Abstract—From 1995 to 1998, we collected female black rockfish (*Sebastes melanops*) off Oregon in order to describe their basic reproductive life history and determine age-specific fecundity and temporal patterns in parturition. Female black rockfish had a 50% probability of being mature at 394 mm fork length and 7.5 years-of-age. The proportion of mature fish age 10 or older significantly decreased each year of this study, from 0.511 in 1996 to 0.145 in 1998. Parturition occurred between mid-January and mid-March, and peaked in February. We observed a trend of older females extruding larvae earlier in the spawning season and of younger fish primarily responsible for larval production during the later part of the season. There were differences in absolute fecundity at age between female black rockfish with prefertilization oocytes and female black rockfish with fertilized eggs; fertilized-egg fecundity estimates were considered superior. The likelihood of yolked oocytes reaching the developing embryo stage increased with maternal age. Absolute fecundity estimates (based on fertilized eggs) ranged from 299,302 embryos for a 6-year-old female to 948,152 embryos for a 16-year-old female. Relative fecundity (based on fertilized eggs) increased with age from 374 eggs/g for fish age 6 to 549 eggs/g for fish age 16.

Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*)

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Many fish species in the North Pacific have a long reproductively active life span, which increases the likelihood of producing offspring during periods of favorable environmental conditions. This bet hedging reproductive strategy reduces the impact of environmental variation on reproductive success (Goodman, 1984; Leaman and Beamish, 1984; Schultz, 1989). In species with age-structured spawning schedules, a broad age distribution will maximize the length of the spawning season. The more protracted the reproductive period, the greater the likelihood that some spawning will occur during conditions favorable for larval survival (Lambert, 1990). Age-related differences in the timing of spawning have been observed in many fishes; usually larger, older fish spawn earlier (Simpson, 1959; Bagenal, 1971; Berkeley and Houde, 1978; Shepherd and Grimes, 1984; Lambert, 1987), but in some cases younger fish spawn earlier in the season (Hutchings and Myers, 1993).

Age truncation, an inevitable result of fishing, can increase recruitment variability by reducing the length of the spawning season or by selectively removing older, more fit individuals from the population. Factors that might affect individual reproductive success include the number of eggs produced, the quality of eggs (e.g., yolk or oil globule volume), and the size or health of eggs and larvae. Off

the coast of Oregon, widow rockfish (*Sebastes entomelas*) have exhibited increased absolute fecundity, and more importantly have increased relative fecundity, with age (Boehlert et al., 1982). Individual populations of shortbelly rockfish (*Sebastes jordani*), have been found to produce larvae with differing lipid and protein compositions and consequently potentially differing rates of survival (MacFarlane and Norton, 1999). Zastrow et al. (1989) reported that striped bass eggs stripped from wild fish increase in quality with maternal age due to increased amounts of proteins and lipids, although relative concentrations remain unchanged.

Black rockfish (*Sebastes melanops*), like most other rockfish, are long-lived, moderately fecund livebearers with long reproductive life spans. Although their longevity and low rate of natural mortality is presumed to be an adaptation to allow successful reproduction over their lifespan despite long periods between favorable environmental conditions, it also makes them more susceptible to overexploitation. The objective of our research presented in the present article is twofold. First, we describe the basic reproductive life history of black rockfish, with an emphasis on the ovarian developmental cycle and maturity schedule. Second, we investigate age-specific fecundity and temporal patterns in parturition and

discuss their effect on reproductive success in a population undergoing truncation of the upper end of its age distribution.

Materials and methods

We collected female black rockfish during the months of peak female reproductive development, November through March, for three successive years from 1995–96 through 1997–98. Female black rockfish were primarily obtained from recreational charter boat landings in Newport, Depoe Bay, and Charleston, Oregon, in addition to some fish from commercial landings from Port Orford, Oregon (Fig. 1). We also collected fish by rod and reel and spearfishing. When possible, the sex of all available black rockfish was determined, and females were staged as immature or mature. Immature females were measured (FL), and mature females were returned to the laboratory. On extremely busy days when numerous charter boats were fishing, all mature females were collected, but immature fish were not measured. In total we collected 1643 female black rockfish. Immediately upon return to the laboratory, we recorded fork length, total weight when possible (most samples from charter boats were carcasses only), liver weight, and ovary weight. Ovaries were assigned a maturity stage based on macroscopic appearance and preserved in 10% buffered formalin. We initially followed the gross maturity stage scheme of Nichol and Pikitch (1994) for darkblotched rockfish (*Sebastes crameri*) but ultimately abandoned their classification of maturity stages in favor of the simplified maturity stages reported by Gunderson et al. (1980) (Table 1). Sagittal otoliths were removed and stored dry for age determination. All aging was done by an expert age reader from the Oregon Department of Fish and Wildlife (ODFW), who used the break-and-burn technique (Beamish and Chilton, 1982). Ten percent of the otoliths were randomly selected for a second reading to ensure consistency in interpretation of annuli. It should be noted that black rockfish ages have not been validated. However, ages have been validated for yellowtail rockfish (*Sebastes flavidus*), a closely related species (Leaman and Nagtegaal, 1987), by using otoliths; moreover, the break-and-burn aging method is widely accepted as valid for aging rockfish (MacLellan, 1997), and ages thus derived are routinely used in rockfish stock assessments. Because our sample included all mature females that we encountered, we used these data to estimate the age distribution of mature females in each time period, and the age distribution of parturition during each time interval.

