well as among species.

Results

In some cases, analysis of covariance (ANCOVA) revealed statistically significant differences in the relationship of standard length and age among the various sweeps conducted within a year (i.e., bocaccio in 1987, chilipepper in 1988, widow rockfish in 1987, and yellowtail rockfish in 1986). It is notable, however, that these cases represented only 4 of the 15 species-year combinations for which data were available. Further examination of the data revealed that in one of these cases significance was due to a very small sample obtained during one sweep. Moreover, in the other three instances there was no regular pattern of either increasing or decreasing growth rate as the season progressed and the magnitude of differences was small. For these reasons a single regression equation describing the annual growth of each species was generated by pooling the age data obtained in a year, ignoring the sweep of origin.

Growth

Shortbelly rockfish There was a linear relationship between standard length (mm) and age (days) for shortbelly rockfish over the size range collected in each year during 1983–88 (Fig. 2). A simple linear growth model was fit to each year individually (Table 2). Annual estimates of pelagic juvenile shortbelly rockfish growth rate ranged from 0.524 mm/day in 1985 to 0.638 mm/day in 1983. Results from ANCOVA (Table 3) showed that significant differences (P 0.019) occurred in annual growth rates (i.e., slopes) among the six years sampled. Growth rates were relatively low in 1985 and 1986, were medium in 1984 and 1988, and were high in 1983 and 1987. To test for differences in estimates of annual growth rate, pairwise comparisons were made using LSD tests (Fig. 3).
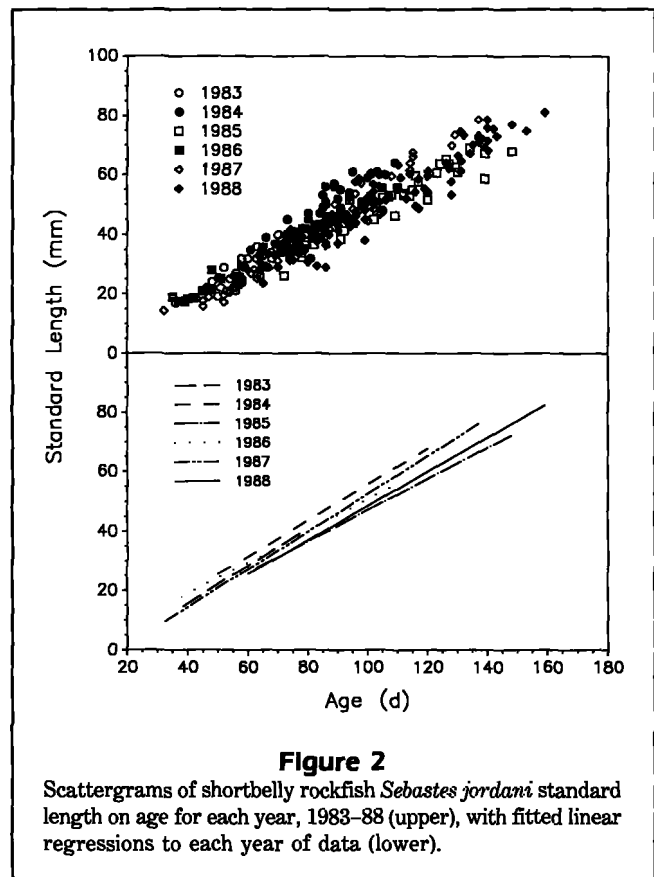

Figure 2

Scattergrams of shortbelly rockfish *Sebastes jordani* standard length on age for each year, 1983–88 (upper), with fitted linear regressions to each year of data (lower).

Table 2

Annual regression statistics for the linear growth model.

