

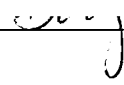
AN ABSTRACT OF THE DISSERTATION OF

Stephen J. Bobko for the degree of Doctor of Philosophy in Fisheries Science
presented on May 2, 2002.


Title: Effects of Maternal Age on Reproductive Success in Black Rockfish, *Sebastes melanops*.

Abstract approved:

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Douglas F. Markle

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Steven A. Berkeley

From 1996 through 1998 I collected mature female black rockfish off Oregon and examined ovaries and otoliths to estimate weekly, age-specific larval production. In all reproductive seasons, older black rockfish extruded larvae earlier in the season, followed by progressively younger fish. Each year, beginning in May, I collected young-of -the-year (YOY) benthic juveniles that settled out in nearshore waters and determined their birthdates from counts of daily rings of lapillar otoliths. I compared the birthdate distribution of juvenile survivors to the age-specific temporal distribution of larval production to estimate the contribution of each adult female age group, ages 6-8, 9-11, 12-14, and 15+ to juvenile recruitment. The results from 1996 show a disproportionately greater contribution to benthic YOY recruitment by older fish. 1997 results show a relatively even contribution among maternal age groups. In 1998

most of the YOY recruits came from younger fish extruding larvae late in the season. I then examined larvae per recruit (LPR) models to evaluate the effects of fishing mortality on spawning potential of black rockfish, incorporating my estimates of age-specific maternal reproductive success. When it is evident that certain age groups are more successful at reproducing, as observed in black rockfish, changes in that population's age composition must be considered beyond simply reducing the estimate of total larval production.

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Effects of Maternal Age on Reproductive Success in
Black Rockfish, *Sebastes melanops*

by
Stephen J. Bobko

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Stephen J. Bobko, Author

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scrubbing coldroom walls with bleach and collecting juvenile rockfish until three in the morning.

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CONTRIBUTION OF AUTHORS

Steven Berkeley was involved in the design, implementation, and analyses of all of my research. He also assisted in the writing of each manuscript. Thomas H. Rippetoe assisted in data collection for the study.

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DEDICATION

To the Bobko's: Mom, Dad, and Melodie

EFFECTS OF MATERNAL AGE ON REPRODUCTIVE SUCCESS IN BLACK ROCKFISH, *SEBASTES MELANOPS*

CHAPTER 1

INTRODUCTION

Overview

For a life history trait to persist in any environment it must promote maximization of the fitness of the individuals, particularly by increasing the potential for reproductive success. For many fish species in the North Pacific, longevity with extreme iteroparity, is a trait which partitions progeny production over many years, increasing the likelihood of spawning during periods of favorable environmental conditions and thereby reducing the impact of environmental variation on reproductive success (Leaman and Beamish, 1984; Goodman, 1984; Schultz, 1989).

There are two principal ways a fish population with long-lived individuals benefits from being composed of a broad distribution of spawning age classes. The first, only recently receiving significant interest, is proportionally greater reproductive contributions by older aged fish. Secondly, in respect to partitioning progeny production over an extended period of time on an annual basis, multiple aged spawners will tend to extend annual spawning seasons, again spreading risk over time.

Spawning potential can increase with age if the fraction of surplus energy devoted to reproduction is age-specific. In many fishes, reproductive effort, often measured in the form of the gonadosomatic index, increases with age (Roff, 1983, 1992; Rijnsdorp, 1990; Leaman, 1991). The means by which increased reproductive effort is manifest in older fish are diverse and may occur through the production of more eggs, eggs with higher quality energy reserves, or eggs and larvae that experience better survival through increased health and/or size.

It is generally accepted that absolute fecundity increases with fish size because of a volumetric increase in body cavity available for ovarian development. Relative fecundity, on the other hand, can increase with fish size only with the production of more eggs per unit somatic weight. Increases in relative fecundity with age have been observed in a diverse group of fishes, including queenfish, *Seriphus politus* (DeMartini, 1991) and haddock, *Melanogrammus aeglefinus* (Hislop, 1988). Boehlert et al. (1982) report that mature widow rockfish, *Sebastes entomelas*, increase relative fecundity from 254.0 eggs per gram of somatic weight at age 6 to 476.8 eggs per gram at age 13.