Histological preparations were made from the ovaries of 175 females collected monthly from March 1996 through March 1997 to track seasonal ovarian development. Females collected in March 1996 and November 1996 through March 1997 were from our regular sampling program, whereas fish collected from April
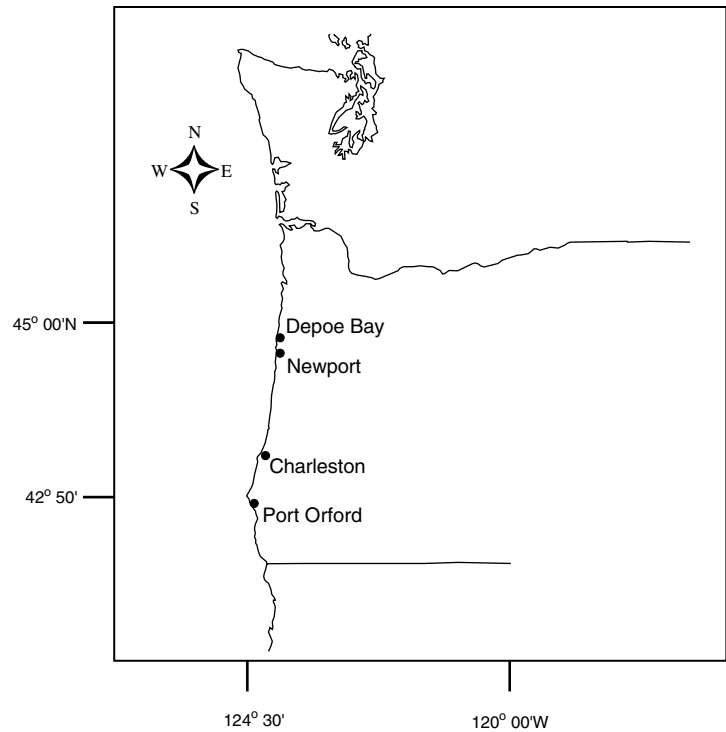

Figure 1

Map of the Oregon coast showing the study area where black rockfish (*Sebastes melanops*) were collected.

through October 1996 were obtained from Newport recreational charter boat landings. Females were randomly selected from each maturity stage observed each month and from as wide a range of ages as available (Table 2). Ovaries were embedded in paraffin, sectioned at 4–5 μm, and stained with gill-3 haematoxylin and eosin y solution.

We determined stage-specific fecundity in black rockfish for females with unfertilized yolked oocytes (n=184) and fertilized eggs (n=85). Postfertilization ovaries were very fragile and tended to rupture easily and release embryos under the slightest pressure. Consequently, for estimating fecundity for these stages, we used only fish collected by ourselves so that we were certain that no eggs or larvae had been released during capture. To ensure that no eggs were lost after capture, these fish were immediately placed into plastic bags in order to retain any eggs that might be extruded before the ovary could be processed. Ovaries were processed following procedures modified from Lowerre-Barbieri and Barbieri (1993) to separate eggs and embryos from connective tissue. Briefly, fixed ovaries were manually manipulated and rinsed with water through a 1-mm square mesh sieve, which retained most of the connective tissue, into another sieve with 0.75-mm mesh. Ovary connective tissue was retained in the coarse sieve, and freed eggs were collected in the fine-mesh sieve. Freed eggs were patted dry, weighed (nearest 0.1 g), and three subsamples were collected, weighed (nearest 0.001 g), and placed in 10% buffered formalin.

Table 1

Macroscopic and histological descriptions of stages used to describe female black rockfish maturity.

Maturity stage	Macroscopic description	Histological description
1 Immature	Small and translucent ovary, pink during months without sexual activity and yellowish (except for very small fish) during months with reproductive activity.	Oocyte cytoplasm intensely basophilic. Densely packed oogonial nests and developing oocytes, with larger oocytes containing small clear vesicles.
2 Vitellogenesis	Ovary firm and yellow or occasionally cream in color. Large range of size, but all with visible opaque eggs.	Oogonia and developing oocytes still visible, but ovary dominated by large oocytes with numerous small red-staining yolk globules.
3 Fertilization	Eggs are golden and translucent. Ovary extremely large in relation to body cavity. Ovary wall thin and easily torn.	Fertilized eggs ovulated and found within the ovarian cavity. Eggs have a single pink-staining yolk mass and clear oil droplet.
4 Eyed larvae	Eyes of developing embryos visible, giving ovary an overall greyish color. Ovary fills a large portion of the body cavity.	Presence of developing larvae with black pigmented eyes. Yolk mass absorbed in late-stage larvae, but oil droplet usually present.
5 Spent	Ovary flaccid, purplish-red in color. Eyed larvae may still be visible.	Early-stage oocytes loosely associated. Extensive network of blood vessels. Possibility of encountering residual larvae.
6 Resting	Ovary again firm and pink in color. Black spots may be visible.	Similar appearance to immature fish. Ovary wall slightly thicker in early summer.

Table 2

Monthly ranges for age, length, and maturity stage of black rockfish collected off Oregon from March 1996 through March 1997 for histological analysis.

Month	Age (yr) range	FL (mm) range	Maturity stage range	n
March	7–25	375–510	1, 4–6	10
April	7–18	364–447	1, 5–6	12
May	7–13	340–465	1 and 6	15
June	5–13	349–432	1 and 6	15
July	5–13	360–475	1 and 6	14
August	5–11	357–493	1–2, 6	15
September	6–16	366–488	1 and 2	12
October	5–16	357–420	1 and 2	11
November	5–11	355–434	1 and 2	16
December	5–14	365–439	1 and 2	10
January	6–17	369–473	1–4	16
February	7–17	378–464	1–5	17
March	6–13	380–467	1, 5–6	12

The number of ova in the subsamples were counted and absolute fecundity was estimated by using the following algorithm:

$$AF = EW \left(\frac{\sum_{i=1}^{3} \frac{SSC_i}{SSW_i}}{3} \right),$$

where AF = absolute fecundity, or the total number of eggs per female;
EW = weight of rinsed eggs (or larvae);
SSC_i = subsample count i, where i=1 to 3; and
SSW_i = subsample weight i, where i=1 to 3.