Rockfish species	Year	N	Slope (mm/d)	(SE)	Intercept (mm)	(SE)	r^2
Shortbelly	1983	32	0.6377	(0.0650)	-9.7612	(3.9387)	0.763
	1984	52	0.6025	(0.0487)	-4.4985	(4.1709)	0.754
	1985	40	0.5239	(0.0258)	-5.3236	(2.7594)	0.915
	1986	34	0.5316	(0.0199)	-2.4195	(1.4332)	0.957
	1987	53	0.6349	(0.0183)	-10.9365	(1.6089)	0.959
	1988	91	0.5735	(0.0197)	-8.7806	(2.0927)	0.905
Bocaccio	1984	50	0.6774	(0.0382)	-16.8644	(3.9810)	0.868
	1985	19	0.9737	(0.1076)	-56.4082	(12.0249)	0.828
	1986	48	0.5627	(0.0226)	-11.2418	(1.7521)	0.931
	1987	90	0.7346	(0.0209)	-24.6335	(1.9917)	0.934
	1988	53	0.7339	(0.0449)	-30.7046	(5.5366)	0.840
Chilipepper	1985	36	0.4028	(0.0336)	-2.5392	(3.3381)	0.808
	1986	27	0.3990	(0.0365)	0.3622	(2.8803)	0.827
	1987	74	0.5553	(0.0190)	-9.9867	(2.0029)	0.922
	1988	74	0.5500	(0.0239)	-16.8179	(2.7082)	0.881
Widow	1985	25	0.5647	(0.0762)	-13.9356	(8.8497)	0.705
	1986	9	0.2986	(0.0978)	13.2109	(9.5706)	0.571
	1987	45	0.6070	(0.0316)	-13.4434	(3.0735)	0.896
	1988	49	0.5696	(0.0231)	-13.2175	(2.7276)	0.928
Yellowtail	1985	18	0.1944	(0.0830)	20.4415	(9.6333)	0.255
	1986	9	0.4634	(0.0263)	-6.3261	(2.2973)	0.978
	1987	23	0.4620	(0.0655)	-1.7767	(6.9320)	0.703
	1988	24	0.4016	(0.0353)	-1.9092	(3.7319)	0.855

Table 3

Analyses of covariance testing for differences in slopes and adjusted means (i.e., elevation) of annual (1983–88) linear growth curves for each of five species of pelagic juvenile rockfish. Tests for adjusted means were done only when the test of equality of slope was not significant. Dependent variable = SL, covariate = age, treatment variable = year.

Rockfish species Source	df	Sum of squares	Mean square	F	P
Shortbelly					
Equality of slopes	5	219.30	43.86	2.74	0.019
Error	290	4,637.14	15.99		
Bocaccio					
Equality of slopes	4	705.01	176.25	6.16	0.001
Error	250	7,157.92	28.63		
Chilipepper					
Equality of slopes	3	262.68	87.56	5.00	0.002
Error	203	3,557.01	17.52		
Widow					
Equality of slopes	3	75.63	25.21	1.64	0.184
Error	120	1,845.44	15.38		
Equality of adjusted means	3	392.41	130.80	8.38	0.001
Error	123	1,921.07	15.62		
Yellowtail					
Equality of slopes	3	57.41	19.14	2.13	0.104
Error	66	591.95	8.97		
Equality of adjusted means	3	798.09	266.03	28.27	0.001
Error	69	649.36	9.41		

Bocaccio The data presented in Figure 4 show the relationship between standard length and age for the aged subsamples of pelagic juvenile bocaccio in each year during 1984–88. No data were available for 1983. There is some suggestion of curvilinearity in the data, especially in the youngest stages of growth, but this cannot be confirmed due to annual differences in the age domain sampled. For example, specimens ranged in age from 35 to 113 days during 1986, whereas in 1985 they ranged from 84 to 131 days. Thus, differences in slope between these years may be due to a year effect in the linear model, or to violation of the linearity assumption. In spite of the suggestion of nonlinearity in the data when pooled over years, the linear model was used to conform with the analyses performed on the other four species studied and because it fits well on a year-by-year basis.

A simple linear growth model was fit to individual years (Table 2). During the period studied, the highest growth rate
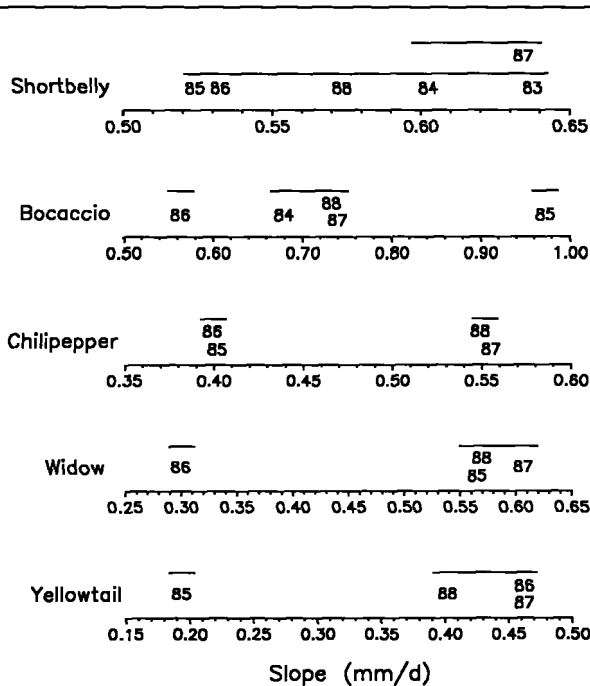

