Abstract—An assessment of the total biomass of shortbelly rockfish (*Sebastes jordani*) off the central California coast is presented that is based on a spatially extensive but temporally restricted ichthyoplankton survey conducted during the 1991 spawning season. Contemporaneous samples of adults were obtained by trawl sampling in the study region. Daily larval production (7.56×10^{10} larvae/d) and the larval mortality rate (Z=0.11/d) during the cruise were estimated from a larval "catch curve," wherein the logarithm of total age-specific larval abundance was regressed against larval age. For this analysis, larval age compositions at each of the 150 sample sites were determined by examination of otolith microstructure from subsampled larvae (n=2203), which were weighted by the polygonal Sette-Ahlstrom area surrounding each station. Female population weight-specific fecundity was estimated through a life table analysis that incorporated sex-specific differences in adult growth rate, female maturity, fecundity, and natural mortality (M). The resulting statistic (102.17 larvae/g) was insensitive to errors in estimating M and to the pattern of recruitment. Together, the two analyses indicated that a total biomass equal to 1366 metric tons (t)/d of age-1+ shortbelly rockfish (sexes combined) was needed to account for the observed level of spawning output during the cruise. Given the long-term seasonal distribution of spawning activity in the study area, as elucidated from a retrospective examination of California Cooperative Oceanic Fisheries Investigation (CalCOFI) ichthyoplankton samples from 1952 to 1984, the "daily" total biomass was expanded to an annual total of 67,392 t. An attempt to account for all sources of error in the derivation of this estimate was made by application of the delta-method, which yielded a coefficient of variation of 19%. The relatively high precision of this larval production method, and the rapidity with which an absolute biomass estimate can be obtained, establishes that, for some species of rockfish (*Sebastes* spp.), it is an attractive alternative to traditional age-structured stock assessments.

An approach to estimating rockfish biomass based on larval production, with application to *Sebastes jordani**

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Shortbelly rockfish (*Sebastes jordani*) is an underutilized species that is distributed from Vancouver Island to northern Baja California (Eschmeyer, 1983), although it is especially abundant along the central California coast. Based on a swept-area bottom trawl survey of demersal rockfish, Gunderson and Sample (1980) estimated there were 24,000 metric tons (t) of shortbelly rockfish in the Monterey International North Pacific Fishery Commission (INPFC) area (35°30′N–40°30′N). This biomass estimate was far greater than that of any other species of rockfish in any area and, significantly, it did not include the midwater portion of the stock. Hydroacoustic estimates of shortbelly rockfish biomass in the shelf-slope area between Ascension Canyon and the Farallon Islands (37°00′–38°00′N), a distance of only 110 km, have ranged from 153,000 to 295,000 t (Nunnely[1]).

Although at present there is no directed fishery for this species (Low, 1991), much is known of its biology. Early work by Phillips (1964) provided basic information about the length-weight relationship, growth as estimated from scale annuli, spawning seasonality (i.e. parturition), fecundity, maturity, and the food habits of shortbelly rockfish. Lenarz (1980) later studied shortbelly rockfish growth using ages from whole otoliths and provided preliminary calculations of the effect of fishing on the stock. He also demonstrated marked spatial variation in age and length composition along both latitudinal and depth gradients. Growth was re-esti-

mated by Pearson et al. (1991) using ages determined from broken and burnt otoliths. From the hydroacoustic biomass estimates cited above and an estimated range for the natural mortality rate (0.20–0.35 yr), they concluded that the maximum sustainable yield (MSY) of the shortbelly rockfish stock in the Ascension Canyon–Farallon Islands area was 13,400–23,500 t.

Shortbelly rockfish is one of the few *Sebastes* spp. that can be readily identified at all life history stages. Descriptions of the early life stages of shortbelly rockfish, from preflexion larvae through the pelagic juvenile stage, were provided by Moser et al. (1977). Extending that work, MacGregor (1986) provided a summary of the spatiotemporal distributions of shortbelly rockfish larvae taken in California Cooperative Oceanic Fisheries Investigation (CalCOFI) cruises conducted in five different years. His results showed that 99.1% of all shortbelly rockfish larvae (~4–10 mm) were captured within 90 km of shore and that 65.4% were sampled during the month of February. Moreover, a strong peak in larval abundance (i.e. 34.7% of the coastwide total) was concentrated in the vicin-

ity of Pioneer Canyon (CalCOFI line 63). Later research by Laidig et al. (1991) resulted in the development of a detailed growth model for young-of-the-year shortbelly rockfish, from extrusion through the late pelagic juvenile stage (~180 d), and verified the feasibility of a daily aging protocol by validating a one-to-one correspondence between counts of daily increments and elapsed time in days. More recent work by Ralston et al. (1996) showed that larval shortbelly rockfish can be accurately aged by using optical microscopy.

For the year 2000 the Pacific Fishery Management Council (PFMC) revised the shortbelly rockfish acceptable biological catch (ABC) downwards from 23,500 to 13,900 t/yr (PFMC[2]). The new ABC is based on the low end of the estimated MSY range presented in Pearson et al. (1991); it was reduced due to a probable natural decline in standing stock during the 1990s arising from poor ocean conditions (MacCall, 1996). The original range, however, was derived by using quite variable data from unpublished hydroacoustic surveys and Pearson et al. (1991) considered it a strictly preliminary estimate. Given that the biomass of shortbelly rockfish along the central California coast was once thought to be very large (Gunderson and Sample, 1980; MacGregor, 1986), and that the species is still probably the single largest rockfish contribution available to the west coast groundfish fishery, data are needed to estimate the size of the stock more precisely than results available from these previous investigations.

The goal of this study was to develop an analytical approach to estimate the total biomass of shortbelly rockfish in the region of Pioneer and Ascension Canyons and to gather field data to evaluate the method. Successful application of the method to shortbelly rockfish would provide to the PFMC information useful for management. On a more fundamental level, it would also assist in developing fishery-independent survey techniques capable of assessing other, more highly exploited, species of rockfish.

The assessment approach

The basic premise of egg and larval surveys is that it is easier to estimate the absolute abundance of ichthyoplankton than it is to estimate that of adults (Saville, 1964; Gunderson, 1993). This is especially true when the spatial distribution of adults exhibits some type of size- or age-specific pattern. Shortbelly rockfish is one such species (Lenarz, 1980) and obtaining a representative sample of the adult population is challenging (Lenarz and Adams, 1980). Conversely, early life history stages (i.e. eggs and preflexion larvae) can be sampled effectively with standard plankton nets (Smith and Richardson, 1977). Due to the direct coupling between egg production and spawning biomass, mediated through population weight-specific

fecundity(Φ[eggs/g]), egg and larval surveys have proven successful for estimating spawning biomass in many applications (e.g. Houde, 1977; Parker, 1980; Richardson, 1981; Lasker, 1985; Armstrong et al., 1988; Hunter et al., 1993).

Members of the scorpionfish genus *Sebastes* are distinctive because they are primitive viviparous livebearers (Wourms, 1991), resulting in parturition of advanced yolksac larvae (Bowers, 1992). This reproductive strategy lends itself to a larval production stock assessment because the age of all spawning products can be accurately determined from otolith microstructure (Laidig et al., 1991; Ralston et al., 1996). In contrast, in egg surveys, egg age is back-calculated to the time of spawning by 1) defining a series of developmental stages, 2) estimating the relationship between stage-specific developmental rates and temperature, 3) assigning a thermal history to each egg, and 4) determining the time required to account for embryo development from spawning to the observed stage (see for example Lo, 1985; Moser and Ahlstrom, 1985). Because a distinctive extrusion check forms on the otoliths of *Sebastes* larvae at the time of parturition (Ralston et al., 1996), a rockfish larval production estimate does not require information on temperature-dependent developmental rates and the ambient thermal history of egg samples.

In the approach presented in the present study, a spatially extensive but temporally restricted ichthyoplankton survey was conducted. The age composition of larvae in each plankton tow was determined by subsampling the catch, aging the subsample, and expanding the subsample age composition back to that of the tow total. The total age-specific abundance of larvae in the study region was calculated by weighting the larval catch-at-age in each plankton sample by the polygonal area around it (see Sette and Ahlstrom, 1948). Characterization of the declining trend in total larval abundance at age with an exponential mortality model allowed estimation of the production rate of day-0 larvae and the larval mortality rate at the time the ichthyoplankton cruise was conducted.

Information on adult reproduction was obtained from contemporaneous data collected during two separate cruises conducted during the spawning season. In particular, the following functional relationships were estimated from the data collected: 1) weight as a function of total length, 2) sex-specific weight at age (i.e. male and female von Bertalanffy growth equations), 3) fecundity as a function of total weight, 4) maturity as a function of age, and 5) the population sex ratio. From these relationships, a life table was constructed, based on an estimate of natural mortality (/yr), that yielded estimates of population weight-specific fecundity (Φ). As defined here, population weight-specific fecundity includes the biomass contributions to total population size from males and immature females.

Together, these estimates (daily larval production and population weight-specific fecundity) can be used to calculate the "daily" total biomass of fish in the population required to produce the observed abundance of larvae. The long-term mean seasonal distribution of shortbelly

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rockfish larvae and spawning activity was then determined by a retrospective analysis of all CalCOFI ichthyoplankton samples collected in the vicinity of Pioneer Canyon. Based upon the timing of our larval survey with respect to the long-term mean distribution of spawning activity, total "annual" biomass was calculated by expansion. Finally, the robustness of the total biomass estimate was evaluated through a simulation study and sensitivity analyses.

Methods

Trawl sampling of adults

Specimens of adult shortbelly rockfish were collected during February–March 1991 by the FV *New Janet Ann* and the RV *Novodrutsk* (Table 1). Shortbelly rockfish aggregations in and around Ascension and Pioneer Canyons (Fig. 1) were targeted from acoustic surveys. A total of 28 trawls (12 bottom and 16 midwater) were conducted over bottom depths ranging from 115 to 384 m, at an average net depth of 126 m (range: 18–210 m). The bottom trawl codend mesh size was 3.8 cm and the midwater trawl mesh was 5.1 cm. Duration of the trawls ranged from 3 to 73 min ($\bar{x}$=26 min). All landings were either fully weighed or subsampled, depending on the size of the catch. Landings were highly variable, ranging from 23 to 36,300 kg.