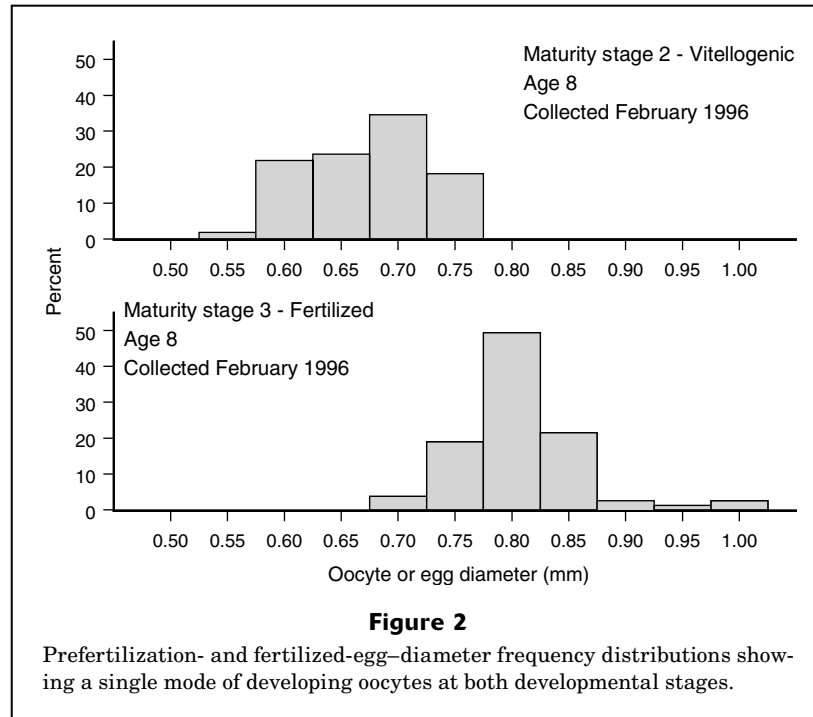Relative fecundity (RF), based on gonad-free somatic weight was estimated by

$$RF = \frac{AF}{TW - GW},$$

where AF = absolute fecundity, or the total number of eggs per female;
TW = total weight; and
GW = gonad weight.

For our analyses of fecundity, we used only fish in which the number of eggs or larvae estimated from the three subsamples had coefficients of variation less than or equal to 5%, and for prefertilization eggs we used only females with average egg diameters of at least 450 μ to ensure inclusion of all developing oocytes. Only one cohort of developing oocytes is present in the ovary of

Figure 2

Prefertilization- and fertilized-egg–diameter frequency distributions showing a single mode of developing oocytes at both developmental stages.

black rockfish, either during development (stage 2) or after fertilization (stage 3) (Fig. 2). Analysis of covariance (ANCOVA) was used to test for annual effects in the relationship between prefertilization fecundity and age and a maturity-stage effect (prefertilization vs. fertilized-egg development stages) on both absolute and relative fecundity at age. We also used ANCOVA to test for a maturity stage effect in the relationship between absolute fecundity and fork length. All ANCOVA analyses were conducted by using multiple linear regression with the function lm in S-PLUS 2000 (MathSoft, Inc., Seattle, WA).

To predict the probability of a female black rockfish being mature based on its fork length, we fitted our maturity-at-length data to a logistic regression. During those months without reproductive activity, late spring through early fall, it was difficult to distinguish between immature and mature-resting ovaries. Consequently, only those females collected during the peak months of reproductive development and from sampling events where all fish, mature and immature, were collected were included in our analysis. Binary maturity observations (0=immature, 1=mature) and fork length were fitted to a logistic model by using the function glm, family = binomial of S-PLUS (S-PLUS 2000). The model used was

$$\pi(FL) = P(Y = 1 \mid FL) = \frac{e^{\beta 0 + \beta 1 FL}}{1 + e^{\beta 0 + \beta 1 FL}},$$

where $P(Y=1 \mid FL)$ = probability of female black rockfish being mature at size FL; and

β_0 and β_1 = regression coefficients for the intercept and fork length, respectively.

For functional purposes, the response variable was interpreted as the percentage of female black rockfish mature at length. Assuming this relationship of fork length to maturity had not changed over time, we applied our logistic model to fork-length data from random sampling conducted by ODFW during the summers of 1992–2000 to calculate the percentage of female black rockfish caught by the recreational fishery off Newport that were mature in each year.

Fork length-at-age data for female black rockfish were fitted with the von Bertalanffy growth function (VBGF) by using the nonlinear function nls() in S-PLUS 2000. Age at 50% maturity was calculated by using our estimate of length at 50% maturity and a VBGF rearranged to the form

$$t_{50\%} = t_0 + \frac{1}{k}\left[\ln\frac{L_\infty}{L_\infty - l_{t50\%}}\right],$$

where $t_{50\%}$ = age at 50% maturity;
L_∞ = asymptotic length;
k = Brody growth parameter;
t_0 = age at zero length; and
$l_{t50\%}$ = length at 50% maturity.

Timing of parturition was estimated by microscopically determining embryo development stages for all females with fertilized eggs following Yamada and

Kusakari's (1991) stages of embryonic development for kurosoi (*Sebastes schlegeli*) modified to reflect the gestation period of 37 days for black rockfish (Boehlert and Yoklavich, 1984). Gestation period is likely to vary with water temperature. In determining gestation period, Boehlert and Yoklavich (1984) held black rockfish in the laboratory at 9–11°C. Mean water temperatures in our study area during the period of egg and larval development (December–April) were 10.9°, 10.1°, and 11.4°C in 1995–96, 1996–97, and 1997–98, respectively (http://co-ops.nos.noaa.gov/data). Even in the strong El Niño year of 1997–98, nearshore water temperature during the winter larval development period was only slightly outside this range. Therefore, we assumed a 37-day gestation period for all years of our study. Using the Boehlert and Yoklavich (1984) equation; (*stage duration* $= 0.0452 \times stage^{1.090}$) we solved for duration at each stage by adding 5 days to account for the time between hatching (stage 32) and parturition (also from Boehlert and Yoklavich, 1984). To calculate the time until parturition for each stage, we subtracted the previous stage durations from the total gestation period of 37. For example, at stage 1, parturition would occur in 37 days. At stage 2, parturition would take place in 37 days – stage-1 duration (~2 days) = 35 days.

For each year of our study, estimated parturition dates for all females in our sample were grouped into one-week time intervals and further subdivided into age categories: 6–8; 9–11; 12–14; and >15. These numbers were then multiplied by the appropriate value for age-class–specific fecundity based on fertilized eggs (Table 3) to estimate relative spawning output by week for each age class.