Figure 3

Results of all possible pairwise least-significant-difference tests of annual differences in growth rate (slope) for each species studied. A bar over and connecting different years (1983–88) indicates lack of significance. No adjustments were made to control the experiment-wide probability of Type I error.
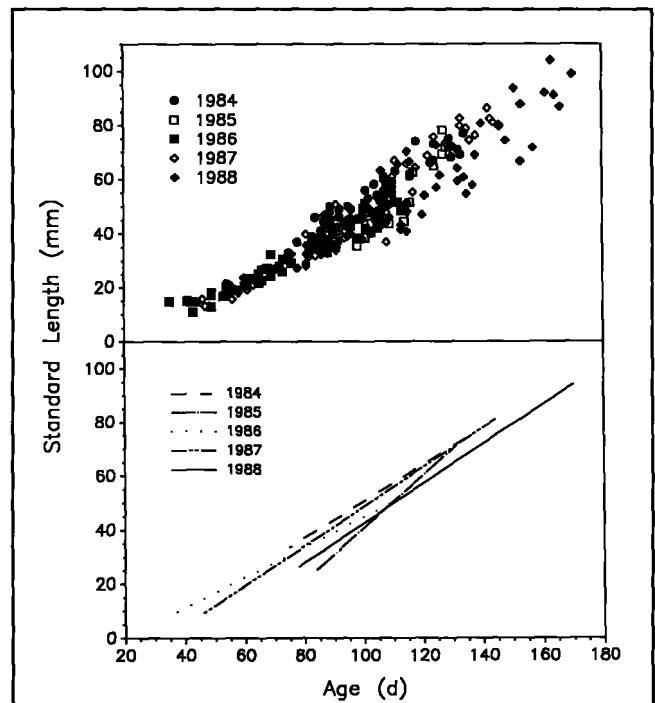

Figure 4

Scattergrams of bocaccio Sebastes paucispinis standard length on age for each year, 1984–88 (upper), with fitted linear regressions to each year of data (lower).

Figure 5

Scattergrams of chilipepper *Sebastes goodei* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).

