

Abstract.—The relationship between length and age of larval and juvenile shortbelly rockfish *Sebastes jordani*, determined from otolith microstructure, is complex. Models that assume size increases smoothly with age may not accurately describe growth in young-of-the-year rockfish. A segmented (piece-wise linear) regression model relating somatic and otolith size was used to back-calculate body length-at-age. The segments of this model coincide with different growth stanzas, which are separated by distinct life-history transitions. The composite function of this model, and a Gompertz curve relating otolith size and age, yielded a good fit to the back-calculated standard length-at-age data. Comparison of back-calculated with actual growth showed no evidence of size-selective mortality. The change in body length, as the number of otolith increments increased, was equal to the observed increase in length per day of a sequentially sampled cohort, validating the daily periodicity of the increments.

Dynamics of Growth in the Early Life History of Shortbelly Rockfish *Sebastes jordani*

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The abundance of young-of-the-year fish, and ultimately the number that reach maturity, varies greatly among years. Much of this variation is unrelated to the size of the spawning stock, and understanding its causes remains a central focus of fisheries research (e.g., Hjort 1914, Sissenwine 1984, Rothschild 1986, Hollowed et al. 1987, Sinclair 1988). Mortality agents, such as starvation (Hjort 1914, Lasker 1975 and 1978, Houde 1977 and 1978, Theilacker 1978 and 1981, Grover and Olla 1986) and predation (Hunter 1981, Hunter and Kimbrell 1980, Sissenwine 1984, Bailey and Houde 1989), can operate strongly during early stages, and it is clear that mortality rates of young fish are higher than those experienced by older fish (Miller et al. 1988). Interannual variation in year-class strength can depend upon the rate of growth early in life (Houde 1987 and 1989, Underwood and Fairweather 1989). Under most conditions, the more rapidly fish grow through early, high-risk stages, the fewer die; small changes in growth rate can thus lead to a major change in recruitment (Houde 1987). Knowledge of the processes affecting growth during the early life history may help predict the occurrence of strong year-classes.

Numerous mathematical models have been developed to describe the growth process, including the Gompertz, von Bertalanffy, logistic, and

exponential functions (Ricker 1979). Although these models usually perform well on adult stages, they commonly falter in predicting growth during the first few weeks of life. For example, Phillips (1964) used a von Bertalanffy function to model growth of shortbelly rockfish *Sebastes jordani*. The model predicted growth of adults well, but its accuracy deteriorated for young-of-the-year fish. Because somatic growth during early stages can be affected by abrupt physiological changes (e.g., flexion, juvenile transformation, and settlement), models that predict growth during this period should reflect (or describe) this complexity (Ricker 1979).

Rockfish (*Sebastes* spp.) are an important component of the west coast groundfish fishery (PFMC 1989). Growth rates of young rockfish have been estimated from linear models relating length to age (Boehlert 1981, Boehlert and Yoklavich 1983, Penney and Evans 1985, Haldorson and Richards 1987, Woodbury and Ralston 1991). Because most of these studies examined a narrow range of ages, linear models fit the data adequately. Although Penney and Evans (1985) showed that a linear model explained much of the variation in length during larval and juvenile stages of redbfish, back-calculated growth rates varied systematically with age; growth rate was relatively slow for young larvae, more rapid

for older larvae, and relatively slow again for juveniles. This suggests that it is possible to improve upon the linear model and provide a more accurate description of growth over the entire range of ages.

Since Pannella (1971) first discovered daily growth increments in otoliths, many researchers have used these microstructural features to study fish growth (see reviews in Campana and Neilson 1985, Jones 1986). By measuring the widths of daily increments within the otolith, and defining the relationship between standard length and otolith radius, one can back-calculate the somatic length of fish at any given age. This approach provides a powerful tool for estimating growth rates (e.g., Thorrold and Williams 1989). In this study, we used otolith microstructure to back-calculate the growth of larval and juvenile shortbelly rockfish *Sebastes jordani*. To do this we (1) determined when daily increments begin to form, (2) validated the daily periodicity of the increments, (3) developed a growth model for back-calculation, and (4) assessed the effects of size-selective mortality on back-calculated estimates of growth.