Results

Ovarian development

Black rockfish off Oregon exhibited group-synchronous oocyte development; and females extruded only one brood of larvae per year (Fig. 2). Based on our observations of ovarian development from all three years of this study, parturition took place from mid-January through mid-March and peaked in February. Following parturition, unextruded larvae were quickly resorbed and the ovary lost much of its vascularization. From April through early August ovaries were in a resting state and contained oogonial nests and slightly larger oocytes with a basophilic cytoplasm and a maximum diameter of 50 μ. Also present at this time were developing oocytes ranging from 50 to 150 μ in diameter with small lipid vacuoles surrounding the nuclear membrane. Yolk deposition (vitellogenesis) began in late August and was observed through the third week of February. In the final stages of vitellogenesis, the largest oocytes were approximately 700 μ in diameter and had numerous oil vacuoles and yolk globules throughout the cytoplasm. The first female with fertilized eggs (stage 3) was observed during the second week of January, and stage-3

Table 3
Age group-specific absolute fecundity (based on fertilized eggs) and age distribution of mature females as a percentage of all mature females, used to estimate larval production. Calculated from data pooled from 1996 through 1998.

Age group (yr)	Absolute fecundity[1]	Percentage of all mature females represented by each age group
6–8	364,183.5	42.19
9–11	558,837.1	38.48
12–14	753,490.7	13.94
15 and older	948,144.3	5.39

[1] Absolute fecundity for each age group is the estimated fecundity (based on fertilized eggs) for ages 7, 10, 13, and 16, respectively.
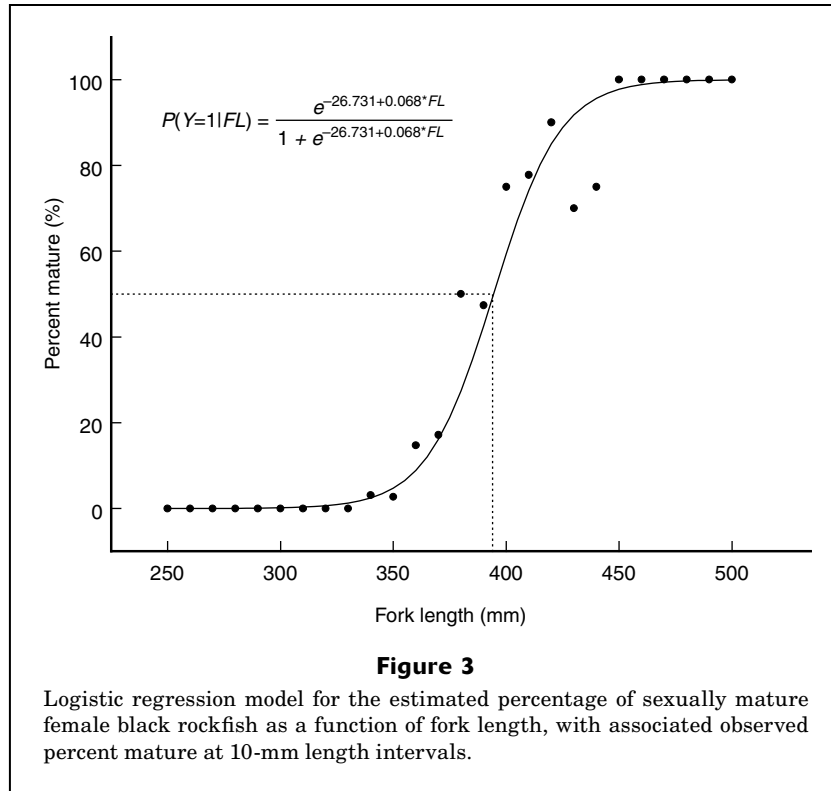
females were observed until the third week of February. Recently fertilized eggs were approximately 850 μ in diameter. The period of parturition as indicated by the occurrence of ovaries containing eyed larvae extended from the second week in January through the second week of March. Spent females were first collected during the last week of January and were most frequently collected in late February and early March.

Sexual maturity

Parameter values for the length-maturity logistic model were $\beta_0 = -26.73$ and $\beta_1 = 0.068$. The smallest mature female black rockfish we observed was 345 mm; all individuals were mature by 450 mm. Fifty percent of females were estimated to be mature at 394 mm fork length (Fig. 3). As reflected in our length-maturity logistic model, there was a decreasing trend in the percent maturity for female black rockfish in recreational landings from ODFW collections from 1992 through 2000 (Fig. 4). The von Bertalanffy parameter estimates for female black rockfish were $L_\infty = 442$ mm, $k = 0.33$, $t_0 = 0.75$ (Fig. 5). Using these estimates, along with the fork length at 50% maturity, we estimated the age at 50% maturity for female black rockfish to be 7.5 years. The median age of mature females decreased in each collection year from 10 years in 1996 to 9 in 1997 and to 7 years in 1998. In addition, we observed a significant decrease in the proportion of mature fish age 10 or older over the three years of our study (Pearson's $\chi^2 = 52.4$, df=2, $P<0.001$). The proportions decreased from 0.511 in 1996, to 0.318 in 1997, and 0.145 in 1998.
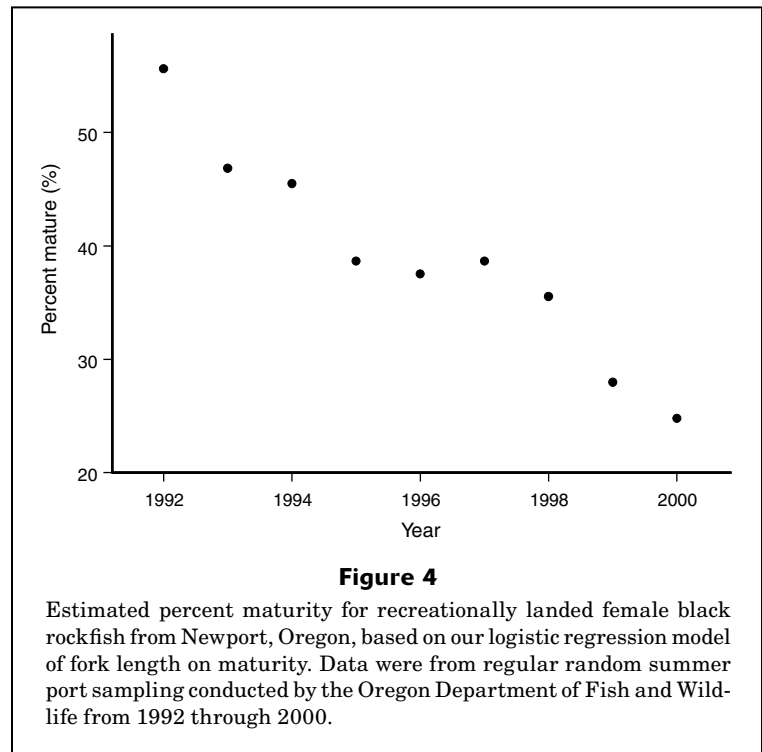
Fecundity