Figure 6

Scattergrams of widow rockfish *Sebastes entomelas* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).
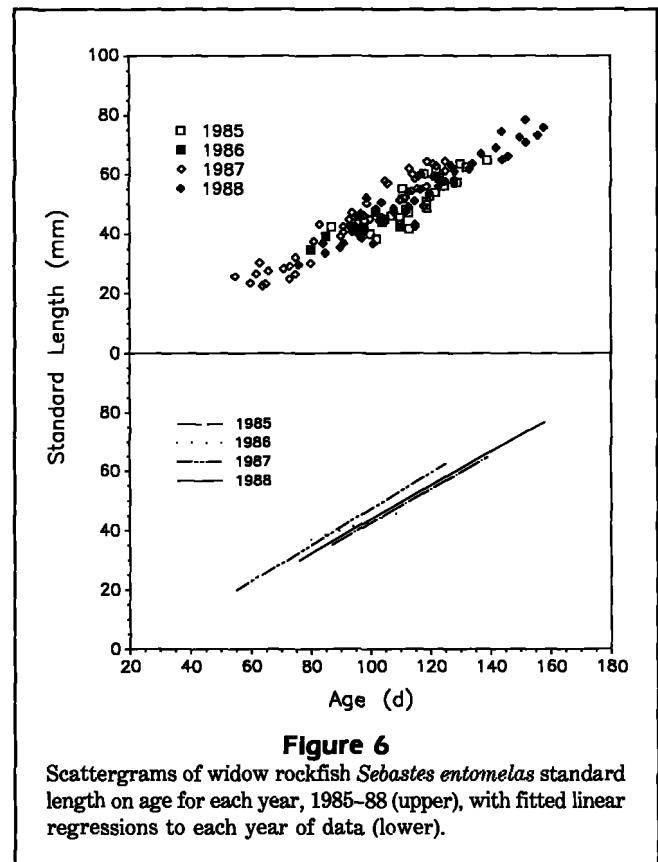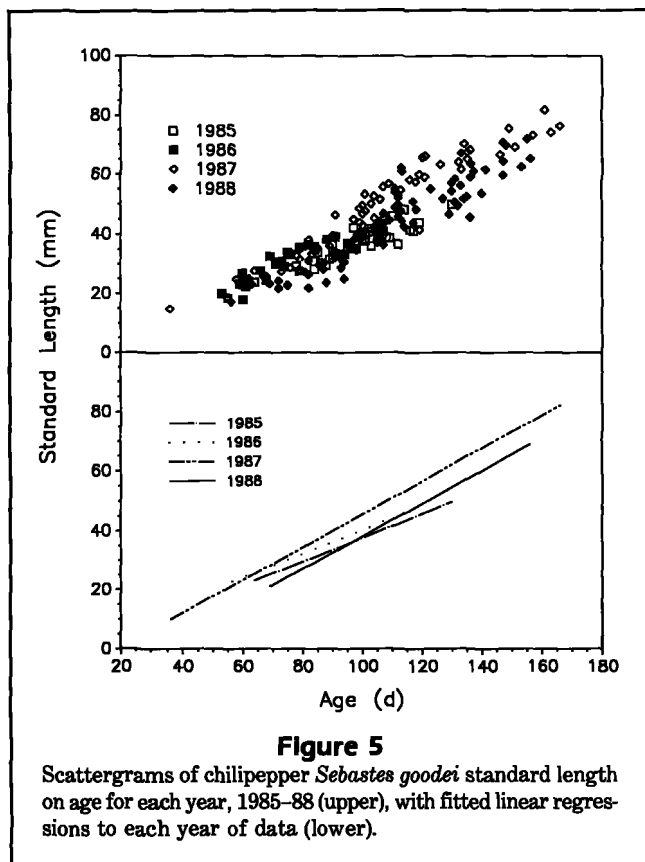
occurred in 1985 (0.974 mm/day), whereas the lowest growth rate (0.563 mm/day) was seen in 1986. Results of ANCOVA (Table 3) show that significant differences (*P* 0.001) in growth rate occurred among years. Results of all possible pairwise LSD tests comparing annual slope estimates (Fig. 3) show that growth in 1985 was distinctly fast. Growth rates were relatively low in 1986 and were moderate and similar in 1984, 1987, and 1988.

Chilipepper Sufficient numbers of fish were collected during 1985–88. Standard length and age data from these years (Fig. 5) indicate an apparent linear relationship. Regression statistics resulting from fitting each year's data to the linear growth model are provided in Table 2. Annual growth rates ranged from a low of 0.399 mm/day in 1986 to a high of 0.555 mm/day in 1987. Results from ANCOVA (Table 3) show that annual differences exist in growth rate (*P* 0.002); pairwise LSD comparisons of slopes (Fig. 3) indicate a very clear separation between the slow growth that occurred in 1985–86 and the relatively fast growth in 1987–88.

Widow rockfish Like chilipepper, widow rockfish were collected in sufficient numbers only in the years 1985–88. The scatter of data (Fig. 6) shows an ap-

parently linear increase in standard length, at least over the range of ages sampled. A problem with the data is that in 1986 only 9 fish were collected, with ages ranging 80–110 days. This resulted in a marked reduction in age contrast (30 days).

The data from each year were fitted separately with linear regression (Table 2), with estimates of growth rate ranging from 0.299 mm/day in 1986 (N 9) to 0.607 mm/day in 1987. When ranked, the descending sequence of estimated annual growth rates (i.e., slopes) was: 1987>1988>1985>1986. Results of ANCOVA (Table 3), however, indicated that slopes did not vary significantly among years (*P* 0.184), although all possible pairwise LSD comparisons (Fig. 3) showed that growth rate in 1986 was slower than in other years. The reason the ANCOVA failed to reveal differences in slope among years was likely due to a small sample size and low age contrast in 1986. An F-test for annual differences in adjusted means (i.e., elevation) did reveal significant differences (Table 3, *P* 0.001). Pairwise LSD comparisons of annual adjusted means indicated that pelagic juveniles were larger in 1987 than in other years. When ranked, the descending sequence of annual adjusted means was: 1987>1986>1988 >1985.

Yellowtail rockfish Juvenile yellowtail rockfish comprised the fewest specimens collected of the five species studied. Sufficient specimens for growth analysis were collected only in the years 1985–88. The scattergram (Fig. 7) shows the smallest range in standard length and age observed. This problem is exemplified in 1985 when the ages ranged only 107–133 days.