Methods

Field collections

Larval and juvenile shortbelly rockfish were collected on four cruises between 1 February and 13 June 1989 (Table 1). All sampling was conducted along the central California coast from Cypress Pt. (Monterey Co.) to Pt. Reyes (Marin Co.). Larval samples were collected with oblique tows to maximum depths of 50–200m, and were towed at depth for 30 seconds, at an approximate ship speed of one knot. Larval samples were collected with a 1 m plankton net (0.505 mm mesh) or, for the 18 February cruise, a 2 × 2 m Isaacs-Kidd trawl (2 mm mesh). For further information on larval hauls, see Appendix A. Larvae were sorted and placed in 80% ethanol. Juvenile samples were collected with a 26 × 26 m midwater trawl (0.945 cm mesh codend liner), towed horizontally at depth for 15 minutes at a speed of approximately one knot. Sampling for the juvenile survey was at fixed stations spread throughout the study area, with target depths of 10, 30, and 100 m, but with most samples taken at the standard depth of 30 m. Juvenile rockfish were removed from hauls and immediately frozen. For further details on procedures for the juvenile survey, see Wyllie Echeverria et al. (1990).

Table 1

Haul and collection data gathered during this study. On the first three cruises, larvae only were collected; on the May–June cruise, both larvae and juveniles were collected.

Dates (1989)	Research vessel	No. hauls	No. collected	No. aged
01 Feb.	RV <i>Ed Rickettes</i>	7	191	153
18 Feb.	RV <i>David Starr Jordan</i>	2	31	31
06 March	RV <i>Ed Rickettes</i>	5	27	10
14 May–13 June	RV <i>David Starr Jordan</i>	168	1262	55

To determine when daily otolith increments begin to form, gestating larvae (rockfish are viviparous live-bearers) were collected and their otoliths examined. Adult female rockfish were collected during the May–June survey and from commercial fishermen at Fort Bragg, California in May. Preextrusion larvae were removed and placed in 80% alcohol for later examination.

Laboratory procedures

The stage of development of the gestating larvae was determined by morphology and pigmentation (Moser et al. 1977). Larvae from four females (two from the May–June cruise and two collected from commercial fishermen in May) were found to be in an advanced stage of development and were used for further analysis.

The standard length (SL) of all larvae and juveniles was measured to the nearest 0.1 mm. Ages were determined for juveniles spanning the entire size range collected and for all planktonic larvae. Sagittae were removed from each fish and affixed whole to slides with a drop of clear fingernail polish. Intact otoliths from larvae (<20 mm) had discernable growth increments with no further preparation. For fish with SL >20 mm, otoliths were sanded in the sagittal plane with 400-grit sandpaper until the nucleus became visible. Concentrated HCl was used to etch the otoliths until growth increments were easily discernable.

All otoliths were viewed at 600–1250× magnification with a compound microscope equipped with a video camera and monitor. Only fish with a dark check mark that clearly encircled the primordium were used in our analysis of growth (see also Penney and Evans 1985). Fish with this mark and no additional increments were given a nominal age of zero. Increments were counted from this mark to the most distal point along the postrostral growth axis. We used a digitizer to record the exact position of each increment; otolith radius (OR) was measured to the nearest 0.1 μm.

Validation

To validate that the increments were formed daily, we only considered samples collected during the May–June survey, because it was the only multiple-day cruise. From the data we identified a well-defined, temporally discrete cohort, and estimated the average change in length of individuals over the duration of the cruise. We compared this rate with the rate of change in length with nominal age from otoliths.

We identified a temporally discrete cohort as follows. Using the 55 aged fish (mainly juveniles) from the May–June cruise, and assuming that the number of increments approximated age in days after extrusion, we linearly regressed age on SL. From the resulting regression equation, we estimated the ages of all juveniles caught (all specimens were measured, but only a subsample of 55 fish from this cruise was aged). By subtracting estimates of age from known dates of capture (measured from the beginning of the year), we estimated the dates when the dark check mark formed for all fish sampled. A plot of frequency of occurrence against estimated dates of check mark deposition was used to identify the cohort. We stress that this procedure was used only to identify the cohort for further consideration. The rate of change in length-per-unit-time for fish sampled from the cohort was found by calculating the rate at which the lengths of captured individuals changed over the course of the 30 day cruise.

Data analysis

Initial exploratory model development involved fitting a number of equations (by least squares) to the data to characterize two functional relationships: $OR = f(\text{age})$ and $SL = g(OR)$. For the former, we used not only the radius of the otolith at the time of collection (terminal OR), but also back-calculated radii measured at earlier ages. Due to the serial correlation present in these data (multiple observations of OR-at-age from the same fish), we used the grouped jackknife technique (Miller 1974) to estimate standard errors of the parameters. In contrast, we used only terminal values of OR and SL when fitting the latter relationship. Once known, the composition of these two functions $\{f, g\}$ defined explicitly the dependence of SL on age, i.e., $SL = g(f(\text{age}))$. This procedure provided a better description of the age-length relationship than did the more usual approach of fitting a growth model to back-calculated SL-at-age data, even when complex formulations were tried (e.g., the two-stage Gompertz function suggested by Zweifel and Lasker 1976).