Many fish produce larger eggs and larvae with each subsequent spawning cycle (Hislop, 1988; DeMartini, 1991; Zastrow et al., 1989). Larger eggs may increase survival by being less susceptible to predation (Rijnsdorp and Jaworski, 1990) and through a positive correlation between egg and larval sizes (Bagenal, 1971; Knutsen and Tilseth, 1985; Hinckley, 1990). In many fish species larger larvae have

greater probabilities of survival than smaller larvae by being able to endure prolonged starvation prior to first feeding (Blaxter and Hempel, 1963), by decreasing stage durations through faster growth rates thereby reducing exposure to high stage-specific mortality rates (Blaxter and Hempel, 1963; Helle, 1989; Monteleone and Houde, 1990), by possessing increased ability to capture prey (Knutsen and Tilseth, 1985), by being able to utilize a greater size range of prey (Hunter, 1981), and by exhibiting increased ability to avoid predators (Miller et al., 1988).

While not directly supporting the “bigger is better” theory, further evidence of the importance of egg size is described by Bailey and Almatar (1989) who report that varying energy available for egg production in herring, *Clupea harengus* L., is primarily manifest in egg number, not in size. During substandard environmental conditions herring will limit the number of eggs produced in order to ensure that eggs produced are of at least a minimum critical size. The authors conclude that egg size is an adaptive feature selected to maximize larval survival and will be maintained at the sacrifice of egg numbers.

Hislop (1988) reports that haddock, *Melanogrammus aeglefinus*, first year spawners produce significantly smaller eggs and have lower relative fecundities than older repeat spawners. Further, Borisov (1978) states that increased mortality of eggs, embryos, larvae, and juveniles are features of females spawning for the first time. While most literature on egg quality is based on aquaculture (Kjorsvik et al., 1990; Lam, 1994), there is some evidence of increased egg quality with age in wild

fish. Zastrow et al. (1989) report 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. In cod, *Gadus morhua* L., egg production and quality are dependent on fish age, nutritional status, batch number, and stress factors (Kjorsvik, 1994).

Regardless of age-specific egg production or egg/larval fitness, a broad age distribution will tend to protract a population's spawning season. Differential timing of spawning events within one season has been observed in many fishes, usually with larger, older fish spawning earlier (Simpson, 1959; Bagenal, 1971; Berkeley and Houde, 1978; Shepherd and Grimes, 1984; Lambert, 1987). In contrast, Hutchings and Myers (1993) report that younger Atlantic cod, *Gadus morhua*, began spawning before older individuals, but with the older fish spawning over a longer period of time and effectively extending the overall reproductive season. Fish stocks with age-specific protracted reproductive periods increase the likelihood of spawning occurring while conditions are conducive to maximizing recruitment (Lambert, 1990). Age-specific egg production is tied to timing of spawning and a mixed-age spawning population leads to protracted spawning which greatly increases the probability of larvae - food match.

Two of the more classical lines of thought on food availability and starvation and their effects on recruitment are Cushing's (1969, 1995) 'match/mismatch' and Hjort's (1926) 'critical period' hypotheses. Both are conceptualized on the premise

that starvation is the primary source of variation in recruitment, with Hjort's hypothesis concerned only with starvation at the first feeding, i.e., the critical period, and Cushing's hypothesis focused on the consequences of starvation at any stage of early development based on larval distribution not coinciding spatially or temporally with peak production. Both hypotheses support the adaptation of spreading reproductive effort over a longer period of time through protracted spawning seasons to increase the probability of a "match" occurring between larvae and adequate prey abundance.