The data were fitted by linear regression for each year (Table 2) resulting in estimates of growth rate that ranged from 0.194 mm/day in 1985 to 0.463 mm/day in 1986. The descending sequence of estimated annual growth rates of yellowtail rockfish was: 1986>1987 >1988>1985. Results of ANCOVA (Table 3) testing for annual differences in slope were borderline (*P* 0.104); all possible pairwise LSD comparisons (Fig. 3) showed that growth rate in 1985 was slower than in other years. An F-test of annual differences in adjusted means was significant (Table 3, *P* 0.001). Like widow rockfish, results from all possible pairwise comparisons of yearly adjusted mean standard length indicated that yellowtail rockfish juveniles were larger in 1987 than in other years, with fish sampled in 1986 and 1988 somewhat larger (*P* 0.05–0.10) than those taken in 1985. The rank order of adjusted mean standard length was identical to that observed in widow rockfish (i.e., 1987>1986>1988>1985).

Annual growth performance

The data presented thus far make it difficult to compare and contrast the growth of the five species on an annual basis. For example, results from bocaccio (lower panel in Figure 4) show that 1985 was characterized by the highest growth rate (0.974 mm/day). Even so, 90-day-old fish in 1985 were estimated to be smaller than in any other year. In this situation it is possible that poor growth performance during early-life-history stages, prior to those sampled, had no lasting effect on growth at the time of sampling. There may even have been some form of compensatory growth response.

To overcome this problem we compared annual growth performance within and among species by estimating length at a selected standard age with the regression statistics presented in Table 2. This is functionally equivalent to integrating annual growth rates up to the selected standard age, providing a common basis for comparison among years. The standard age for each species was determined from the range of ages sampled in the various years. Standard ages were selected to prevent extrapolation of the regressions. Specific ages selected were: shortbelly rockfish 70 days, bocaccio 100 days, chilipepper 90 days, widow rockfish 100 days, and yellowtail rockfish 107 days.
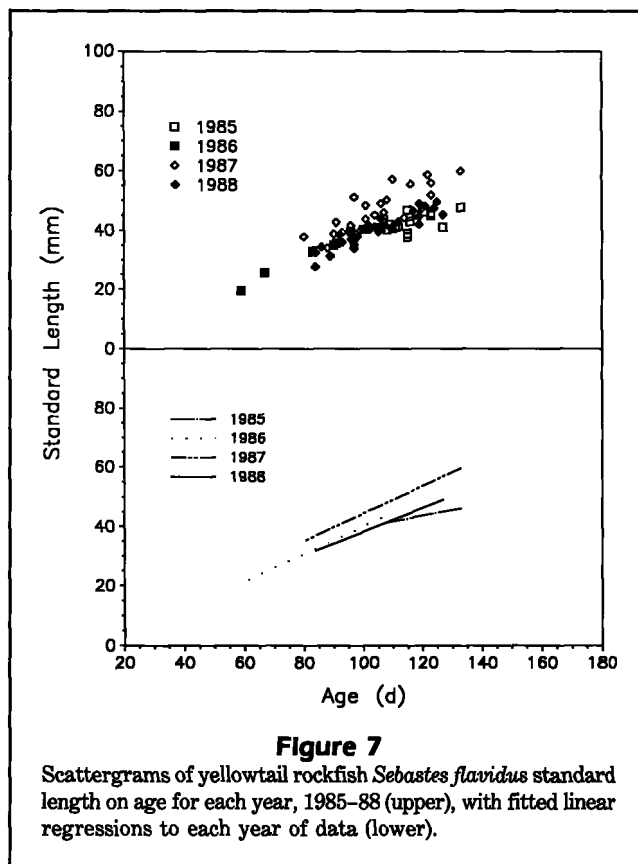

Figure 7

Scattergrams of yellowtail rockfish *Sebastes flavidus* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).
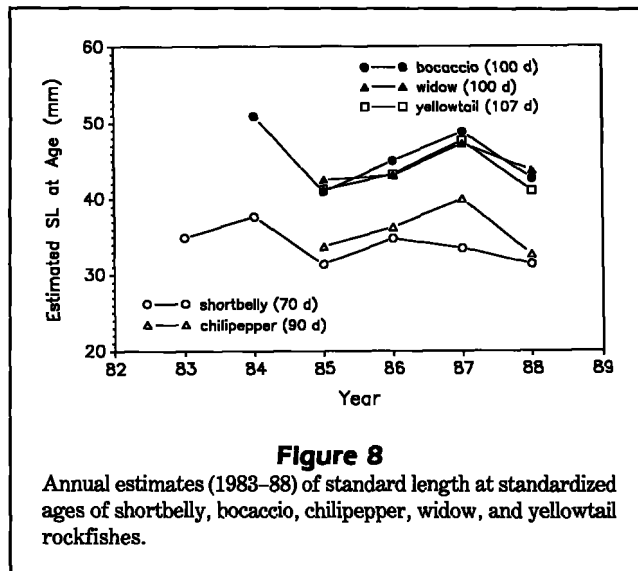

Figure 8

Annual estimates (1983–88) of standard length at standardized ages of shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes.