Two subsamples were taken from each trawl landing. The first was used to determine the overall age, size, sex, and maturity composition of the catch; it was obtained by randomly selecting and examining 100–300 individuals from each trawl, depending on the availability of both time and fish. For these specimens, total lengths (TL) were measured to the nearest mm, gonads were examined to determine sex and to assign gross maturity stages (see below), and otoliths were removed for later age determination by the break-and-burn method (Pearson et al., 1991). A second smaller subsample of 25–50 specimens was also taken to estimate length-weight and fecundity relationships. For each of these fish, TL was measured, weight was determined to the nearest mg, the otoliths were extracted, and late vitellogenic ovaries were dissected from females and fixed in Gilson's fluid.

We rated females in terms of maturity based on gross gonadal condition. A summary of the scale we used is the following: 1.0 = immature; 2.0–2.9 = vitellogenic oocytes (yolk deposition with associated oocyte and ovary enlargement); 3.0–3.9 = fertilized eggs (embryos to hatched larvae); 4.0 = spent; and 5.0 = reorganization and recovery.

Fecundity of female shortbelly rockfish was estimated gravimetrically from vitellogenic ovaries after 2–4 months
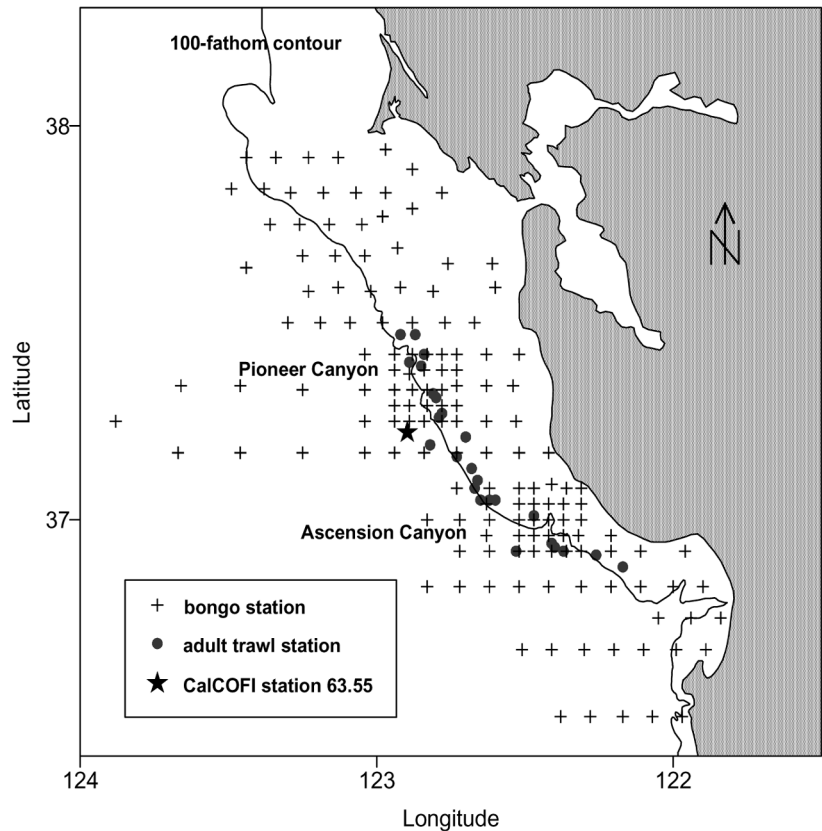

Figure 1

Map of the central California study region showing bongo net and adult trawl sampling locations. The annual spawning season was estimated by the long-term seasonal distribution of shortbelly rockfish larvae at CalCOFI station 63.55.

Table 1

Summary information of trawl collections for adults. Trawl locations are shown as closed circles in Figure 1. NJA = RV *New Janet Ann*; NOV = RV *Novodrutsk*.

Date	Vessel	Trawl type	
		Bottom	Midwater
14 Feb 1991	NJA	3	1
15 Feb 1991	NJA	2	1
22 Feb 1991	NJA	4	1
23 Feb 1991	NJA	3	1
15 Mar 1991	NOV	0	3
16 Mar 1991	NOV	0	3
17 Mar 1991	NOV	0	2
18 Mar 1991	NOV	0	2
19 Mar 1991	NOV	0	2

fixation with periodic stirring. Entire fixed ovaries from each female were blotted dry and weighed to the nearest 1.0 mg. Duplicate subsamples of both ovaries were weighed

to the nearest 0.1 mg and their egg contents counted with the aid of a dissecting microscope. The mean number of eggs per gram from each fish was then expanded to the total ovary weight to estimate annual fecundity (total eggs per individual female).

To estimate population weight-specific fecundity, first the length and weight data were fitted to the power function and the bias-corrected regression equation was used to estimate the weight of every fish that was aged. Next, for each sex, growth equations were obtained by fitting the weight and age "data" to the von Bertalanffy growth model (Ricker, 1975). Maturity was quantified by fitting the logistic equation to the proportion of females that were mature within 5-mm-TL intervals, and fecundity was estimated by fitting fecundity and female weight data to the power function, with appropriate bias-correction. These various functional relationships were then combined in a life table analysis to determine the expected biomass per female recruit and the expected lifetime larval production per female recruit. The ratio of these quantities is the estimated equilibrium cohort weight-specific fecundity (i.e. Φ[larvae/g]) of female shortbelly rockfish. Given an estimate of total age-0 larvae (N_0), the female biomass responsible for the observed larval production can be estimated as $N_0\Phi^{-1}$. Finally, the combined sex biomass can be determined by expanding female biomass using weight-based cohort sex ratio estimates from the life table analysis.

Ichthyoplankton sampling

The primary set of ichthyoplankton samples used in our study was obtained by using bongo nets during a cruise of the NOAA RV *David Starr Jordan* (DSJ-9102) conducted in the winter of 1991. Sampling began at 1500 h on 8 February and ended at 0230 h on 15 February. During that $6\frac{1}{2}$-day period 150 stations were occupied in the region bounded from lat. 36°30′N to lat. 38°00′N and offshore to a maximum distance of 130 km (Fig. 1). The study area included Pioneer and Ascension Canyons—two features in the continental slope known to harbor large numbers of adults (Lenarz, 1980; MacGregor, 1986; Chess et al., 1988). At these sites the sampling density was increased.

Field and laboratory processing of the bongo net samples followed prescribed CalCOFI guidelines (i.e. Kramer et al., 1972; Smith and Richardson, 1977), with minor modification. For example, at every fifth sampling station, the bongo frame was deployed with 333-μm and 505-μm mesh nets to determine the extent of extrusion of small larvae in the standard 505-μm mesh (Lenarz, 1972; Somerton and Kobayashi, 1989). After the nets were washed down, samples from both mesh sizes were preserved in 80% EtOH. At all other stations, the net frame was deployed with two 505-μm mesh nets; one sample was preserved in 80% EtOH (to allow later age determinations from larval otoliths), and the other was preserved in 10% buffered formalin. In addition, because *Sebastes* larvae were believed to occur only in the upper mixed layer (Ahlstrom, 1959), the maximum amount of wire deployed was 200 m, resulting in a maximum depth fished equal to 140 m. Following splitting, sorting, identification, and enumeration of the

larvae in the laboratory, abundance was expressed as the number of shortbelly rockfish per 10 m² of sea surface.

To estimate the age composition of the larval population, the sorted shortbelly rockfish larvae from each of the 150 EtOH-preserved bongo hauls were randomly subsampled for otolith microstructure examination. To determine the size of an age subsample (N_s), based upon the total number of larvae occurring in a haul (N_h), we applied the following rule: 1) for N_h less than or equal to 10, $N_s = N_h$, 2); for N_h greater than 10 but less than or equal to 410, $N_s = 10 + 0.10[N_h - 10]$; and 3) for N_h greater than 410, $N_s = 50$. Otoliths were extracted from each specimen in the haul subsample and individual ages determined by methods outlined in Laidig et al. (1991) and Ralston et al. (1996).

The age composition of the larvae in each bongo sample was then estimated by expanding the percent age-frequency obtained from the subsample to the haul total (N_h). The estimated numbers-at-age of larvae in each haul were standardized to the number per 10 m² of sea surface (n_{Ti} for age T and haul i) by application of standard haul factors (Kramer et al., 1972; Smith and Richardson, 1977).

We expanded the n_{Ti} to the entire survey area by using the method of Sette and Ahlstrom (1948). The Sette-Ahlstrom estimate is calculated by the following equation (see Kendall and Picquelle, 1990):

$$\hat{N}_T = \sum_{i=1}^{k} A_i \times n_{Ti},$$

where for each of k hauls A_i = the area that haul i represents (units of 10 m²); and

N_T = the total abundance of larvae of age T in the entire survey area.

The area for a haul (A_i) is defined as the area circumscribed by a polygon containing all points in space closer to a haul's location than to the location of any other haul. With this definition, we were able to write a simple computer program to calculate Sette-Ahlstrom weights by dividing the study area into a fine grid and assigning each grid point to a haul. Note that this definition and procedure for obtaining Sette-Ahlstrom areas is equivalent to constructing polygons manually using perpendicular bisectors and measuring their areas (Sette and Ahlstrom, 1948).

The mean daily larval production rate during the cruise was estimated as the bias-corrected antilogarithm of the y-intercept of the ordinary least-squares linear regression of $\log_e[\hat{N}_t]$ against larval age. Moreover, the regression slope provides an estimate of the total instantaneous mortality rate of the larvae (Z [/d]). This calculation implicitly assumes that the age distribution of larvae was stationary throughout the $6\frac{1}{2}$-day period of the cruise.

To determine if shortbelly rockfish larvae occur deeper in the water column than 140 m, a series of 1-m² multiple-opening-closing-net with environmental sensing system (MOCNESS) tows was conducted aboard the RV *David Starr Jordan* (cruise DSJ-9203) during the 1992 spawning season. At that time, 21 tows were made in the area of

Pioneer and Ascension Canyons from 1800 h on 21 February to 0600 h on 23 February. Where bottom depth permitted, discrete depth samples were gathered using 505-μm mesh nets, sampling obliquely in the 0–40, 40–80, 80–120, 120–160, 160–200, 200–300, and 300–400 m depth intervals. Sampling was arrayed along seven onshore–offshore transects, each composed of three tows conducted at different bottom depths, i.e. mid-continental shelf (110 m), the shelf-break (183 m), and well off the shelf (550 m). All samples were preserved in EtOH and after sorting, identifying, and enumerating the larvae in the laboratory, we expressed abundances as the number of shortbelly rockfish larvae per 1000 m^3 water sampled.