A single-stage Gompertz growth equation (Ricker 1979) provided a good description of otolith growth.

The model has three parameters (OR_0 , k , and g) and can be expressed as:

$$OR = OR_0 \cdot \exp\{k \cdot [1 - \exp(-g \cdot \text{age})]\}.$$

Our data showed increasing variance in OR with increasing age, so the data and the equation were logarithmically transformed prior to fitting (Zweifel and Lasker 1976).

To regress SL on OR, we developed a model consisting of four linear segments, each describing a different growth stanza (see Appendix B for details). Before selecting this segmented model, we first considered, and then discarded due to lack of fit, a number of continuous models, including the simple two-parameter linear model, the Gompertz function, and three-parameter power and exponential models with separate Y-intercept terms.

Once we had established a relationship between SL and OR, we used this relationship to back-calculate SL at ages younger than the terminal age-at-capture. We used the "body-size proportional" method described by Francis (1990) in our back-calculations, in which the length at age i (some age younger than c , the age of collection) for fish j (SL_{ij}) is given by:

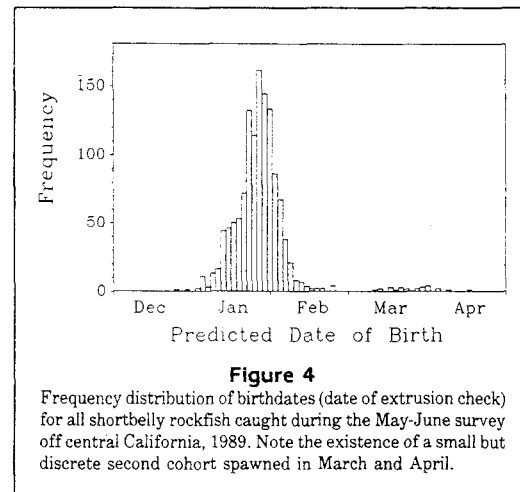
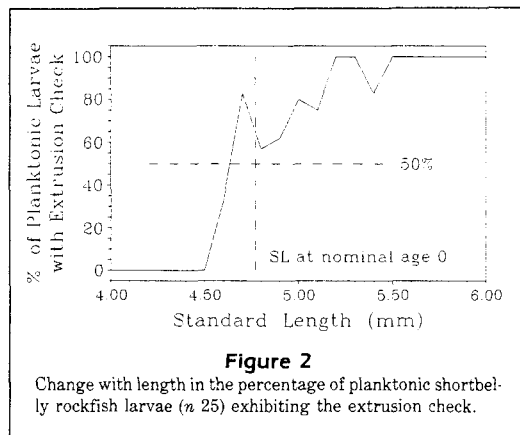
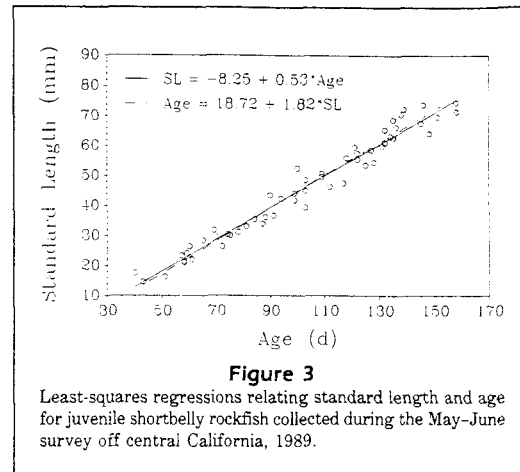
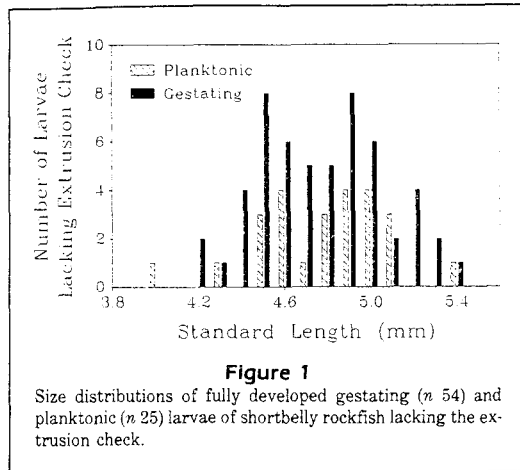
$$SL_{ij} = g(OR_{ij}) \cdot (SL_{cj}/g(OR_{cj})),$$

where, as above, $g(\cdot)$ is the regression equation we developed to predict expected SL from OR, and SL_{cj} is the measured length of fish j at the time of capture. Note that this method corrects for the deviation between the length predicted by the regression model and actual length at the time of capture. The well-known Fraser-Lee method, which also takes into account actual length of an individual at the time of capture, is inappropriate here because of the non-linear relationship between SL and OR (Campana 1990, Francis 1990). The fit of $SL = g(f(\text{age}))$ to the "observed" back-calculated estimates of SL_{ij} was then evaluated by examining a plot of the residuals ($SL_{ij} - \widehat{SL}$).