Results show coherent differences in growth performance from year to year (Fig. 8). Among the five species over the last four years of the study, 1985 consistently produced the smallest fish and, with the exception of shortbelly rockfish, 1987 yielded the largest fish observed. Although only represented by two

Figure 9
Composite annual back-calculated birthdate distributions of shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes (1983–88).
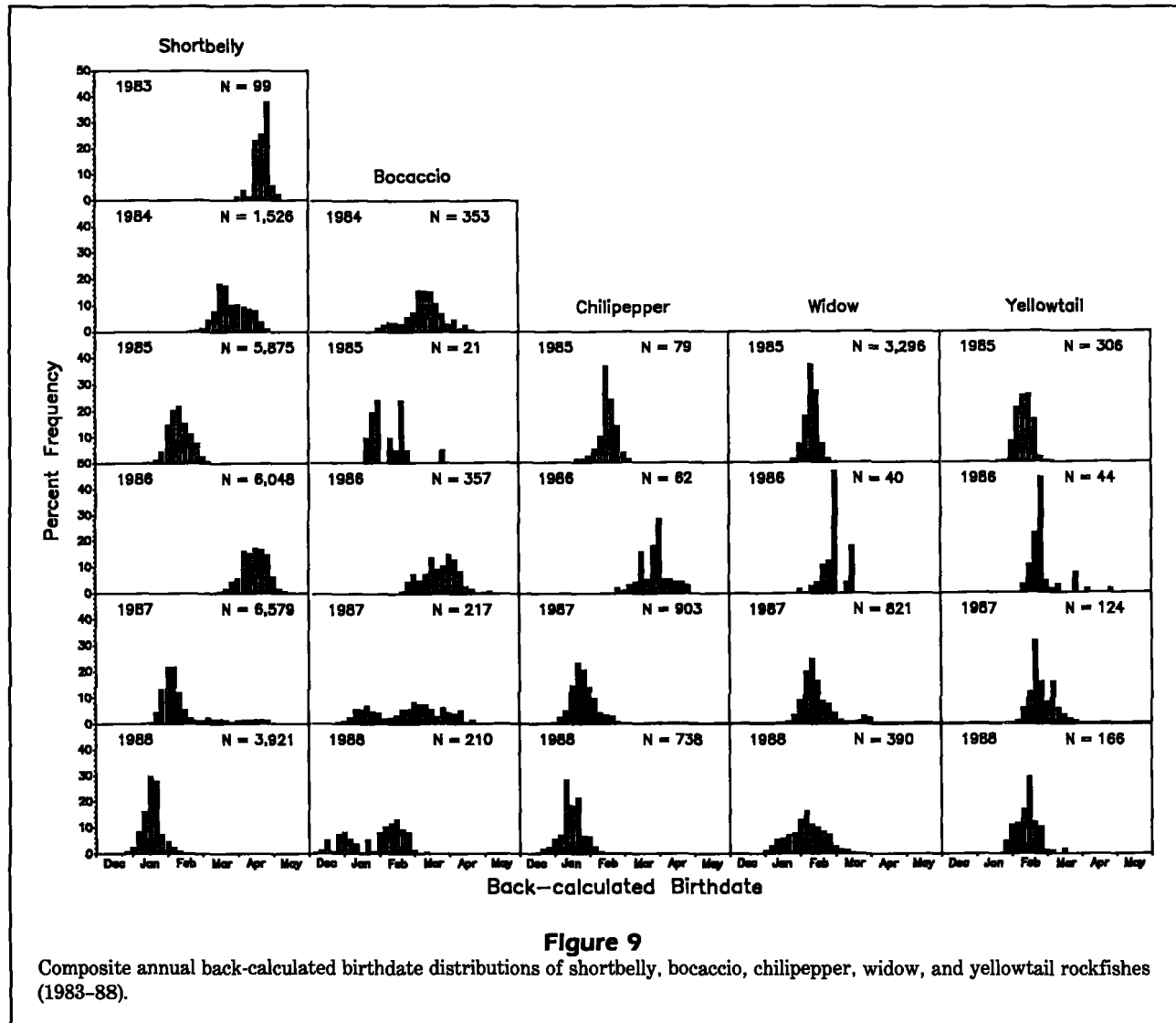
species (bocaccio and shortbelly rockfish), 1984 produced faster growth than in any other year.