Spawning seasonality

At its inception, this assessment was intended to be an application of the fecundity reduction method described by Lo et al. (1992, 1993). However, samples from the February and March adult trawl surveys showed that a higher proportion of females had completed spawning in the earlier cruise in comparison with the later cruise, an indication that sampling was not representative during one or both of the cruises. Consequently, the fecundity reduction method was abandoned and an alternative approach was devised. Instead, we estimated the seasonal distribution of spawning activity based on the temporal distribution of preflexion shortbelly rockfish larvae in samples collected as part of the CalCOFI program from December to April from 1952 to 1984 (see Ahlstrom et al., 1978). We then used this seasonal spawning pattern to expand our estimate of the daily spawning biomass from the short period represented by our 1991 plankton samples to the entire year.

To estimate the seasonal spawning distribution, we first identified the appropriate samples from CALCOFI station 63.55 in the vicinity of Pioneer Canyon by using results from MacGregor (1986) as a guide. Plankton samples at this location (Fig. 1) were re-examined and the total number of preflexion shortbelly rockfish larvae were enumerated from *Sebastes* subsets. These samples amounted to 41 plankton tows (bongo and ring nets) taken in 21 different years.

Next, we calculated the mean density of preflexion larvae for each month, assigned these densities to the midpoint day of the month, and used nonlinear least-squares regression to fit the normal curve to approximate the seasonal spawning pattern, i.e.

$$\hat{N}_p(t) = \frac{\psi}{\hat{\sigma}_p \sqrt{2\pi}} e^{-\frac{(t-\hat{\mu}_p)^2}{2\hat{\sigma}^2}},$$

where $\hat{N}_{p(t)}$ = the estimated density of preflexion larvae on calendar day t (for December t is negative);

$\hat{\mu}_p$ = the expected value of the seasonal distribution of preflexion larvae;

$\hat{\sigma}_p$ = the standard deviation of the distribution; and

Ψ = a "nuisance" scaling constant.

To determine the seasonal distribution of age-0 larval production that generates the seasonal distribution of preflexion larvae, we assumed that the preflexion larval period has a duration of 15 days (Laidig et al., 1991) and that larvae experience the estimated preflexion mortality rate (see above). As with preflexion larvae, we approximated the seasonal distribution of age-0 larval production with a normal curve, with mean μ_0 and standard deviation σ_0. Given particular values for μ_0 and σ_0 we calculated the corresponding relative numbers of age-0 larvae produced during each day of the spawning season, and the integrated seasonal distribution of preflexion larvae, i.e.

$$N_p^*(t) = \sum_{i=0}^{15} N_0(t-i) e^{-iZ}.$$

We started the estimation with trial values of μ_0 and σ_0 and then recursively adjusted the parameter estimates until the mean and standard deviation of the inferred seasonal distribution of preflexion larvae ($N_{p(t)}^*$) converged on the empirical estimates of $\hat{\mu}_p$ and $\hat{\sigma}_p$.

Lastly, based on the timing of the larval survey within the long-term mean spawning distribution, total biomass was calculated by simple expansion. Specifically, the midpoint of the 1991 bongo survey was 11 February (i.e. calendar day 42). Consequently we calculated λ, which is the proportion of annual spawning under the age-0 larval production curve that occurs from day 41.5 to 42.5. Total population biomass was then estimated by multiplying the estimate of "daily" biomass by $1/\lambda$. This calculation implicitly assumes that the seasonal progression of spawning has been stable over years. Therefore, the sensitivity of the biomass estimate to a violation of this assumption was evaluated by profiling over a range of values for the mean date of spawning (μ_0), which has a substantial effect on λ.

Precision of the biomass estimate

The determination of total biomass requires the estimation of numerous statistical relationships, each with its own parameter set. The results of fitting these functions were then combined algebraically to produce the final biomass estimate. We calculated the precision of the final biomass estimate by using the delta method (Seber, 1982, p. 8), i.e.

$$V[g(\theta)] = \sum_i V[\theta_i]\left(\frac{\partial B}{\partial \theta_i}\right)^2 + 2\sum_{i<j}\sum \text{cov}[\theta_i, \theta_j]\frac{\partial B}{\partial \theta_i}\frac{\partial B}{\partial \theta_j},$$

where g(θ) = the algebraic combination of functions used to produce the final biomass estimates; and

θ = the full set of estimated parameters.

Application of this method requires estimates of variances for each parameter, covariances among parameters, and partial derivatives of estimated biomass with respect to each parameter ($\partial B/\partial \theta$). Partial derivatives of the final biomass estimate with respect to the parameters were calculated numerically by using central differencing by per-

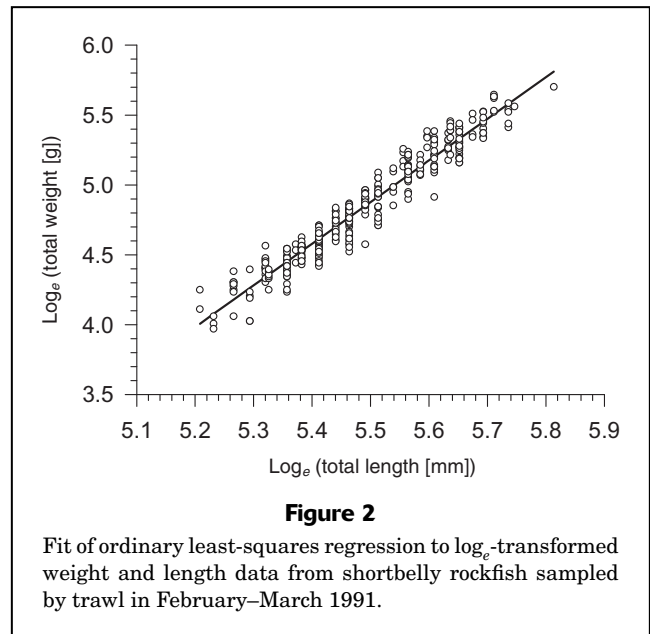turbing each parameter ±1% and calculating the resulting effect on biomass.

In some instances, variance estimates (i.e. squared standard errors) and covariances were extracted directly from computer output produced by the SAS (1987) procedures PROC REG and PROC NLIN. In the case of linear regressions, these are the usual estimates of these quantities (e.g. Draper and Smith, 1981), whereas for nonlinear regression, these are asymptotic variances and covariances (e.g. Seber and Wild, 1992). In addition, following the assumptions of normal-based regression, the residual error parameter estimates ($\hat{\sigma}^2_{mse}$) used in bias adjustments are independent of other regression parameters (i.e. covariances are zero) and $n\hat{\sigma}^2_{mse}/\sigma^2_{mse}$ has a chi-square distribution with k degrees of freedom, where k is the degrees of freedom associated with $\hat{\sigma}^2_{mse}$ (e.g. for a linear regression $k=n-2$). This chi-square distributed random variable, i.e.

$$\text{var}\left(\frac{n\hat{\sigma}^2_{mse}}{\sigma^2_{mse}}\right) = 2k,$$

was then used to estimate the variance of the mean square errors (Larsen and Marx, 1981)

$$\text{var}(\hat{\sigma}^2_{mse}) = \left(\frac{\hat{\sigma}^4_{mse}}{n^2}\right) \times 2k.$$

This straightforward approach to obtaining variances and covariances is appropriate when a suite of parameters estimated by a regression procedure is based on a data set that could reasonably be expected to be independent of data sets used to estimate other parameters, and when values of other estimated parameters were not used as "known" constants during a regression or estimation procedure. In two cases, however, estimates of other parameters were treated as known constants during a regression or estimation procedure. These cases were 1) estimation of the mean and standard deviation of the seasonal distribution of age-0 larvae, and 2) estimation of von Bertalanffy growth equation parameters. In the case of the seasonal distribution of age-0 larvae, parameter estimates depended upon the natural mortality rate estimated for larvae (Z). Hence, variances for these parameters calculated directly from the regression procedure are conditional on the estimated mortality rate. Imprecision associated with estimating this rate adds to variances of these parameters, and influences their covariance. Likewise, for von Bertalanffy growth, the weight "data" used were calculated on the basis of the estimated relationship between weight and length. Hence regression estimates of variance and covariances for the von Bertalanffy parameters are conditional on the parameters for the weight-length relationship. Uncertainty associated with the estimates of the weight-length parameters influences the unconditional variances and covariances of the von Bertalanffy parameters, sets up covariances between the two suites of parameters, and because the same weight-length relationship was used for both sexes, also sets up

Figure 2

Fit of ordinary least-squares regression to $\log_e$-transformed weight and length data from shortbelly rockfish sampled by trawl in February–March 1991.

covariances among the von Bertalanffy parameters for males and females.

For these cases, a generalized version of the delta method was used to estimate covariances (and variances):

$$\text{cov}[g(x,y), h(x,z)] = \sum_{ij}\sum \text{cov}[x_i, x_j]\frac{\partial g}{\partial x_i}\frac{\partial h}{\partial x_j}$$

(Seber, 1982, p. 9). Here g and h represent regression procedures by which two specified parameters are estimated, x represents a set of shared values (assumed known parameters and data) used by the two regression procedures, y and z represent distinct data or parameters with no covariance among them, and partial derivatives are calculated as described above.

Results

Population weight-specific fecundity and sex ratio

The weight (W) of a fish is equated to its length (TL) by use of the power function, i.e.

$$W = \alpha TL^\beta,$$

where α and β are fitted parameters (Ricker, 1975).

In our study, weight (gm) and TL (mm) data were collected from 352 fish sampled during the two adult trawl cruises. The data from these fish were $\log_e$-transformed and fitted by linear regression (Fig. 2, Table 2). The fit was good, as indicated by a high r^2 value (0.94), and the distribution of residuals did not deviate from normality ($P=0.109$). To predict weight at length on the untransformed scale, a

Table 2

Functional relationships, estimated parameters, statistical results, and sensitivity analyses of shortbelly rockfish larval production biomass estimate.