Results

We measured SL of 1511 larval and juvenile shortbelly rockfish. Ages were determined for 249 fish that ranged in size from 4.5 to 74.5 mm SL. Of these, 194 (4.5–15.2 mm SL) were from the three single-day cruises and 55 (14.6–74.5 mm) were from the May–June cruise (Table 1).

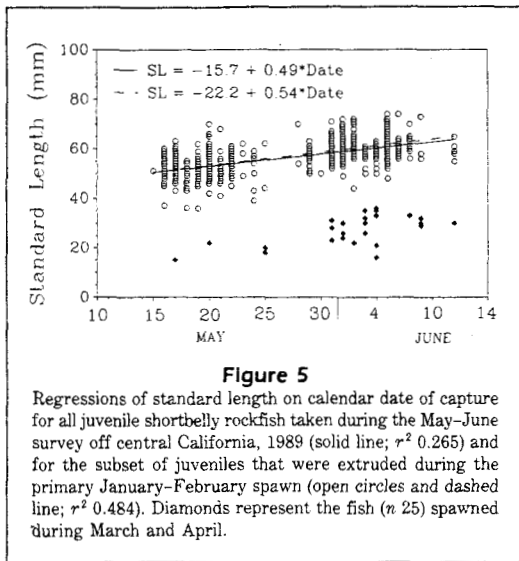
None of the gestating preextrusion larvae that we examined possessed the dark check mark that we used as the starting point for increment counts. Because of this, and the presence of increments in most of the



smallest planktonic larvae, we believe this mark was formed at, or shortly after, extrusion. The size distribution of the few planktonic larvae that lacked this feature (henceforth called the extrusion check) was similar to the size distribution of full-term, gestating larvae (Fig. 1). Thus, shortbelly rockfish do not appear to grow substantially from the time of extrusion to the time the extrusion check is formed. Likewise, all planktonic larvae greater than 5.5 mm in length had an extrusion check and more than 50% had the extrusion check, at a size of 4.7 mm (Fig. 2). The average size of the full-term gestating larvae we measured was 4.7 mm, and we take this as an estimate of the size-at-extrusion, which is independent of our growth models.

Validation

We compared how the mean SL of fish in a cohort changed over a 30-day period, with the growth rate estimated from a regression of SL on nominal age determined independently by examining otoliths. For the 55 fish we aged from the extended May-June cruise, a linear relationship existed between assumed daily age and SL, with a slope of 1.82 days/mm (SE 0.0484) and an r^2 of 0.963 (Fig. 3). The distribution of estimated birthdates for all juveniles caught during the cruise ($N = 1262$) contained a small secondary mode ($N = 25$) in March and April (Fig. 4). In our primary analysis, we considered only those fish with birthdates occurring in January or February ($N = 1237$).

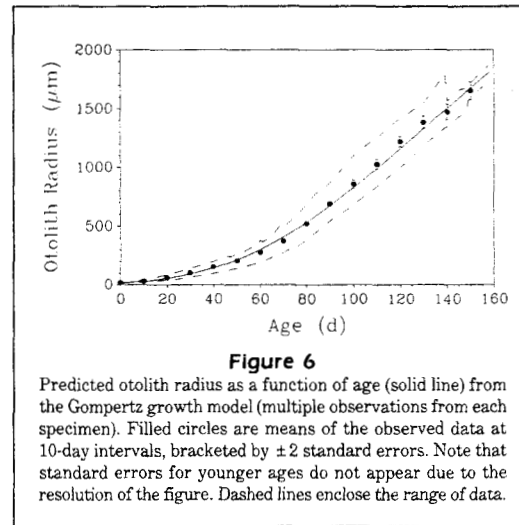


For the juveniles from the first cohort, the slope of the regression of SL on date of capture was 0.54 mm/day (SE 0.0158; Fig. 5). This compares with a slope of 0.53 mm/increment (SE 0.0140) obtained from a regression of length against the number of increments counted for the 55 aged fish (Fig. 3). Moreover, the slope of a regression of the predicted ages of the fish from the first cohort on their date of capture was 0.96 increments/day (SE 0.028). This rate is not significantly different ($P > 0.05$) from the expected 1:1 correspondence between increments and days ($t = 1.43$, df 1235).