Absolute fecundity for prefertilization female black rockfish ranged from 482,528 oocytes for a 5-year-old female to 998,050 oocytes for a 19-year-old female. The results of ANCOVA (Table 4) over a common age

Figure 3

Logistic regression model for the estimated percentage of sexually mature female black rockfish as a function of fork length, with associated observed percent mature at 10-mm length intervals.

The equation shown in the figure:

$$P(Y=1|FL) = \frac{e^{-26.731+0.068*FL}}{1 + e^{-26.731+0.068*FL}}$$

range showed no evidence of differences in slopes among the years 1996–98 ($P=0.161$). ANCOVA also showed no significant difference in elevations ($P=0.632$), indicating no annual effect and allowing one model to be fitted to the pooled data (Fig. 6). Absolute fecundity for females with fertilized eggs ranged from 299,302 embryos for a 6-year-old to 948,152 embryos for a 16-year-old. Because of the low number of females with developing embryos collected in 1996 and 1998, 19 and 4 females, respectively, and based on the results of prefertilization females, all data were pooled and fitted with one model (Fig. 7). Although we were able to pool the data for all years for fecundity-age regressions for both prefertilization females and fertilized females, there was evidence of interaction (i.e., unequal slopes) between stage-specific absolute fecundity and age (2-tailed t-test, $P=0.020$) requiring separate linear regressions to be fitted to the data (Fig. 8).

Similar to the ANCOVA results for absolute fecundity, there were no differences in slopes or elevations for relative fecundity for prefertilization females for the years 1996–98 (Table 4). Again, based on the results of the ANCOVA for prefertilization females and due to the low number of fertilized females collected in 1996 and 1998, all relative fecundity data for females with fertilized eggs were pooled. Unlike the results for the

Figure 4

Estimated percent maturity for recreationally landed female black rockfish from Newport, Oregon, based on our logistic regression model of fork length on maturity. Data were from regular random summer port sampling conducted by the Oregon Department of Fish and Wildlife from 1992 through 2000.
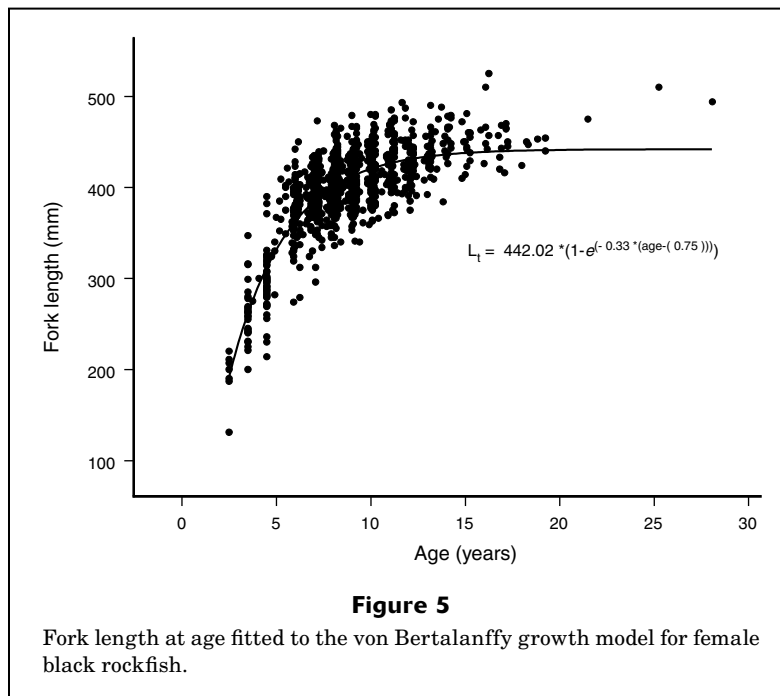
relation between absolute fecundity and age there was no evidence of interaction (i.e., unequal slopes) between stage-specific relative fecundity and age (2-sided *t*-test

Table 4

Results of analyses of covariance testing for differences in slopes and elevations of annual absolute fecundity-age relation and annual relative fecundity-age relation. Response variables = AF and RF, treatment factors = year, and covariate = age.

Source of variation	df	Sum of squares	Mean square	F	P
Absolute fecundity (based on prefertilization oocytes)					
Equality of slopes	2	105,347	52,674	1.85	0.161
Error	160	4,564,320	28,527		
Equality of elevation	2	168,544	84,272	0.29	0.747
Error	162	3,459,048	288,254		
Relative fecundity (based on prefertilization oocytes)					
Equality of slopes	2	259.04	129.52	0.58	0.559
Error	160	35,452.22	221.58		
Equality of elevation	2	799.52	399.76	1.81	0.166
Error	162	35,711.26	220.44		

$$L_t = 442.02 *(1-e^{(-0.33 *(age-(0.75)))})$$

Figure 5

Fork length at age fitted to the von Bertalanffy growth model for female black rockfish.

(2-tailed t-test, $P<0.0001$,) of a stage effect (i.e., unequal elevations) which necessitated that the data be fitted with a parallel-line multiple linear regression model (Fig. 10).