Function	Parameter	Estimate	Standard error	% Effect on biomass −1 SE	% Effect on biomass +1 SE
Length-weight relationship $\log_e(W) = \log_e(\alpha) + \beta\,(\log_e[TL])$	$\log_e(\alpha)$	−11.512	0.2225	0.00%	0.00%
	β	2.980	0.0405	0.09%	−0.08%
	σ^2_{MSE}	0.008820	0.000667	0.00%	0.00%
Female von Bertalanffy growth $W_\female = W_{\infty,\female}\{1-\exp[-K_\female(T-t_{0,\female})]\}^\beta$	$W_{\infty,\female}$,	248.1	2.6245	0.64%	−0.63%
	$K_\female$	0.2843	0.00917	1.73%	−1.58%
	$t_{0,\female}$	−0.78	0.11026	−0.91%	0.96%
Male von Bertalanffy growth $W_\male = W_{\infty,\male}\{1-\exp[-K_\male(T-t_{0,\male})]\}^\beta$	$W_{\infty,\male}$,	209.9	3.0872	−0.67%	0.67%
	$K_\male$	0.2432	0.00984	−2.05%	2.01%
	$t_{0,\male}$	−1.48	0.15183	1.55%	−1.54%
Adult survival $\log_e(N_T) = \log_e(\eta_0) - M(T)$	$\log_e(\eta_0)$	3.194	0.30662	0.00%	0.00%
	M	0.2616	0.02656	−1.46%	1.53%
Fecundity at weight $\log_e(F) = \log_e(\phi) + \delta(\log_e[W])$	$\log_e(\phi)$	3.8155	0.1732	18.91%	−15.90%
	δ	1.1416	0.0366	19.88%	−16.61%
	σ^2_{MSE}	0.2972	0.01827	0.92%	−0.91%
Maturity at length $S = 1 + \nu/\{1+\exp[-\rho(TL - TL')]\}$	ν	2.888	0.0237	0.00%	0.00%
	ρ	0.6046	0.10318	0.00%	0.00%
	TL'	135.05	0.85515	−0.15%	0.00%
Larval production and survival $\log_e(N_T) = \log_e(N_0) - Z(T)$	$\log_e(N_0)$	−0.3775	0.1737	−15.97%	19.01%
	Z	0.1107	0.01157	0.70%	−0.67%
	σ^2_{MSE}	0.1960	0.05659	−2.79%	2.87%
Spawning seasonality $N_p(t) = (\Psi/\sigma_p\sqrt{2\pi})\exp[-(t-\mu_p)^2/2\sigma_p^2]$	Ψ	5.2×10^4	2.36×10^3	0.00%	0.00%
	μ_p	37.88	1.1250	4.02%	−3.45%
	σ_p	17.39	1.1042	−4.58%	4.78%

bias-correction term ($\hat{\sigma}^2_{mse}/2$) was applied prior to exponentiation (Miller, 1984). However, because $\hat{\sigma}^2_{mse}$ was small (0.00882), the correction had little effect on predictions of weight at TL. Moreover, predicted values of weight at length did not differ materially from those given in Phillips (1964) and Lenarz (1980).

A total of 586 female shortbelly rockfish were aged from trawl samples. The weights (g) of these fish were individually estimated from measurements of TL (mm) by using the regression results described above. The derived weight-at-age (yr) data were then fitted to the von Bertalanffy growth equation by using a nonlinear regression routine (SAS, 1987). The specific form of the fitted model was

$$W_\female = W_{\infty,\female}\,[1 - e^{-K_\female(T - t_{0,\female})}]^\beta,$$

where $W_\female$ = female weight (g)
$W_{\infty,\female}$ = the asymptotic mean weight of females at a hypothetically infinite age (g);
$K_\female$ = the instantaneous growth coefficient specific to females (/yr);
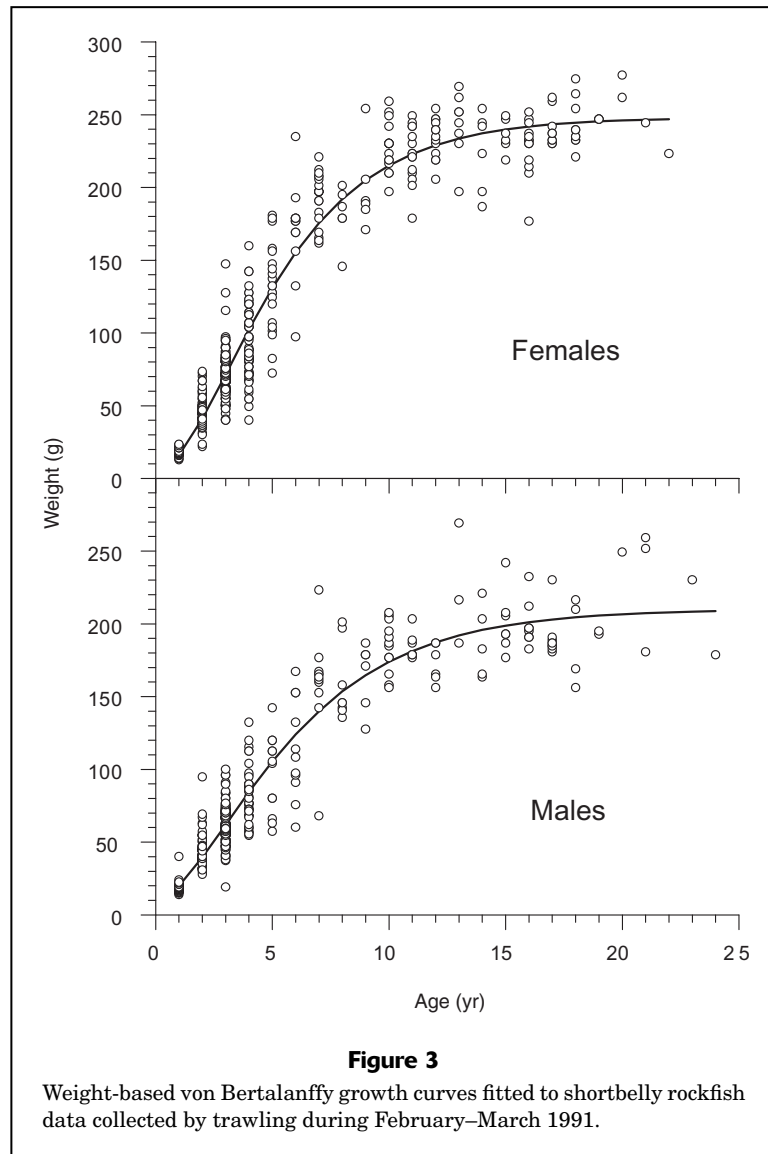T = age (yr);

$t_{0,\female}$ = the x-intercept of the growth curve (yr); and
β = the allometric growth parameter estimated from the regression of weight on length (Ricker, 1975).

The β parameter is often set equal to 3.0, implying isometric growth, although β was fixed at 2.980 in this application (see above). Likewise, 535 adult male fish were aged, their weights estimated from measurements of TL, and the data fitted to the weight-based von Bertalanffy growth model. Regression results for both sexes are presented in Figure 3 and Table 2.

A simple exponential mortality model is used to describe the observed pattern of shortbelly rockfish abundance with age. The model is of the form

$$N_T = \eta_0 e^{-MT},$$

where N_T = the number of individuals alive at age T (yr);
η_0 = the extrapolated number at age T=0; and
M = the instantaneous rate of natural mortality (/yr).

Figure 3

Weight-based von Bertalanffy growth curves fitted to shortbelly rockfish data collected by trawling during February–March 1991.

In this application a term for fishing mortality is assumed to be unnecessary because there is no commercial or recreational harvest of shortbelly rockfish. The model was fitted by a weighted linear regression of $\log_e(N_T)$ on T, where the statistical weights were derived from expansions of the aged subsamples to the full trawl catches. Results showed a declining trend in abundance with age (Table 2, Fig. 4), and an estimated adult natural mortality rate of 0.26/yr.

Like the weight-length relationship, fecundity is typically related to fish size with the power function (Bagenal and Braum, 1968), which is linearized by logarithmic transformation, i.e.

$$F = \phi W^\delta,$$

$$\log_e(F) = \log_e(\phi) + \delta \times \log_e(W),$$

where F = individual annual fecundity (larvae/female);

W = female weight (g); and
$\log_e[\phi]$ and δ = fitted parameters.

In our study fecundity estimates were gathered from 531 females taken during the trawl surveys and the transformed data were fitted by simple regression (Fig. 5, Table 2). There was considerable residual variability in the fecundity at weight relationship (r^2=0.65; $\hat{\sigma}^2_{mse}$ =0.29715) and, in this instance, the addition of a bias-correction term had a noticeable effect on back-transformed predictions of fecundity at weight on the arithmetic scale. Although the distribution of regression residuals deviated significantly from normal (P=0.0001), due in large part to negative skewness, the overall fit was deemed adequate. Predictions of fecundity at weight were ~25–35% less than the results presented in Lenarz (1980), although his equation is based on only the 10 data points provided in Phillips (1964).
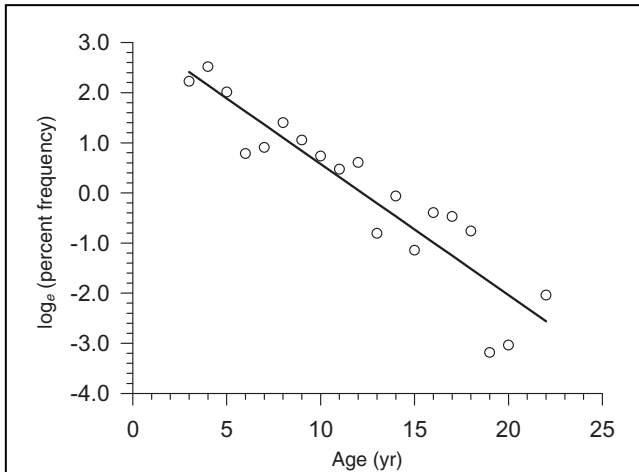
Figure 4

Weighted linear regression of $\log_e$-transformed shortbelly rockfish abundance on age (statistical weights based on expansions of aged subsamples to full trawl catches; all samples collected by trawling during February–March 1991).
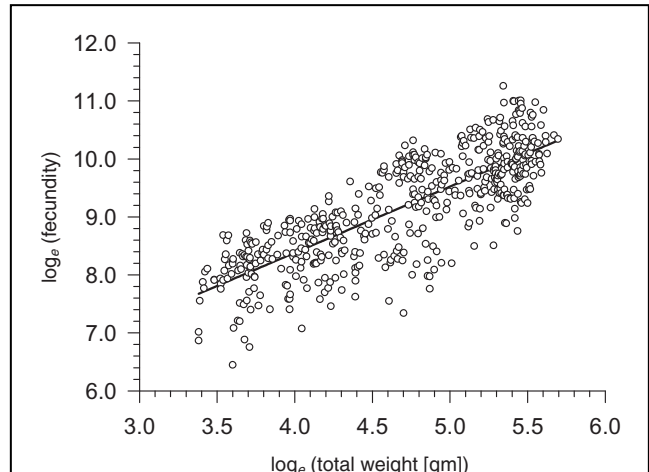

Figure 5

Fit of ordinary least-squares regression to $\log_e$-transformed fecundity and weight data from shortbelly rockfish sampled by trawling during February–March 1991.