While longevity compensates for varying environmental conditions, it also makes the fish more susceptible to over-exploitation. The removal of older age classes through fishing mortality can be detrimental to a long-lived fish species not only by removing biomass and lowering egg production, but by truncating the upper end of the age distribution of spawners and their potentially higher reproductive potential (Borisov, 1978; Beverton, 1986; Leaman and Beamish, 1984). It is critical that these older individuals not be addressed solely in terms of biomass, but their relative reproductive contribution and the repercussions of their removal from the population be considered.

Fisheries stock assessments and catch predictions are typically based upon female spawning stock biomass and/or population egg production. While age-specific fecundity is often utilized in fisheries models, changes in a stock's age composition through the removal of older age classes are not considered beyond reducing the

estimate of total potential egg production. If eggs produced by young age spawners have a lower chance of survival but are regarded as equal to eggs from older spawners, management decisions will overweight the contribution of young spawners. This is critical even for a species that spawns over many years. As fishing pressure truncates older fish from the range of age classes spawning it results in a higher proportion of eggs produced in any given year coming from the youngest spawners. Leaman (1987, 1991) discusses the importance of incorporating some measure of reproductive value or potential into stock monitoring and assessment programs, but unfortunately consideration of the existence of differential reproductive success with age is usually disregarded.

My research is concerned with investigating differing reproductive success, measured here as the proportion of progeny surviving to demersal juvenile stage, as a function of maternal age in a long-lived species, black rockfish, *Sebastes melanops* using simulation modeling techniques. If present, disproportionately greater contribution to recruitment by older fish should generate considerable concern for fisheries biologists, managers, and, of course, fishermen. As Leaman and Beamish (1984) and Leaman (1991) have warned, managing long-lived species using strategies based on fisheries characteristics of short-lived stocks may result in rapid over-exploitation and prolonged periods of recovery.

Black rockfish are ideal subjects for studying age-related variability in reproductive success. They are relatively long-lived, with fish reaching a maximum

age of 38 years (Stewart, 1993). Adult fish usually restrict movements to a small home range, with only 3 % of recoveries of fish tagged off Newport and Garibaldi caught further than 10 nautical miles from their release sites (Butler, 1986; Stewart, 1993). Black rockfish are viviparous, with gestation estimated to be 37 days at 10°C (Boehlert and Yoklavich, 1984). This reproductive strategy enables age specific development to be tracked over the entire range of stages, from egg to larva. Juvenile fish are also quite abundant and easily captured in bays and tide pools (Laroche and Richardson, 1980; Bayer, 1981). Black rockfish have also been experiencing an increased popularity in the Oregon sport fishery comprising as much as 80% of all landed groundfish in some ports (Stewart, 1993).

Objectives

(1) The first objective is to determine if reproductive potential and strategy differ with maternal age. This objective is multi-faceted and will be achieved through:

- * Determining age-specific fecundity;
- * Identifying temporal patterns of reproductive development through seasonal increases in egg diameters and timing of spawning determined by macro and microscopic staging ovaries; and
- * Identifying age related temporal patterns in parturition.

- (2) Investigate the existence of differential survival of recruits relative to my estimates of age-specific spawning output. Birthdates will be determined using the otolith increment technique on juvenile fish collected after recruiting to nearshore demersal habitats. The distribution of birthdate frequencies will be compared with the observed age-specific temporal distribution of spawning output (larval production) extrapolated to the population level.
- (3) The ultimate goal of this research is to combine data from objectives (1) and (2) with existing data from the literature to produce population simulation models of the effects of maternal age on reproductive success.

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CHAPTER 2

MATURITY SCHEDULE, OVARIAN CYCLE, FECUNDITY, AND
AGE-SPECIFIC PARTURITION OF
BLACK ROCKFISH, *SEBASTES MELANOPS*,
OFF THE OREGON COAST

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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 percentage of all mature fish aged 10 or older decreased each year of this study, from 51.1% in 1996 to 14.5% in 1998. Parturition occurred between mid January and mid March, with a peak in February. We observed a trend of older females extruding larvae earlier in the spawning season, with younger fish responsible for larval production during the later part of the season. The likelihood of yolked oocytes reaching the developing embryo stage increased with maternal age. Absolute fertilized fecundity estimates ranged 299,000 embryos for a 6 year-old to 948,000 embryos for a 16 year-old.