Overall, growth performance shows remarkable coherency in this time series. This conclusion is further reinforced with results from principal component analysis. Following ordination, 83.3% of the variation in growth-performance standard scores was accounted for by the first principal component (λ_1 4.16). First component scores (ζ_1) for each year were ranked in descending order as follows: 1987 (ζ_1 2.74)>1986 (ζ_1 0.36)>1988 (ζ_1 -1.40)>1985 (ζ_1 -1.71). These values follow the general pattern evident in Figure 8.

Back-calculated birthdate distributions

As with the aged subsample data, the birthdate frequency distributions that were generated from length-

frequency data were pooled across sweeps within each year, even though in some cases significant differences occurred. Although sweep-to-sweep differences would be useful in elucidating within-season patterns of mortality, movement, and growth, we ignored them because an analysis of the components of variance showed that, with the exception of yellowtail rockfish, variation of this kind was quite minor in comparison to yearly fluctuations in birthdate distributions.

Results of back-calculating time of birth (Fig. 9) show that, typically, surviving juveniles were born during a two-month period. For most species-year combinations, a unimodal distribution is evident. Bocaccio display somewhat broader birthdate distributions than the other species, perhaps reflecting their multiple spawning capability in southern California waters (MacGregor 1970). Positive skewness in the birthdate

distributions of all five species was evident in 1987, being particularly marked in shortbelly, chilipepper, and widow rockfish. What is most striking in these data, however, is the broad coherence among the species in the yearly shifts that occurred in the distributions (Fig. 10). For example, 1986 was a year in which successful parturition occurred late in the season for all species examined. Conversely, 1985 and 1988 were years marked by earlier birthdate distributions.

Principal component analysis demonstrates the great degree to which these data are coherent in time (1985–88). Results show that 92.9% of the variation in mean back-calculated calendar birthdate standard scores was accounted for by the first principal component (λ_1 4.64). Given the tight coupling that occurred between bocaccio and shortbelly rockfish in 1984–85, these values may well have been higher if data had been available for all species in all years (1983–88). First component scores for each year were ranked in descending order as follows: 1986 (ζ_1 2.93)>1987 (ζ_1 0.13)>1985 (ζ_1 −1.16)>1988 (ζ_1 −1.89). This sequence mirrors the interannual shifting of distributions evident in Figures 9 and 10.

Discussion

Growth

Growth rates of field-collected larval and pelagic juvenile *Sebastes* spp. have been determined by others using otolith microstructure (reviewed in Kendall and Lenarz 1987, Moser and Boehlert 1991). It is noteworthy that in all cases a linear growth model fitted the data best, similar to results reported here (Figs. 2, 4–7). Data for *S. melanostomus* (*N* 4) indicated that at 15–30 mm SL the growth rate was 0.24 mm/day (Moser and Ahlstrom 1978). Research on *S. diploproa* (Boehlert 1981) showed a growth rate of 0.19 mm/day for fish 10–40 mm SL. Both studies were conducted off southern California. Penney and Evans (1985) estimated that redfish (composite of *S. marinus*, *S. mentella*, and *S. fasciatus*) from the northwest Atlantic grew at the rate of 0.11–0.16 mm/day when in the range 8–25 mm TL.

These growth rates are somewhat lower than those presented in Table 2. Our data show growth rates ranging 0.52–0.64 mm/day for shortbelly rockfish, 0.56–0.97 mm/day for bocaccio, 0.40–0.56 for chilipepper, and 0.30–0.61 mm/day and 0.19–0.46 mm/day for widow and yellowtail rockfishes, respectively. This is likely due to the span of ages and/or sizes caught, since our fish were larger and older than in these other studies. It is conceivable, however, that the growth rates of pelagic juvenile *Sebastes* spp. along the central California coast
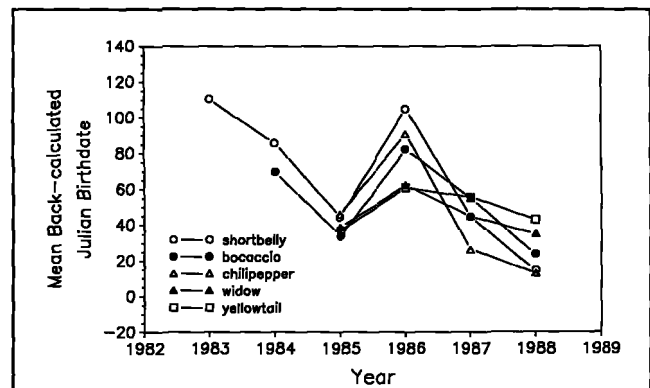