There was no evidence that the sex ratio of the fish sampled during the 1991 spawning season (n=1121 from February and March cruises combined) varied with age. A two-way test for independence of age and sex yielded χ^2=27.55, df=23, P=0.23. Moreover, there was no evidence that the overall population sex ratio was other than 50:50 ($N_{\female}$=586, $N_{\male}$=535; χ^2=2.32, df=1, P=0.14). From these results, we concluded that females and males both enter the population at approximately the same rate and thereafter they experience a similar natural mortality rate.

The maturity stage data were used to establish a maturity schedule for female shortbelly rockfish collected during the 1991 winter spawning season. Fish were first stratified by size class (5-mm-TL intervals), and for each size group, the mean coded ovarian stage was computed. The data were then fitted by nonlinear regression (SAS, 1987) to a logistic model of the form

$$S = 1 + \frac{\nu}{1 + e^{-\rho(TL - TL')}},$$

where S = the mean coded maturity stage;
          TL = total length (mm); and
ν, ρ, and TL' = fitted parameters.

Results show (Fig. 6, Table 2) an abrupt change in ovarian condition at a length of 135 mm. At the time of sampling (February–March), virtually all fish above that size were gestating or had already released their larvae, whereas fish smaller than that cutoff size were almost exclusively immature. All females were therefore assumed to be reproductively mature if TL was greater than 135 mm. The proportion of fish in each age class that exceeded 135 mm TL was used to define an empirical age-based
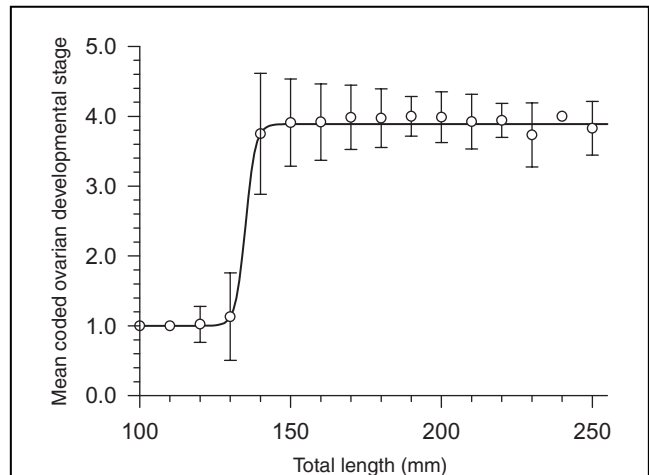

Figure 6

Fit of the logistic maturity function to coded ovarian developmental stage data. Circles are means, which are bracketed by ±1.0 standard deviation (all samples collected by trawling during February–March, 1991).

maturity ogive. Results indicated that 7.9% of 1-yr-old fish spawned, whereas 99.0% of 2-yr-old females reproduced.

When coupled with some type of recruitment model, the four functional relationships given in Figures 3–6 can be used to estimate population weight-specific fecundity and a weight-based population sex ratio. These latter two variables are presented in Table 3 as part of a life table projection for shortbelly rockfish. In the table, age is incremented discretely in one year steps to a maximum life span of 30 yr, which extends well beyond the maximum observed age of 22 years (Pearson et al., 1991). All calculations were

Table 3

Life table for shortbelly rockfish (*Sebastes jordani*) based upon samples of adults obtained during the 1991 spawning season (February–March).

Age (yr)	♀ or ♂ numbers	♀ Wt (g)	♀ Cohort Wt (g)	Fecundity (larvae/♀)	Weight-specific fecundity (no. of larvae/g of female)	Proportion mature	Cohort fecundity (larvae)	♂ Wt (g)	♂ cohort Wt (g)
1	1.0000	15.9	15.85	1235	77.90	0.079	98	19.9	19.89
2	0.7698	41.0	31.54	3651	89.11	0.990	2783	39.6	30.50
3	0.5926	71.5	42.37	6893	96.42	1.000	4085	62.0	36.72
4	0.4562	102.4	46.72	10,390	101.45	1.000	4740	84.4	38.50
5	0.3512	130.8	45.93	13,736	105.03	1.000	4824	105.3	36.99
6	0.2704	155.3	41.98	16,710	107.61	1.000	4518	124.0	33.52
7	0.2081	175.6	36.55	19,227	109.50	1.000	4002	140.0	29.14
8	0.1602	192.0	30.76	21,291	110.89	1.000	3411	153.6	24.60
9	0.1233	205.0	25.28	22,943	111.93	1.000	2830	164.7	20.32
10	0.0950	215.1	20.43	24,245	112.70	1.000	2302	173.9	16.51
11	0.0731	223.0	16.30	25,258	113.27	1.000	1846	181.3	13.25
12	0.0563	229.0	12.89	26,040	113.70	1.000	1465	187.2	10.54
13	0.0433	233.6	10.12	26,640	114.02	1.000	1154	192.0	8.32
14	0.0333	237.2	7.91	27,098	114.26	1.000	904	195.8	6.53
15	0.0257	239.8	6.16	27,446	114.44	1.000	705	198.8	5.10
16	0.0198	241.8	4.78	27,710	114.58	1.000	548	201.1	3.98
17	0.0152	243.4	3.70	27,910	114.68	1.000	425	203.0	3.09
18	0.0117	244.5	2.86	28,061	114.76	1.000	329	204.5	2.39
19	0.0090	245.4	2.21	28,175	114.82	1.000	254	205.7	1.85
20	0.0069	246.1	1.71	28,261	114.86	1.000	196	206.6	1.43
21	0.0053	246.5	1.32	28,326	114.89	1.000	151	207.3	1.11
22	0.0041	246.9	1.02	28,375	114.92	1.000	117	207.9	0.85
23	0.0032	247.2	0.78	28,412	114.94	1.000	90	208.3	0.66
24	0.0024	247.4	0.60	28,440	114.95	1.000	69	208.7	0.51
25	0.0019	247.6	0.46	28,461	114.96	1.000	53	208.9	0.39
26	0.0014	247.7	0.36	28,476	114.97	1.000	41	209.1	0.30
27	0.0011	247.8	0.28	28,488	114.97	1.000	32	209.3	0.23
28	0.0009	247.8	0.21	28,497	114.98	1.000	24	209.4	0.18
29	0.0007	247.9	0.16	28,504	114.98	1.000	19	209.6	0.14
30	0.0005	247.9	0.13	28,509	114.98	1.000	14	209.6	0.11
Total			411.37				42,028		347.65

based on a discrete time origin that was centered in the spawning season and it was assumed that samples were obtained at that time.

For simplicity, constant annual recruitment to the population at age 1 is assumed, although this particular assumption is later relaxed and its specific effect on estimates of population weight-specific fecundity is evaluated. To start the simulated population, recruitment was arbitrarily set equal to $N_1 = 1.0$/yr for both females and males. Then, given female weight at age (Fig. 3) and female numbers at age (Fig. 4), one can calculate age-specific female cohort biomass as the product of numbers and individual weights (Table 3), which when summed over all ages yields the total equilibrium female biomass (411.37 g/female recruit). Likewise, age-specific cohort fecundity is calculated as female numbers at age, multiplied by estimates of individual female fecundity (Fig. 5), multiplied by the proportion of females

that are mature (Fig. 6), which when summed over all ages classes yields the expected lifetime larval production of a cohort (42,028 larvae). The ratio of these two quantities (Φ=102.17 larvae/g of female) estimates the population weight-specific fecundity of female shortbelly rockfish. This population statistic can be compared with individual age-specific estimates presented in Table 3. These weight-specific fecundities range from 77.90 larvae/g of female for the mature 1-yr-old females, to 114.98 larvae/g of female for the oldest fish.

It is also revealing to compare predicted weight-specific fecundity at age from the life table analysis (Table 3) with the observed data calculated directly from individual fish (Fig. 7). Results show a great deal of variability in the observed data, which is consistent with the extensive residual variability in fecundity (see Fig. 5, Table 2). Life table predictions were generally similar to, but slightly higher than, the observed data. This slight difference is
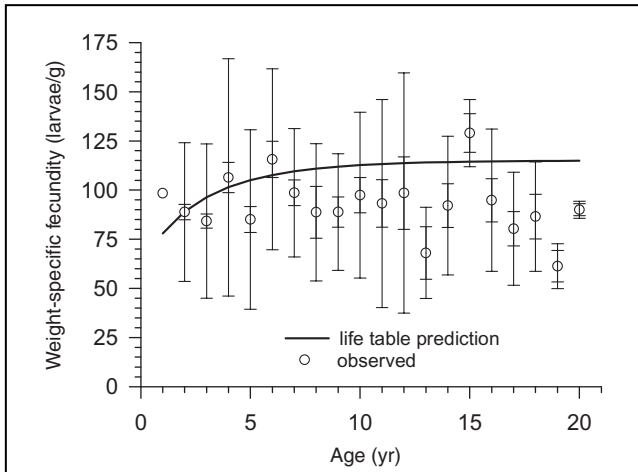
Figure 7

Weight-specific fecundity and its dependency on age. Observed values are means of measured females, bracketed by ±1.0 standard error and ±1.0 standard deviation (all samples collected by trawl during February–March, 1991). The solid line, which is not fitted to the "observed" points, is the predicted relationship from the life table analysis presented in Table 3.

Figure 8

Results of Monte Carlo simulation evaluating the effect of recruitment stochasticity on calculations of shortbelly rockfish population weight-specific fecundity.

due to the bias correction that occurs when the fecundity relationship, which was fitted on the log-scale, is back-transformed to the arithmetic scale. Irrespective of the type of data, however, it is evident that weight-specific fecundity is only weakly dependent on age. This finding implies that changing the equilibrium age structure of the population, as mediated through an alteration in the natural mortality rate (M), will have little effect on the population's weight-specific fecundity.