Introduction

Many fish species in the North Pacific have long reproductive life spans, which partitions progeny production over many years, increasing 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 with larger, older fish spawning earlier (Simpson, 1959; Bagenal, 1971; Berkeley and Houde, 1978; Shepherd and Grimes, 1984; Lambert, 1987), but in some cases younger fish spawning earlier in the season (Hutchings and Myers, 1993).

Increased recruitment variability in marine fishes can result from the removal of a component(s) of a population with a disproportionate contribution towards reproductive success. Factors that might affect individual reproductive success include the number of eggs produced, the quality of eggs (e.g., amount of yolk), and the size or health of eggs and larvae. Off the coast of Oregon, widow rockfish, *Sebastes entomelas*, exhibited increased absolute fecundity, and more importantly increased relative fecundity, with age (Boehlert et al., 1982). Individual populations of shortbelly rockfish, *Sebastes jordani*, were 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. While their longevity

and low rate of natural mortality may compensate for varying environmental conditions, it also makes them more susceptible to over-exploitation. The objective of our research presented here is twofold. First, we describe the basic reproductive life history of black rockfish, with emphasis on the ovarian development 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 2,575 black rockfish from October 1995 through March 1998 from Newport, Depoe Bay, Port Orford, and Charleston, Oregon (Figure 2.1). From December through March, the months of peak female reproductive development, collections were made every day fish were available from the recreational fishery. Outside this period, fish were collected monthly. Black rockfish were primarily obtained from charter boat landings, and consequently only carcasses were normally available. We also collected whole fish by rod and reel and spearfishing. When possible, all available black rockfish were sexed, and females staged as immature or mature; males and immature females were measured (mm), and mature females were returned to the laboratory. On extremely busy days with numerous charter boats fishing, only mature females were sampled. Immediately upon return to the laboratory, we recorded fork length (FL, mm), total weight (g) when possible, liver

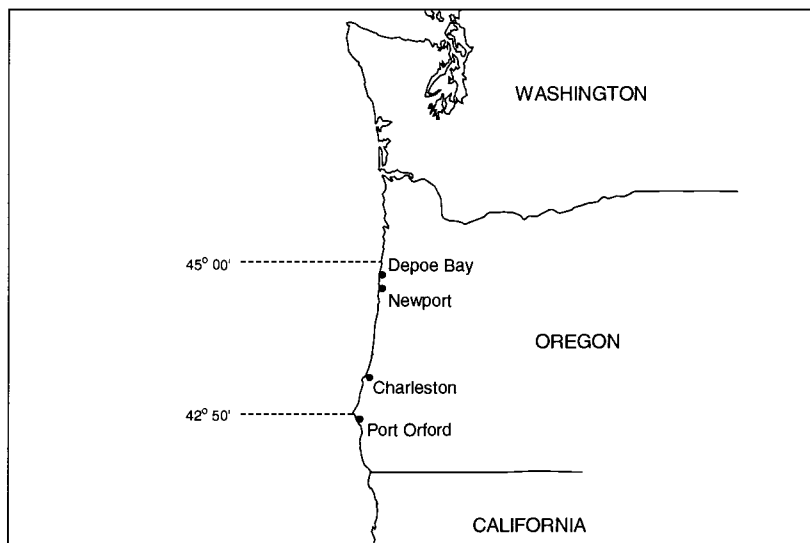


Figure 2.1. Map of the Oregon coast showing the study area where black rockfish were collected.

weight (g), and ovary weight (nearest 0.1 g). 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 “maturing” classification in favor of the simplified maturity stages reported by Gunderson et al. (1980) (Table 2.1). Sagittal otoliths were removed and stored dry for age determination. All ageing was done by personnel from the Oregon Department of Fish and Wildlife (ODFW) using the break and burn technique (Beamish and Chilton, 1982).