Figure 10
Annual trends (1983–88) in the means of back-calculated birthdate distributions for shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes.

are enhanced in response to superior feeding conditions and increased ration (Brett 1979), a consequence of elevated production associated with coastal upwelling (Smith 1968). Dietary studies of these fishes show that they feed primarily on various life stages of euphausiids and calanoid copepods (Reilly et al. In prep.).

Interannual variation in growth performance has been implicated as a major factor affecting year-class strength (Miller et al. 1988). Houde (1987) showed with simple calculations that, in some situations, a doubling of the instantaneous growth rate during the early life history can increase the number of recruits by nearly 100-fold. Moderate and significant interannual variations in growth rates/performance were evident for the species in this study. Likewise, widow rockfish year-class strength has varied 10-fold during the 1974–89 period (Hightower and Lenarz 1989). These results are, therefore, consistent with the hypothesis that fluctuations in rockfish recruitment are due, at least in part, to interannual variation in growth rate.

Birthdate distributions

Back-calculation of birthdate distributions using daily increment data has been reported before (e.g., Bolz and Lough 1983, Brothers et al. 1983, Methot 1983, Jones 1985, Penney and Evans 1985, Thorrold 1989). One difficulty with this approach is that estimates of the numbers born by date should be adjusted for differences in mortality (Penney and Evans 1985), i.e., to have appeared in our samples, older juveniles must have survived for a longer period of time than younger ones. However, without an estimate of early larval and juvenile mortality rates we were unable to adjust for

this effect. In this sense, the histograms presented in Figure 9 represent the birthdate distributions of the fish that survived to the time of sampling.

The distributions are also influenced by other factors. For example, there are differences among the species in duration of the pelagic phase. This is especially true for widow and yellowtail rockfish, which tend to settle at a relatively young age. Results may also be biased if parturition occurs unusually late in the year. In this case the larvae/juveniles might not be large enough to be captured by the gear we used. However, our sampling occurred annually at similar times, and marked differences in the distributions were still noted. The early birthdate distributions characterizing bocaccio, chilipepper, and shortbelly rockfish in 1988 were due to the prevalence of relatively old fish, whereas fish sampled in 1986 were relatively young. Although these shifts may be influenced by settlement and gear selectivity, they nonetheless provide a conservative representation of interannual differences.

Two possible hypotheses accounting for interannual variation in the means of back-calculated birthdate distributions are (1) annual variation in the seasonal timing of parturition, and (2) year-specific seasonal variation in the expression of mortality rates within fixed parturition seasons. Although at present we have no basis to distinguish between these two alternatives, this topic is currently under detailed investigation.

Oceanographic conditions

It is well known that temperature has a major influence on larval growth at sea. There is evidence that sea-surface temperature (SST) affects the growth performance of pelagic juvenile rockfish off central California (lat. 36–39°). In this area mean January SST from 1983–87 (Cole and McLain 1989) was positively associated with growth performance. For example, in 1984 shortbelly rockfish were estimated to be 37.7 mm SL at a standard age of 70 days. This represented this species' best growth during the 1983–88 period, and in this year mean January SST was a very warm 13.12°C. In contrast, in 1985, when mean January SST was at its lowest value in the time series (12.05°C), estimated length at age was lowest also (31.3 mm SL).

Similar to growth, there is evidence that sea-surface temperature has a strong influence on interannual shifting of back-calculated birthdate distributions. Cold years were associated with early successful parturition. Our results show that for shortbelly rockfish the annual mean of the birthdate distribution was at its minimum in 1985 (8 February) when mean January SST was only 12.05°C. By comparison, in 1983 (an El Niño year) the birthdate mean was at its maximum value (21 April) in association with warm January SST

(13.16°C). These findings are intriguing and form the basis of ongoing investigations into the establishment of year-class strength in *Sebastes* spp.

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