The assumption that recruitment is constant and uniform does not appear to appreciably bias the estimate of population weight-specific fecundity derived from the life table analysis (102.17 larvae/g of female). Population weight-specific fecundity was also estimated in a Monte Carlo life table simulation that used a more realistic lognormal recruitment model (Fogarty, 1993). Annual recruitments in that simulation were determined as N_1 = $\exp(\mu + \sigma X)$, where N_1 is the number of recruits at age 1, $\mu = \log_e[10,000]$, $\sigma = 0.921$, and X is a standard normal deviate (i.e. $X \sim N[0,1]$). This level of variability in lognormal recruitment is comparable to that observed in the widow rockfish fishery (Bence et al., 1993; Hightower and Lenarz[3]), where 20-fold differences in recruitment have been observed in a 10-yr time period. Results of the simulation showed that fluctuating, lognormal recruitment can
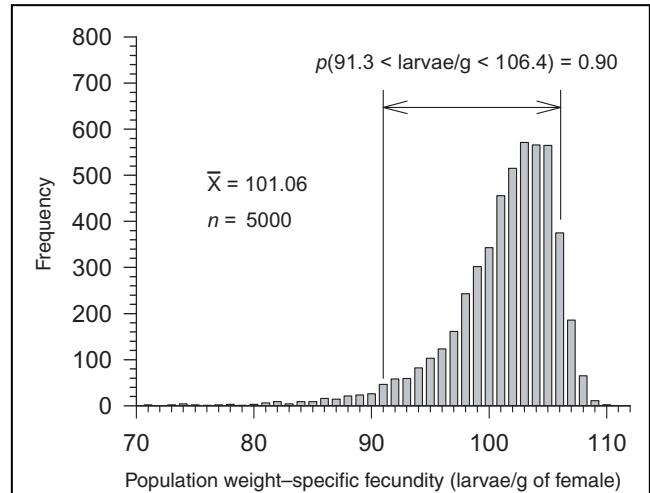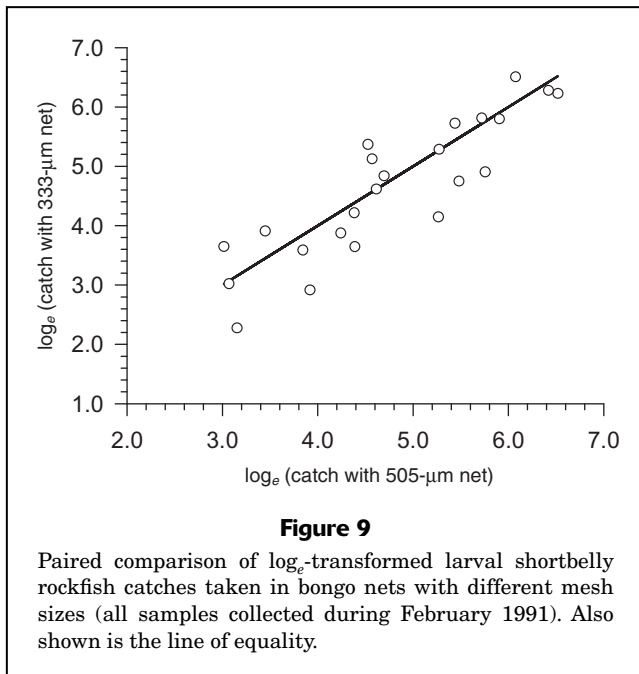
produce values of population weight-specific fecundity that range from 71 to 110 larvae/g of female, depending on the exact sequence of year classes and their resulting affect on age structure (Fig. 8). Even so, the mean of the sample distribution ($\bar{x}=101.06$ larvae/g of female, $n=5000$) did not differ significantly from the life table calculation that had no recruitment variability. In addition, 90% of all the lognormal recruitment realizations were within ±10% of the constant recruitment result.

By definition, population weight-specific fecundity represents the number of larvae produced by one gram of female biomass (including immature 1-yr-olds). We expanded female biomass to total biomass including males. Results presented in Table 3 show that age-specific male cohort biomass, like that of females, is calculated as the product of numbers-at-age and individual weights-at-age, which when summed over all ages yields the total equilibrium male biomass (347.64 g/male recruit). Total population biomass (i.e. females+males) is then 759.01 g, of which females comprise 54.2% by weight. Thus, the total biomass is estimated by applying a 1.845 expansion factor to female biomass.

Larval production

Sampling with different mesh-size bongo nets (333 and 505 µm) allowed an assessment of whether a portion of smaller larvae retained by the smaller mesh was lost with the standard 505-µm mesh. Although shortbelly rockfish are relatively large and stout at parturition (~5.0 mm, Moser et al., 1977), undersampling of small, young larvae could seriously bias larval production estimates. Results presented in Figure 9 show, however, that the standardized catches of larvae (number/[10 m²]) in the two net sizes were quite similar. A paired t-test of catches (333 minus

[3] Hightower, J. E., and W. H. Lenarz.   1990.   Status of the widow rockfish fishery in 1990.   *In* Status of the Pacific coast groundfish fishery through 1990 and recommended acceptable biological catches for 1991. Stock assessment and fishery evaluation, appendix vol. 2, 48 p.   Pacific Fishery Management Council, Portland, OR.
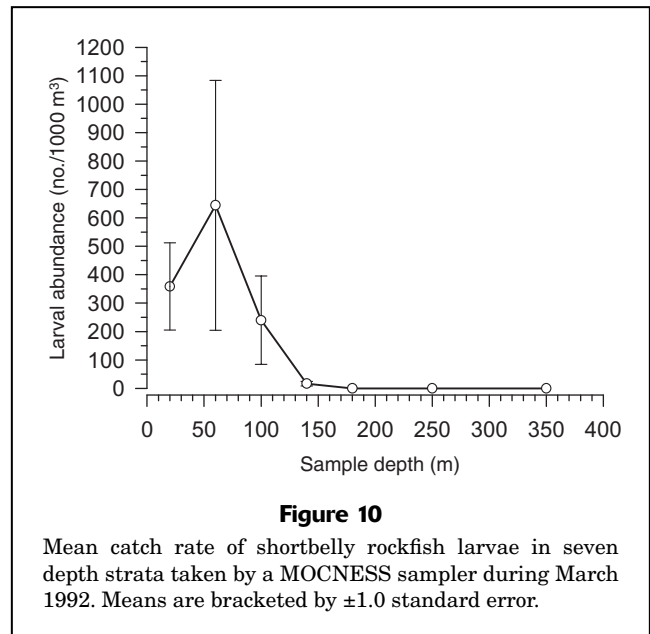
Figure 9

Paired comparison of $\log_e$-transformed larval shortbelly rockfish catches taken in bongo nets with different mesh sizes (all samples collected during February 1991). Also shown is the line of equality.

Figure 10

Mean catch rate of shortbelly rockfish larvae in seven depth strata taken by a MOCNESS sampler during March 1992. Means are bracketed by ±1.0 standard error.

505) resulted in $\bar{x}$ = –0.1458, n = 23, t = –1.24, and P = 0.23, indicating no difference in the catch of the larger mesh net in relation to the smaller net. We conclude that the 505-μm net was an effective sampler of rockfish larvae.

Examination of the standardized catches from the MOC-NESS tows conducted in 1992 revealed that shortbelly rockfish larvae were not caught in depths below the 120–160 m interval (Fig. 10). The mean catch rate in that depth range was 16.8 larvae/1000 m³, which amounted to only 1.3% of the combined average catch at all depths, i.e. 98.7% of all larvae were captured at depths < 120 m. Because the bongo net was deployed to a maximum depth of 140 m in 1991, and because the mixed layer depth was depressed during MOCNESS sampling in 1992 due to strong El Niño conditions (Lynn et al., 1995), we concluded that the 1991 bongo net survey sampled the entire depth range where shortbelly rockfish larvae occurred.

For this assessment, a total of 2203 shortbelly rockfish larvae were subsampled from the 505-μm bongo net catches and were aged by using optical microscopy (see Ralston et al., 1996). Results from that work indicated that the ages were quite precise (84% agreement among three readers to within ±1 d) and there were, moreover, no increment interpretation differences between optical observations and those made with a scanning electron microscope (SEM).

The horizontal distribution of very young (0–2 d) short-belly rockfish larvae was strongly associated with the continental shelf break (Fig. 11) and, latitudinally, with the Pioneer Canyon area. Due to the coincidence of this distribution with the locus of adult sampling sites (Fig. 1), we concluded that the trawl survey sampled the adults that produced the larvae captured in the ichthyoplankton survey. This finding supports the coupling of our population weight-specific fecundity statistic (102.17 larvae/g of female) with larval production to estimate the total bio-

mass of shortbelly rockfish in the Pioneer Canyon region. Although not shown, older age classes of larvae tended to be more dispersed and to occur increasingly to the north-west—a pattern consistent with hydrographic conditions at the time of the survey (Sakuma et al., 1995).

When Sette-Ahlstrom weights were used to expand age-specific standardized bongo net catches to the entire study region, the composite age-frequency distribution of short-belly rockfish larvae appeared to support a $\log_e$-linear model with constant exponential mortality (Z [/d]), i.e.

$$N_T = N_0 e^{-ZT}, \log_e(N_T) = \log_e(N_0) - ZT,$$

where N_T = the total abundance of larvae of age T (d);
Z = the instantaneous larval mortality rate (/d); and
N_0 = the larval renewal rate (i.e. daily production of larvae).

The model was fitted over the first 25 days of life, which largely represents the preflexion stage. In addition, the N_T were first coded by scaling all observations to 1×10^{11} and 0.5 was added to all larval ages as a continuity correction (see Ralston et al., 1996). Results show (Fig. 12, Table 2) a satisfactory fit, although there is some suggestion of an aberrant, serially correlated pattern in the residuals from age 0–9 d. The y-intercept term ($\log_e[N_0]$ = –0.3775), when back-transformed (with bias-correction) yields $\hat{N}_0$ = 7.562×10^{10} age-0 larvae.