Temporal patterns in parturition

From 1996 through 1998 we estimated relative larval production for four age groups: 6–8; 9–11; 12–14; and 15 years and older (Fig. 11). In each year parturition took place from mid-January until mid-March, and older, larger fish extruded larvae earlier than younger fish. In 1996 and 1997, the 9–11 year-old fish dominated larval production, responsible for 60.1% and 49.6% of all larvae extruded, respectively (Table 5). In 1998 age 6–8 fish produced the largest percentage of larvae (65.3%). In all years, relative larval production was lowest for the oldest age group (15+), declining to near 0 by 1998.

Discussion

Ovarian development for black rockfish in Oregon was similar to the developmental cycles reported for other rockfish species (Moser, 1967; Bowers, 1992; Nichol and Pikitch, 1994) with the exception of seasonal timing and stage duration. Females underwent vitellogenesis for up to six months before fertilization, which occurred from December through February. In all three years, parturition off the Oregon coast occurred between mid-January and mid-March and peaked in February. Wyllie Echeverria (1987) observed similar timing for parturition of black rockfish off north-central California, with a peak in February but with parturition occurring through May.

$P=0.096$). There was, however, strong evidence (2-tailed t-test, $P<0.001$,) of a stage effect (i.e., unequal elevations) which necessitated that the data be fitted with a parallel-lines multiple linear regression model (Fig. 9).

Absolute fecundity for prefertilization female black rockfish ranged from 443,671 oocytes for a 381-mm-FL female to 1,135,457 oocytes for a 495-mm-FL female. For fertilized females, absolute fecundity ranged from 283,618 oocytes for a 381-mm-FL female to 1,073,356 oocytes for a 510-mm-FL female. The results of AN-COVA over a common size range showed no evidence of differences in slopes between maturity stages (2-sided t-test $P=0.206$). There was, however, strong evidence

All female black rockfish, except the smallest immature females, followed a seasonal cycle in which their ovaries developed an orange coloring during the months of reproductive activity—a pattern observed in olive rockfish (Love and Westphal, 1981). Similarly, Nichol and Pikitch (1994) observed darkblotched rockfish undergoing an "immature cycling" and even assigned these fish a maturity stage. After the reproductive season, the ovaries of immature black rockfish once again became pale pink in color. Because these fish were functionally immature and there was no way to project when they would become sexually mature, they were combined with those small, young females undergoing no seasonal ovarian development and were staged as immature.

Our estimate of fork length at 50% maturity for female black rockfish off Oregon was similar to the 400 mm estimate reported for north-central California females (Wyllie Echeverria, 1987), but lower than the estimate of 422 mm from Washington (Wallace and Tagart, 1994). Our estimated age at 50% maturity of 7.5 years was similar to the estimates of 7.9 and 7 years from Washington and north-central California, respectively. McClure (1982) reported that over 50% of examined female black rockfish collected off Depoe Bay, Oregon, were mature by age six. The difference between our estimate and McClure's was most likely due to using whole otoliths to age fish, which resulted in underestimates of age, and to assigning maturity stages only during summer months, which we have already described as problematic. Both absolute and relative fecundity increased with age for female black rockfish in Oregon waters, although there was a great deal of variation not accounted for by age. The low r^2 values for absolute fecundity regressions for pre- and postfertilization females (0.25 and 0.45 respectively) are due largely to the relatively poor correspondence between age and size (Fig. 5). Black rockfish, like many slow growing, long-lived fish grow slowly after sexual maturity. The rate of growth during their first few years can be quite variable depending on oceanographic conditions and food availability. As a result, young fish can be as large or larger than much older fish (Fig. 5). Length is a better predictor of fecundity than age as judged by the goodness-of-fit of the multiple linear regression model (Fig. 10; r^2=0.70).

An increase in absolute fecundity with age was observed in both prefertilization and postfertilization
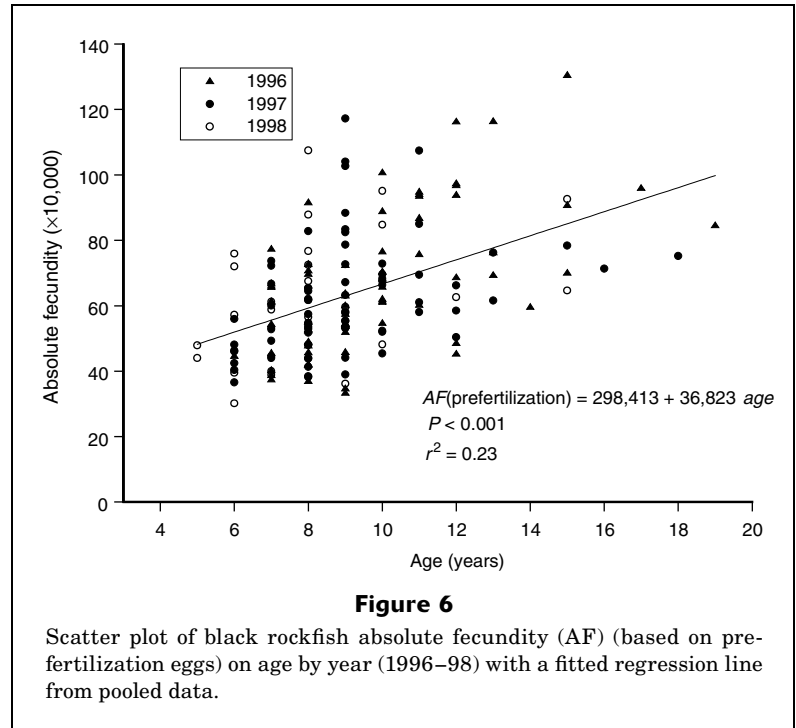