Most of the fish from the second cohort (Fig. 4) were captured late in the May-June cruise, probably because selectivity of the net did not allow their capture at the beginning of the cruise when they were smaller. Because fish from the second cohort were smaller and were caught later in the cruise, excluding them improved the agreement between the observed rate of change in length over time and the growth rate estimated from daily otolith increments of aged fish (Fig. 3). We feel that the exclusion was warranted because of the clear separation between the cohorts (Fig. 4). In any case, relatively few fish (25 out of 1262) were excluded, and the effect on our estimated rate of change in length of the cohort was slight ($\sim 10\%$; Fig. 5).

Growth of the otolith

Otoliths of shortbelly rockfish grow at a generally increasing rate from birth to ~ 90 days in age (Fig. 6).

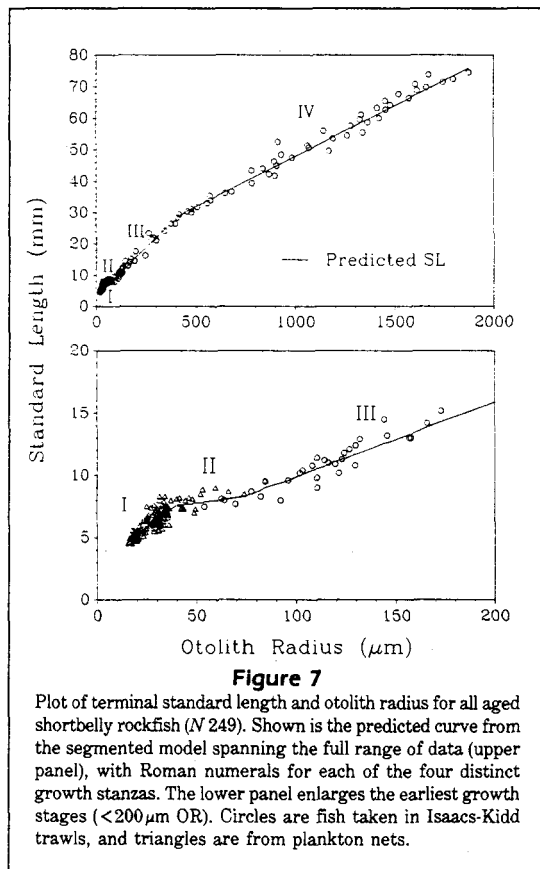


Thereafter, there is substantially less curvature in the data. Results of fitting the Gompertz growth function to the data yielded estimates of $OR_0 = 16.00 \mu\text{m}$ (SE 0.0374), $k = 5.4223$ [dimensionless] (SE 0.0235), and $g = 0.01298/\text{day}$ (SE 0.000106), with an r^2 of 0.991. The curve (solid line in figure) fit the data well except for a minor lack of fit at about 70 days of age.

Standard length vs. otolith radius and back-calculation of length

The segmented linear model (after Bacon and Watts 1971) provided a good fit when SL was regressed on OR (Fig. 7, Table 2). There was no discernable pattern to the residuals, and the r^2 value was quite high (0.998). In addition, the model's estimate of body length at the mean otolith radius at the extrusion check ($17 \mu\text{m}$) was 4.9 mm SL; this approximated independent estimates of length-at-extrusion (5.4 mm [Moser et al. 1977], 4.0 mm [MacGregor 1986], and 4.7 mm SL [this study, Figs. 1, 2]). The intersections of the four linear segments relating SL to OR were at 38.7, 73.1, and 431.3 μm OR, and the corresponding lengths were 7.7, 8.4, and 29.9 mm SL, respectively.

Larvae were collected with two types (sizes) of nets. A possible source of bias in our results could arise from different selectivities of the nets (Somerton and Kobayashi 1989). For example, differential sampling by the nets may be responsible for the segmenting seen in Figure 7, although we do not believe this is the case. Even though, on average, the nets collected different sized fish, both types of nets captured fish in the range



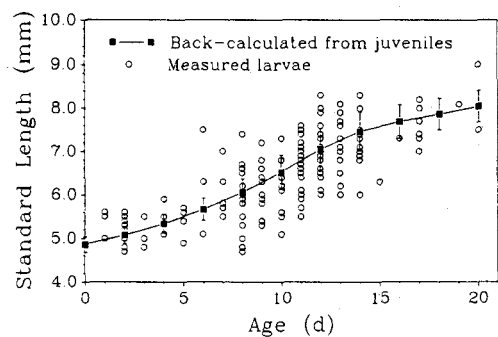
of 7.5–10.0 mm SL (lower panel of Figure 7). Within this range, the relationship of SL to OR did not differ significantly between the nets ($t=0.50$, $df=4$, $P>0.05$).