Given estimates of daily larval production (7.562×10^{10} larvae) and population weight-specific fecundity (Φ= 102.17 larvae/g of female), we calculated from the ratio of these two quantities that 740 t of female shortbelly rockfish spawned each day during the bongo net cruise (DSJ-9102), which is equivalent to a daily biomass of 1366 t/d (sexes combined).
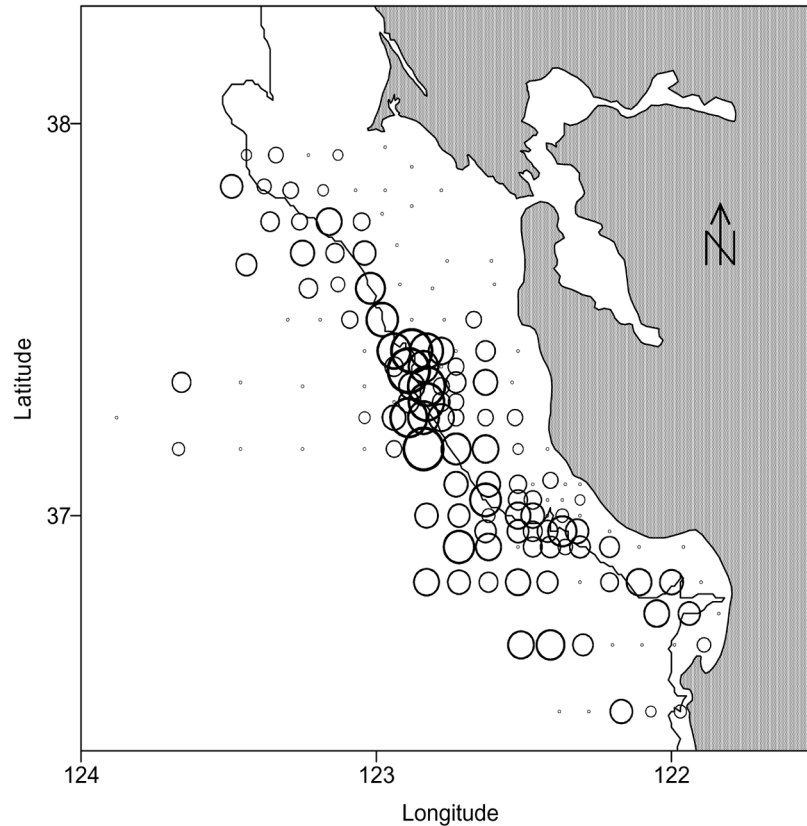
Figure 11

Map showing the spatial distribution of very young (0–2 d) shortbelly rockfish larvae sampled during February 1991. The size of the circles is proportional to $\log_e(\text{catch}+1)$.

Historical data from CalCOFI station 63.55 (Fig. 1) showed that in the vicinity of Pioneer Canyon the seasonal availability of preflexion shortbelly rockfish larvae peaks during January–March (see "observed" in Fig. 13). These data were fitted to a normal curve (see "predicted" in Fig. 13) and indicated that the distribution of preflexion larvae is centered on 7 February (calendar date $\hat{\mu}_p=$ 37.88) and the spawning season typically lasts ~70 d ($\hat{\sigma}_p$=17.39). Assuming that preflexion larvae represent a pool of fish 1–15 d old (Laidig et al., 1991) that experience a daily instantaneous mortality rate of $Z = 0.11$/d (Table 2), the distribution of age-0 larval production is centered earlier in the spawning season, i.e. 2 February (calendar date $\hat{\mu}_0$ =32.62) and the spawning season is slightly less protracted ($\hat{\sigma}_0$=16.86). The estimated long-term mean distribution of age-0 larval shortbelly rockfish production at CalCOFI station 63.55 (Fig. 1) is depicted in Figure 13 as a solid line.
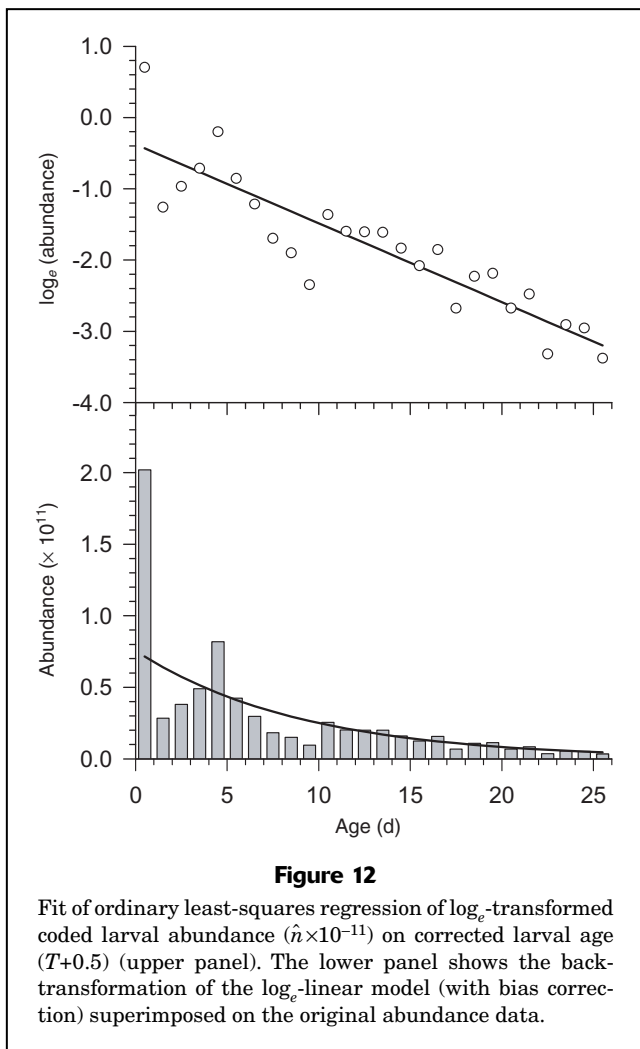
The midpoint of the 1991 bongo-net survey (DSJ-9102) was 11 February (calendar date 42). If larval production were normally distributed and centered at $\hat{\mu}_0$ = 32.62, with $\hat{\sigma}_0$ = 16.86, we calculated that the area under the curve from 41.5 to 42.5 is 0.02026. This represents the estimated fraction of the total annual larval production that occurred per day at the midpoint of the cruise and is the area under the curve between the two vertical lines

shown in Figure 13. Thus, we expanded by 49.35 spawning d/yr (1/0.02026) the estimated daily biomass (1366 t/d) to 67,392 t/yr, which is the estimated total stock biomass of shortbelly rockfish in the study area. The standard error of this estimate, based upon delta-method computations, is 12,900 t/yr, yielding a coefficient of variation of 19%.

Sensitivity of the biomass estimate

Presented in Table 2 is a simple sensitivity analysis of all parameters estimated in the larval production spawning stock biomass assessment of shortbelly rockfish. For each of the 23 parameters, the coefficient of variation (expressed as a percentage) is given. In addition, the effects of individual parameter perturbations on the final estimate of spawning stock biomass are shown. In each case, a parameter (Θ) was altered by plus or minus one standard error of the estimate (s_Θ) and the resulting overall effect on the assessment was expressed as the percentage change of the perturbed biomass estimate in relation to the unperturbed value, i.e.

$$\Delta_e = 100\left[\frac{B_\theta - B_0}{B_0}\right],$$

Figure 12

Fit of ordinary least-squares regression of $\log_e$-transformed coded larval abundance ($\hat{n} \times 10^{-11}$) on corrected larval age (T+0.5) (upper panel). The lower panel shows the back-transformation of the $\log_e$-linear model (with bias correction) superimposed on the original abundance data.

where Δ_Θ = the relative sensitivity of the assessment to parameter "Θ";

B_Θ = the resulting biomass after altering parameter "Θ" by $\pm s_\Theta$; and

B_0 = the original unperturbed biomass estimate (67,392 t/yr).

Perturbations equal to $\pm 1\, s_\Theta$ were selected to reflect the level of statistical uncertainty in the parameters themselves. Results showed that within this range of uncertainty, certain parameters had essentially no effect on the final estimate of spawning stock biomass (e.g. $\log_e[\eta_0]$, v, ρ, Ψ), and others had a more substantial effect. In particular, the assessment was most sensitive to estimates of the two fecundity parameters ($\log_e[\phi]$ and δ) and to the intercept term of the larval production and survival model ($\log_e[N_0]$); both of these findings are consistent with intuition.

Also note that the estimate of adult natural mortality rate (M) has only a minor influence on projected biomass. Low sensitivity to this parameter is important because M alone governs the adult age-structure, implying that variation in age-structure has little effect on the overall

stock assessment. This conclusion was portended by results presented in Figures 7 and 8, which illustrate the relative insensitivity of weight-specific fecundity to age. Fundamentally, this conclusion is due to the nearly linear relationship between individual female fecundity and specimen weight (δ=1.14, Table 2, Fig. 5); that is, a fixed mass of mature females produces roughly the same larval output, irrespective of its age composition.

This property is quite useful because it suggests that an accurate estimate of M is not required to make useful projections of total biomass. As discussed previously, obtaining a representative sample of adult rockfish is difficult (Lenarz and Adams, 1980); yet such a sample is usually needed to estimate mortality. Pearson et al. (1991) also highlighted the problem of estimating the natural mortality rate of shortbelly rockfish. Using empirical longevity estimates ($T_{max,\female}$=22 yr, $T_{max,\male}$=20 yr) as inputs to Hoenig's (1983) regression equation and sample size model, they concluded that for shortbelly rockfish $0.20 \leq M \leq 0.35$/yr. Even over this rather broad range of plausible natural mortality values, our results indicate that biomass estimates vary by only ~9% (Fig. 14).

In contrast, mis-specification of the temporal progression of spawning could have a very large effect on the total biomass estimate. Results presented in Figure 15 show the sensitivity of the total biomass estimate to a range of values for μ_0. Because this parameter depends directly on μ_p and σ_p, which were estimated with good precision (Table 2), the expected effect on the total biomass estimate is relatively minor. Even so, if the mean of the spawning distribution actually occurred two weeks earlier (i.e. 18 January instead of 2 February), the biomass estimate would be grossly in error.

Discussion

It is widely recognized that most age-structured stock assessments depend critically on the availability of auxiliary information to adequately constrain solutions to these complex models (Deriso et al., 1985; Hilborn and Walters, 1992; NRC 1998; Quinn and Deriso, 1999). However, even with lengthy time series of landings, discards, age compositions, length compositions, survey CPUE data, and logbook effort statistics, it is by no means certain that complex stock assessment models will precisely or accurately estimate total stock biomass (NRC, 1998). Faced with this dilemma, simple procedures like the one presented here become far more attractive, particularly because the coefficient of variation on the final biomass estimate from this pilot study was relatively precise (i.e. 19%). Moreover, the estimate of absolute biomass does not depend on the development of a long time series of data and it can be obtained rather quickly.