Figure 6
Scatter plot of black rockfish absolute fecundity (AF) (based on prefertilization eggs) on age by year (1996–98) with a fitted regression line from pooled data.
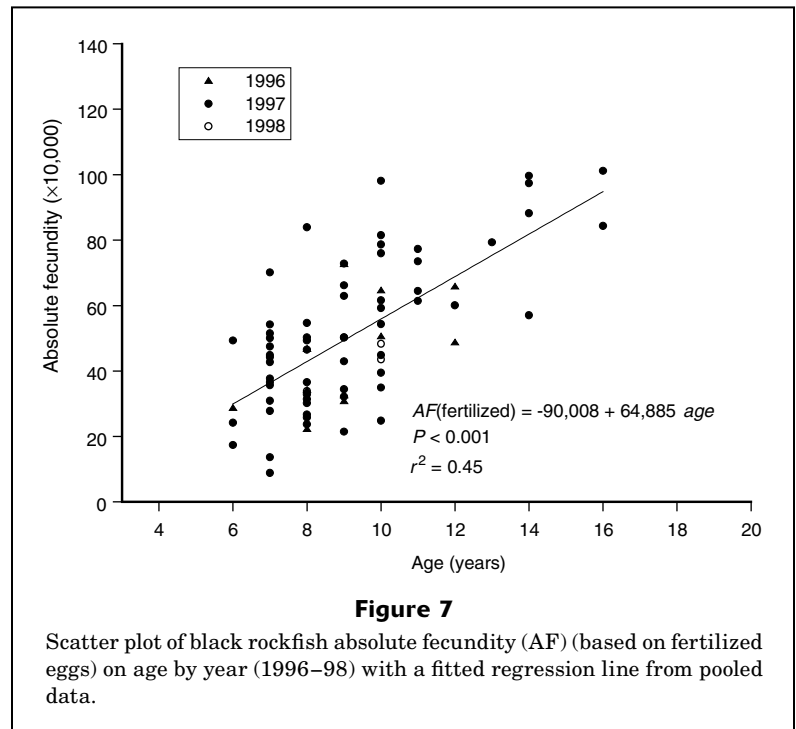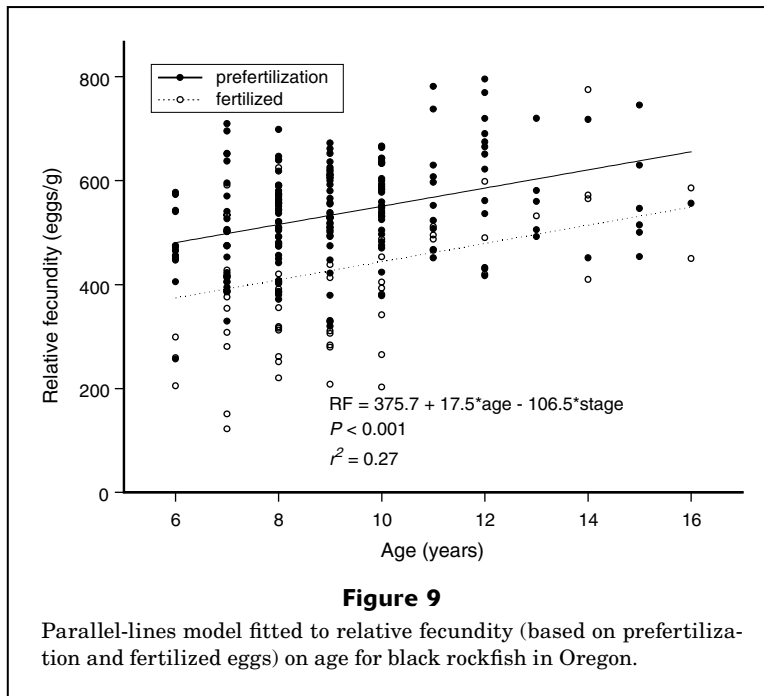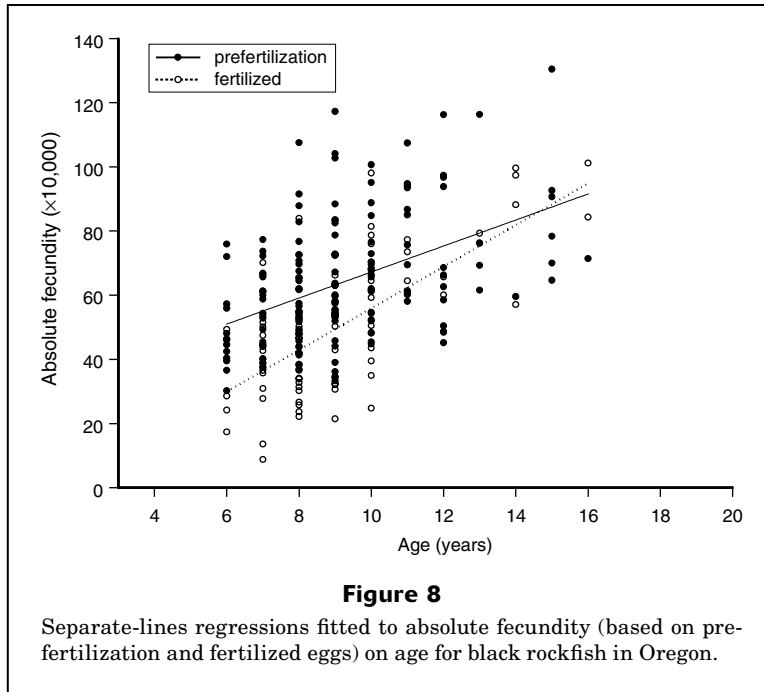

Figure 7
Scatter plot of black rockfish absolute fecundity (AF) (based on fertilized eggs) on age by year (1996–98) with a fitted regression line from pooled data.

females, but they occurred at different rates. As illustrated in Figure 8, the absolute fecundity for a postfertilization 6-year-old black rockfish was only 58% of the estimated absolute fecundity for a prefertilization fish of the same age. By age 15 absolute fecundity

Figure 8

Separate-lines regressions fitted to absolute fecundity (based on pre-fertilization and fertilized eggs) on age for black rockfish in Oregon.