Standard length vs. age

Our back-calculation of standard length-at-age (SL_{ij}) is based on the implicit assumption that the mean back-calculated length at any particular age is similar to the mean length of fish actually captured at those earlier ages. Violation of this assumption is the so-called Rosa Lee's phenomenon (Ricker 1979), which can arise when mortality rates are size-selective and from a number of other causes, such as biased sampling. However, our data show that mean length-at-age during the first 20 days of life, back-calculated from juveniles at least 60 days old, passes through the observed values of SL and age at the time of capture for young larvae (Fig. 8). This result suggests

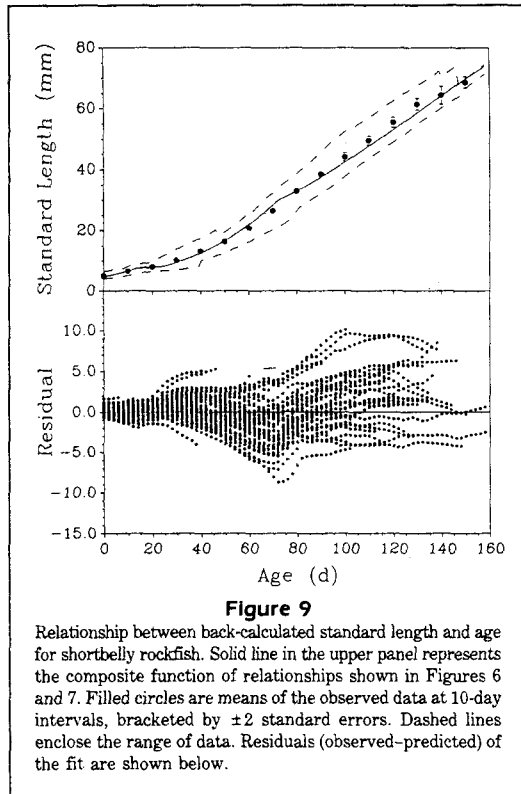
Table 2
Parameter estimates for the segmented regression model describing the relationship between standard length (mm) and otolith radius (OR, μm); Y-intercept (a), slopes for each segment (b_1 – b_4), and intersection points of the segments (c_1 – c_3) on the X (OR) axis. Note that, except for c_1 – c_3 , these are algebraic transformations of the actual parameters fitted by the regression procedure (see Appendix B). Estimates of length for a given OR based on the values given below ignore the smoothing described in Appendix B, but will be close approximations of the values that would be obtained using the original parameterization.

Transformed parameter	Estimate
a	2.92
b_1	0.1233
b_2	0.0219
b_3	0.0599
b_4	0.0327
c_1	38.72
c_2	73.10
c_3	431.31



that Rosa Lee's phenomenon is unlikely to distort our findings to any appreciable degree.

The predicted fit of the composite function [$\widehat{SL} = g(f(\text{age}))$] to the back-calculated size data was good (Fig. 9). Note that individual fish followed their own growth trajectories, producing serial correlation in the residuals. The slight lack of fit around age = 70 days (see Figure 6) is also seen more easily in this figure.



Discussion

Our goal was to develop a model that could be used to provide accurate estimates of back-calculated growth from the otolith microstructure of larval and juvenile shortbelly rockfish. A crucial assumption of the study was that the increments were formed daily. Many authors have stressed the importance of validating the daily periodicity of otolith growth increments (Jones 1986, Geffen 1987). Without validation, growth rates may be biased and their use in models of juvenile dynamics and recruitment could lead to serious errors. For validation purposes, we followed a cohort of fish through the May-June time period, measuring their progressive change in average length. We found that the rate of change in length of this cohort agreed with the estimated growth rate based on a regression of length against number of growth increments enumerated for aged fish. From this result, we conclude that the increments we counted were formed daily. It is noted, however, that the daily periodicity of these increments is validated only for the size ranges and dates

observed during the extended May-June cruise, but we have no reason to assume that the increments are not daily at earlier stages of growth.

Other evidence exists that daily increments form in otoliths of *Sebastes* spp. Yoklavich and Boehlert (1987) demonstrated the daily periodicity of increment formation in otoliths of black rockfish *S. melanops* by marking the otoliths with oxytetracycline (OTC) and by autoradiography. Also, Laidig (unpubl. data) found no difference between increment counts and the number of days following a fluorescent OTC mark, verifying that the increments of brown rockfish *S. auriculatus* were interpreted correctly as daily.