We note that in comparison with previous hydroacoustic assessments, which ranged from 153,000–295,000 t,[1] our estimate of the total biomass of shortbelly rockfish in the vicinity of Pioneer and Ascension Canyons (67,400 t) is substantially lower. Because one of the primary goals of our study was to obtain a more precise biomass estimate than the hydroacoustic estimates, it is important to care-
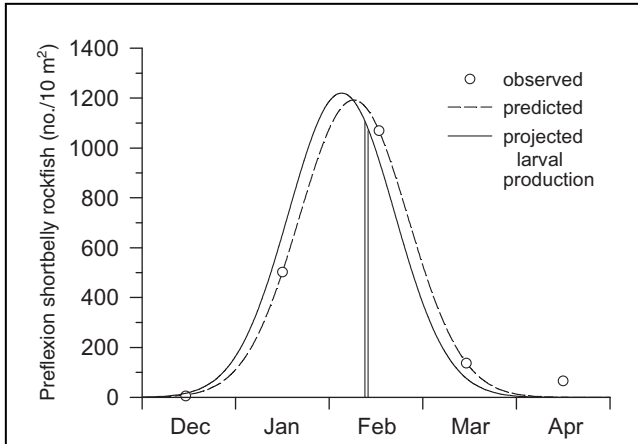
Figure 13

Seasonal pattern in the catch of preflexion shortbelly rockfish larvae at CalCOFI station 63.55 (Pioneer Canyon; see Fig. 1). Observed data were fitted with a normal curve; projected larval production assumes $M = 0.11/d$.
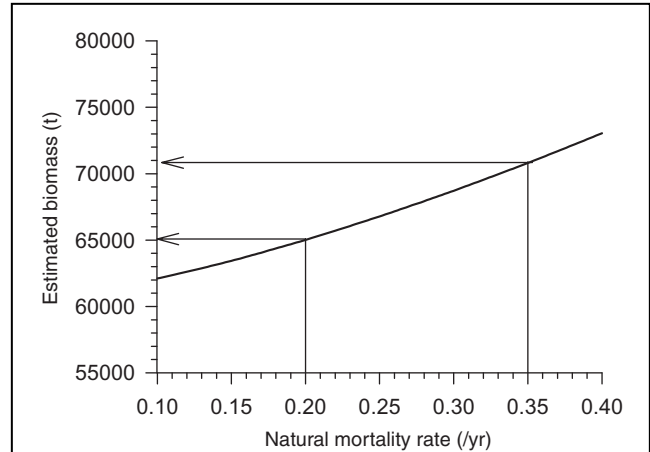

Figure 14

Sensitivity of the larval production estimate of shortbelly rockfish total biomass to the estimated natural morality rate. Vertical dashed lines extending up from the abscissa encompass the likely range of shortbelly rockfish natural mortality (Pearson et al., 1991).
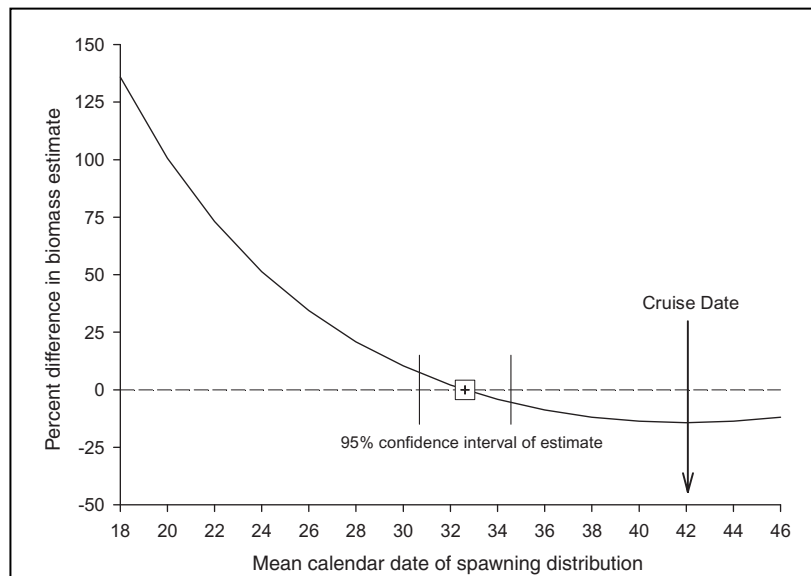

Figure 15

Sensitivity of the total biomass estimate to the mean of the seasonal distribution of shortbelly rockfish larval production, based on CalCOFI samples collected at station 63.55. The estimated mean ($\mu_0 = 32.62$) is represented by the square, which is bounded by its 95% confidence interval. The effect of mis-specifying μ_0 over a broader range (i.e. ±2 weeks) is also shown.

fully consider sources of error and uncertainty in the larval production estimate.

Results presented in Table 2 show that errors in estimating the six growth curve parameters had negligible effects on the biomass estimate, ranging at most from –2.05% to +2.01%. However, estimation errors in the logarithmically transformed power function regression of fecundity on weight had a considerably greater effect. Parameter perturbations in this function altered biomass estimates by ~15–20%. In contrast, errors in estimating the parameters of the logistic maturity ogive had virtually no effect.

We have shown that weight-specific fecundity was only weakly dependent on age (Fig. 7). If these variables were independent, the age structure of the stock would have no influence on population fecundity; that is, a ton of 5-yr-old fish would have the same reproductive output as a ton of 20-yr-old fish. Thus, if age and weight-specific fecundity are independent, the natural mortality rate (M) has no influence on the estimation of biomass, which agrees with the relative insensitivity of the total biomass estimate to estimated natural mortality rate (Table 2, Fig. 14). This a highly desirable characteristic of the assessment methods proposed here. Unlike stock assessments that are predicated on measuring the abundance of ichthyoplankton, results from standard age-structured stock assessment models often depend critically on what is almost always an assumed value of M (e.g. Ralston and Pearson[4]). This can have the effect of reducing an entire stock assessment modeling exercise to guesswork.

Daily larval production ($\log_e[N_0]$) is the other estimated parameter that most strongly influences the calculation of biomass, with parameter perturbations of ±1.0 standard error that result in a 16–19% effect on estimated stock biomass (Table 2). This parameter was determined by assuming a constant mortality rate model, which yielded $Z = 0.11$/d. However, we view the selection of a specific mortality model to be of considerable importance and wish to emphasize that other alternatives to the exponential survivorship case are available, including the Pareto model (Lo et al., 1989). Researchers who wish to apply the method that we outline here would be well-advised to examine this particular issue carefully because the estimate of daily larval production (N_0) will depend critically on the mortality model used.

Another underlying assumption of the larval production method is that over the period represented by the data, the larval production rate and the mortality rate remained constant. Violations of this assumption could cause patterns like those evidenced in Figure 12. However, we conclude that the existing data do not allow us to distinguish between explanations based on correlated estimation errors and those based on time-varying larval production rates. Also, the ichthyoplankton survey took place over a 6½-day period and samples close together in space were also close together in time, which further complicates the issue. Possible future approaches might consist of sampling designs that include spatial and temporal replication.

Another major source of uncertainty in our assessment lies in the expansion of "daily" total biomass to "annual" total biomass. Based upon the long-term mean distribution of spawning activity (Fig. 12), we calculated that the annual biomass was ~50 times larger than the daily biomass on 11 February. Use of the long-term mean distri-

bution has obvious limitations, however, if the spawning season varies interannually (see Fig. 15).

Results presented in MacGregor (1986) can be used to examine the assumption that spawning seasonality is the same every year. He sorted all shortbelly rockfish larvae from all plankton samples that were collected as part of CalCOFI surveys conducted in 1956, 1966, 1969, 1972, and 1975. In each of these years, cruises were conducted in every month and he presented monthly total larval abundances by year in tabular form. His findings showed that, within the region bounded by CalCOFI lines 60–137 (i.e. San Francisco, CA, to Magdalena Bay, Mexico), the mean date of preflexion larval abundance (μ_p) encompassed only four days among those five years, which together spanned two decades. Similarly, with the exception of 1972 (an El Niño year) the standard deviation of the preflexion larval distribution (σ_p) varied by only five days. These results are consistent with other studies that have shown a remarkable consistency in the timing of fish reproduction (Cushing, 1969; Anderson, 1984; Pedersen, 1984; Picquelle and Megrey, 1993; Gillet et al., 1995; but see Hutchings and Myers, 1994). Thus, although misspecification of the mean time of spawning has the potential to seriously impact the biomass estimate, the observed data suggest that in this application the effect is negligible.

Perhaps a more important structural assumption we have made is that the spawning season can be represented by a normal distribution. Although Saville (1956, 1964) advocated use of the normal distribution for this purpose, we question the generality and accuracy of this symmetric function when used to model spawning seasonality. In the case of shortbelly rockfish, the fit of the five data points to the distribution was reasonably good (dashed line in Fig. 13). Even so, we note that the observed data were monthly means and the April value did not conform well to expectation. Therefore, in future applications of the larval production method we recommend strongly that a well-defined year-specific estimate of the seasonal distribution of spawning activity (i.e. the production rate of age-0 larvae) be obtained. In principle these data could be gathered by high-frequency sampling of either the larval or adult portions of the stock, and even through monitoring the maturity of females in commercial landings.

It is also true that the entire spatial distribution of early larvae must be surveyed in order for the larval production estimate ($\hat{N}_0$) to represent the complete spawning stock. This concern is not unique to this assessment, however; it is a requirement that must be satisfied whenever egg and larval surveys are used to estimate the absolute biomass of a fish stock. Nonetheless, in this application it is not likely to have been fully met (Fig. 11). Although the primary spawning concentration of shortbelly rockfish along the central California seems to have been largely encompassed, there is evidence that the offshore extent of very young larvae was not fully captured

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[4] Ralston, S., and D. Pearson. 1997. Status of the widow rockfish stock in 1997. *In* Status of the Pacific coast groundfish fishery through 1997 and recommended acceptable biological catches for 1998. Stock assessment and fishery evaluation, appendix, 54 p. Pacific Fishery Management Council, Portland, OR.

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