RF = 375.7 + 17.5*age − 106.5*stage
$P < 0.001$
$r^2 = 0.27$

Figure 9

Parallel-lines model fitted to relative fecundity (based on prefertilization and fertilized eggs) on age for black rockfish in Oregon.

estimates for fertilized and prefertilization females were approximately equal. Yolked oocytes from older females were more successful in reaching the developing embryo stage. This may be attributed to higher rates of fertilization, greater viability of embryos, or a combination of both in older female black rockfish. Regardless of the mechanism there should have been signs of greater atresia in the ovaries of young fish, which we did not

observe in our histological preparations. This may have been due to rapid resorption of unfertilized oocytes or an artifact of the fragile nature of fertilized ovaries, which made it difficult to obtain representative histological preparations. Nevertheless, these results suggest that fecundity in black rockfish is best described after fertilization, but care must be taken to minimize embryo loss. These results also suggest that current

estimates of reproductive potential, in which fecundity for prefertilization females is used, may overestimate actual larval production because an increasing proportion of the stock consists of young fish.

We observed a recurring trend of older, larger fish extruding larvae earlier in the reproductive season and larval output being increasingly dominated by younger and younger fish. Eldridge et al. (1991) reported that larger (and most likely older) yellowtail rockfish (*Sebastes flavidus*) spawned earlier in the season than smaller fish—a pattern also reported for darkblotched rockfish (*S. crameri*) by Nichol and Pikitch (1994). Reduced food availability has been suggested as a potential cause for delayed reproduction in *Sebastes* for smaller, younger individuals with high metabolic requirements for somatic growth (Larson, 1991). We feel that limiting the amount of energy that can be spent on reproductive development would cause lower fecundity or reduced yolk content, but not necessarily a delay in reproductive development that would result in suboptimal timing of parturition.

Stock assessments rarely consider changes in population age composition resulting from the removal of older age classes except to the extent that total egg and larval production is reduced. The decreasing representation of mature female black rockfish age 10 and older in the three years of our study indicates that age truncation is occurring in black rockfish in Oregon. This truncation not only removes biomass and potential larval production, but truncation of the upper end of the age distribution eliminates mature females with higher fecundity per individual, a greater success in carrying eggs through to the larval stage, and an age group that extends the overall parturition season. Further research is necessary to explore the controlling mechanisms of differential reproductive success with age and to determine how best to incorporate these findings into stock assessment models.
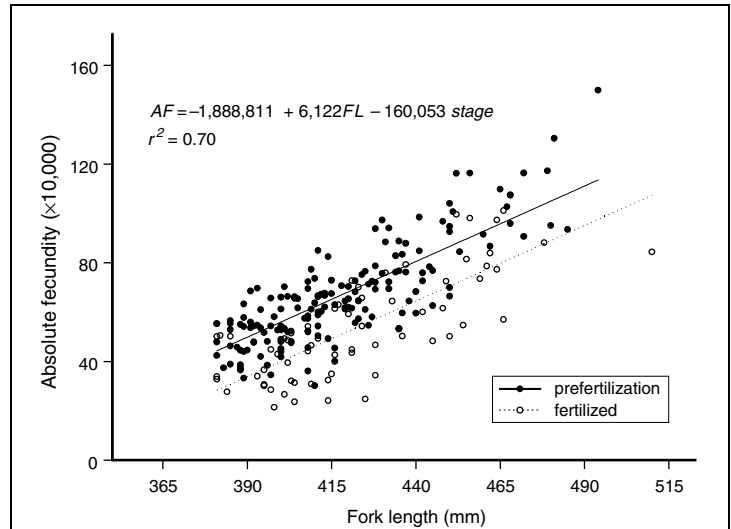
Acknowledgments

Figure 10

Parallel-lines model fitted to absolute fecundity (based on prefertilization and fertilized eggs) on age for black rockfish in Oregon.
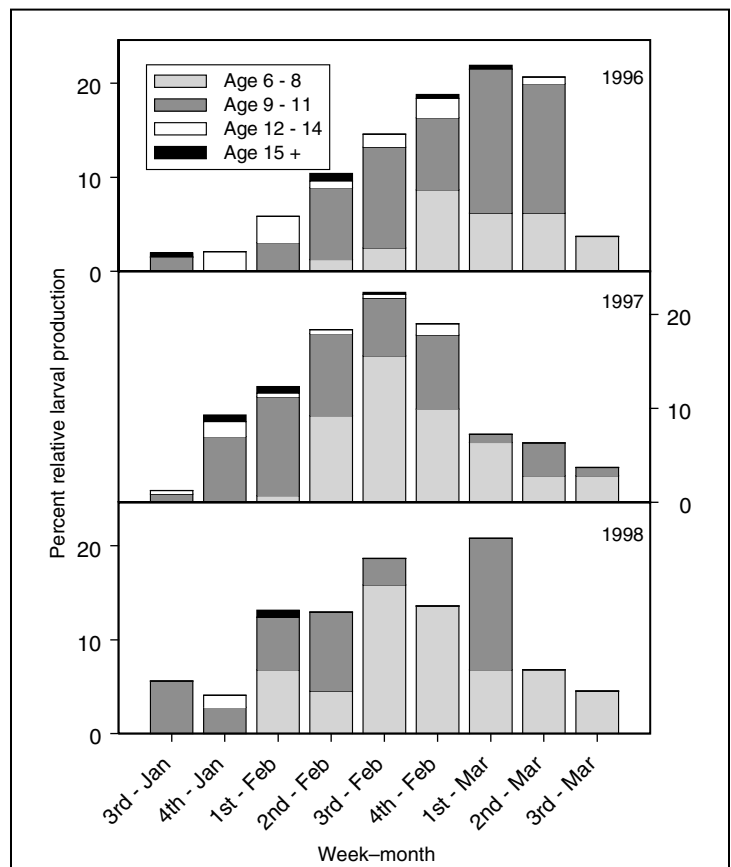

Figure 11

Percent relative larval production estimated from observations of larval development and age-group–specific absolute fecundity (based on fertilized eggs) for all mature females belonging to each age group of black rockfish collected in Oregon during 1996–98.

Table 5

Age group-specific relative larval production for 1996–98 for female black rockfish off Oregon.

Age group	Percentage of relative larval production		
	1996	1997	1998
6–8	26.4%	43.1%	65.3%
9–11	60.1%	49.6%	32.9%
12–14	11.3%	5.8%	1.8%
15 and older	2.2%	1.5%	0.0%

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