Our segmented model of fish size versus otolith size, for use in back-calculating fish length, may describe significant events during the early life of *S. jordani*. The first major events following extrusion, in the early life of rockfish, are first feeding, flexion, and transformation from larva to juvenile. Moser et al. (1977) noted that shortbelly rockfish larvae undergo flexion at 8.0-10.0 mm SL. This range essentially corresponds to the size of fish in segment II. The slope of this segment was much reduced, suggesting that although fish length increases little during flexion, the otolith continues to grow. Likewise, Moser et al. (1977) found that juvenile transformation began after 27 mm SL, and we observed that the intersection of segments III and IV occurred at a length of about 30 mm SL. It is possible, of course, that the segments we have described are peculiar to the time and place that we collected the fish. For example, the slope of the fish size to otolith size relationship could have changed at specific points in time in response to altering oceanographic conditions (see also the discussion on "buffering" below). Before this type of alternative explanation can be discarded, similar SL-OR regressions need to be established in other years.

Relative to the entire organism, the sagittal otolith is a simple structure, especially during early life history. During the first 160 days of life, the sagitta develops from a spherical primordium into an oval-saucer shape. During this time a single Gompertz curve (Fig. 6) adequately described growth along one of its dimensions (i.e., the postrostral axis).

In contrast, the whole organism is morphologically and developmentally complex. Although a simple Gompertz curve, when fitted to back-calculated length (SL_{ij}) against age, resulted in a high r^2 value, an unacceptable pattern was evident in a plot of the residuals. Other authors also have found that smooth models (e.g., Gompertz and von Bertalanffy curves) did not accurately fit SL-at-age data in young-of-the-year fish (Uchiyama and Struhsaker 1981, Bailey 1982, Rosenberg and Laroche 1982, Campana 1984, Boehlert and Yoklavich 1985). Although these simplified models

often perform well on adult fish, they are sometimes unable to depict the complex growth processes characterizing the complete life history. In such cases, segmented models should be considered because they allow for life history changes and growth stanzas (Ricker 1979). For example, Watanabe et al. (1988) found that for Pacific saury *Cololabis saira*, two Gompertz curves produced a better fit to the relationship of length and the number of daily otolith increments than did a single Gompertz curve. Zweifel and Lasker (1976) showed that a two-stage Gompertz curve described the growth of anchovy *Engraulis mordax* larvae better than a simple single-stage Gompertz curve. These authors also noted that although other models had high coefficients of determination, they exhibited unacceptable predictions for small larvae. Likewise, Nishimura and Yamada (1988) found that three linear segments described the relationship between otolith length and total length for walleye pollock *Theragra chalcogramma*, and that the intersection points between segments represented changes from larval to juvenile growth and juvenile to adult growth.

Changes in growth stages or stanzas are characterized by a fundamental alteration or discontinuity in development, such as hatching, first feeding, maturation, or a change in habitat (Ricker 1979). Above we presented and reviewed some evidence for this idea from studies of fish. The concept is likely to have validity for many organisms. For example, allometric relationships for physiological rates in *Daphnia* are stage-dependent (McCauley et al. 1990).

Some authors (Reznick et al. 1989, Secor and Dean 1989) have shown that otolith growth rate is relatively insensitive to factors that cause more extensive variation in somatic growth rate (e.g., alterations in temperature and food ration). Under extreme conditions, however, daily increment deposition arrests or is otherwise seriously perturbed (Tanaka et al. 1981, Campana 1983, Neilson and Geen 1985; reviews in Campana and Neilson 1985 and Jones 1986). Nonetheless, in many instances the otolith can be considered a conservative growth structure that is buffered from environmental factors affecting somatic growth. The otolith continues to record significant events, such as transitions to other life stages, even when somatic growth is seriously impaired. Conversely, this buffering tends to obscure the otolithic record of somatic growth fluctuations arising from exogenous factors, e.g., temperature fluctuation, changes in prey density, and turbidity.

Insulation of the otolith to ambient conditions can lead to a somatic:otolith size ratio that is positively related to growth rate. Recently, Campana (1990) showed that this can lead to biased estimates of length-at-age and the appearance of Rosa Lee's phenomenon,

when lengths are back-calculated by the Fraser-Lee method. He noted that this problem is unlikely to be significant when the intercept is well fixed by aging young larval fish, or through use of independent biological measurements. In our study, many of the aged fish were young larvae. In addition, the estimated length of a fish with an otolith radius equal to the mean radius at the extrusion check was in good agreement with the mean length of late-stage gestating pre-extrusion larvae. Lastly, we found no evidence that back-calculated lengths of fish captured as juveniles differed from directly measured lengths of fish captured as larvae.

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Appendix A

Detailed information on individual larval hauls.

Date	Research vessel	Gear type	Max. depth	Lat.	Long.	No. caught	No. aged
2/1	RV <i>Ed Ricketts</i>	Plankton net	150	36°48.2'	121°51.9'	22	15
2/1	"	"	150	36°48.1'	121°52.7'	42	27
2/1	"	"	100	36°47.8'	121°54.0'	27	5
2/1	"	"	100	36°47.8'	121°54.7'	48	34
2/1	"	"	200	36°47.9'	121°53.7'	32	18
2/1	"	"	80	36°48.4'	121°53.2'	36	33
2/1	"	"	100	36°48.3'	121°52.4'	13	4
2/18	RV <i>David Starr Jordan</i>	Isaacs-Kidd trawl	200	37°16.6'	122°49.1'	0	0
2/18	"	"	200	37°16.7'	122°49.0'	32	31
3/6	RV <i>Ed Ricketts</i>	Plankton net	100	36°48.2'	121°52.7'	2	1
3/6	"	"	120	36°47.8'	121°53.7'	5	4
3/6	"	"	140	36°47.2'	121°55.2'	6	6
3/6	"	"	130	36°46.4'	121°59.6'	4	4
3/6	"	"	60	36°47.2'	121°50.6'	12	8

Appendix B

Here we describe the regression model used to relate standard length to otolith radius, which consisted of a series of four linear segments, each describing a different growth stanza. We start with the following equation:

$$SL = \begin{cases} a + b_1x & \text{for } x < c_1 \\ a + b_1c_1 + b_2(x - c_1) & \text{for } c_1 \leq x < c_2 \\ a + b_1c_1 + b_2(c_2 - c_1) + b_3(x - c_2) & \text{for } c_2 \leq x < c_3 \\ a + b_1c_1 + b_2(c_2 - c_1) + b_3(c_3 - c_2) + b_4(x - c_3) & \text{for } c_3 \leq x \end{cases} \quad (1)$$

where a is the y -intercept of the first segment, x is the otolith radius, b_1 , b_2 , b_3 , and b_4 are the slopes of the four segments, and c_1 , c_2 , and c_3 are the points on the x axis corresponding to the intersections. Because not all individuals would be expected to make the transition from one stanza to the next at identical sizes, it is reasonable to smooth the relationship at the segment intersections. We therefore applied the technique described by Bacon and Watts (1971) to smooth the transition between linear segments, assuming that most fish made the transition from one stanza to the next over a small size range. Specifically, we assumed that the probability that an individual fish made the

transition from one stanza to the next was described by the logistic cumulative distribution function, $F(z) = 1/(1 + \exp(-z))$, where $z = (x - c_i)/g$. Note that g is a constant chosen so that 95% of all transitions occur within $\pm 0.3 \mu\text{m}$ OR of each intersection. (We assumed this rapid rate of transition rather than evaluating the transition rate from the data because preliminary analyses, with g as an estimated parameter, indicated that the density of measurements on the x axis was not sufficient to yield unique solutions. Runs with different starting parameters did not converge to the same parameter estimates.) Following Bacon and Watts (1971), we rewrote the model as:

$$SL = e + d_1(x - c_1) + d_2(x - c_1)s_1 + d_3(x - c_2)s_2 + d_4(x - c_3)s_3 \quad (2)$$

where the terms relate to equation 1 as follows:

$$\begin{aligned} s_i &= 2 * (F((x - c_i)/g) - 1); \quad i = 1, 2, 3; \quad g = 0.1, \\ d_1 &= (b_1 + b_4)/2, \quad d_2 = (b_2 - b_1)/2, \\ d_3 &= (b_3 - b_2)/2, \\ d_4 &= (b_4 - b_3)/2, \text{ and} \\ e &= a + ((b_1 + b_4)/2)c_1 - ((b_2 - b_1)/2)c_1 - ((b_3 - b_2)/2)c_2 - ((b_4 - b_3)/2)c_3. \end{aligned}$$

Our estimates of the above parameters and their standard errors are in Appendix Table 1.

Parameter	Estimate	SE
e	12.375	0.411
d_1	0.0780	0.0078
d_2	-0.0507	0.016
d_3	0.0190	0.014
d_4	-0.0136	0.00091
c_1	3.872	0.480
c_2	7.310	2.044
c_3	43.131	2.128