Histological preparations were made from the ovaries of 175 females collected monthly from March 1996 through March 1997 to track seasonal ovarian development in black rockfish. We selected females from all maturity stages observed in each month and as wide a range of ages as possible (Table 2.2). Ovaries were embedded in paraffin, sectioned at 4-5 μm , and stained with Gill-3 Haematoxylin and Eosin Y Alcoholic. Histological preparations were made by the Diagnostic Laboratory of the College of Veterinarian Medicine, Oregon State University.

We determined stage-specific fecundity in black rockfish for females with unfertilized yolked oocytes ($n=192$) and fertilized eggs ($n=85$). Post fertilization ovaries were very fragile and tended to rupture easily and release embryos under the slightest pressure. Consequently, for these stages, only fish with no evidence of embryo loss were used to estimate fecundity, which were predominately fish that we

Table 2.1. Macroscopic and histological description 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 relative 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 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 2.2. 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	<i>n</i>
March	7-25	375-510	1, 4-6	10
April	7-18	364-447	1, 5-6	12
May	7-13	340-465	1 & 6	15
June	5-13	349-432	1 & 6	15
July	5-13	360-475	1 & 6	14
August	5-11	357-493	1-2, 6	15
September	6-16	366-488	1 & 2	12
October	5-16	357-420	1 & 2	11
November	5-11	355-434	1 & 2	16
December	5-14	365-439	1 & 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

collected by hook and line and spearfishing and immediately placed into plastic bags upon collection. Ovaries were processed following procedures modified from Lowerre-Barbieri and Barbieri (1993) to separate eggs/embryos from connective tissue. Briefly, fixed ovaries were manually manipulated and rinsed with water through a 1mm-square mesh sieve, which retained most of the connective tissue, into another sieve with 75 μ mesh. Ovary connective tissue was retained in the coarse sieve, while freed eggs were collected in the fine mesh sieve. Freed eggs were patted dry, weighed (nearest 0.1 g), and three subsamples, collected, weighed (nearest 0.001 g), and placed in 10% buffered formalin. The subsamples were counted by hand and absolute fecundity estimated by the calculation

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

where AF = absolute fecundity, or the total number of eggs per female;

EW = rinsed egg/larvae weight;

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 FL and assuming isometric growth, was estimated by

$$RF = \frac{AF}{FL^3} \times 10^4.$$

For our analyses of fecundity, we only included fish with coefficients of variation of egg/embryo counts less than or equal to 5%, and for pre-fertilized eggs we only included females with average egg diameters of no less than 350 μ to ensure full recruitment of developing oocytes. Analysis of covariance (ANCOVA) was used to test for differences in the relationships between fecundity and age between years and pre-fertilized vs. fertilized egg development stages.

We used logistic regression to predict the probability of female black rockfish being mature based on fork length. 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 this analysis. Binary maturity observations (0 = immature, 1 = mature) and fork length were fitted to a logistic model using the function `glm, family = binomial` of S-PLUS (S-PLUS, 1999). The model used was

$$\pi (FL) = P(Y = 1 | FL) = \frac{e^{\beta_0 + \beta_1 * FL}}{1 + e^{\beta_0 + \beta_1 * FL}},$$

where $P(Y = 1 | FL)$ = 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 percent of female black rockfish mature at length. Assuming this fork length-maturity relationship 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 percent maturity of recreational female black rockfish landings off Newport.

To estimate age at 50% maturity, our length-at-age data, which were primarily from mature females, were combined with length-at-age data from two through four-year-old female black rockfish collected by ODFW off Newport, Oregon in 1998 and fitted with the von Bertalanffy growth function (VBGF). Using the VBGF in the form

$$t = t_0 + \frac{1}{k} \left[\log \frac{L_\infty}{L_\infty - l_t} \right]$$

with our VBGF parameter estimates and estimated length at 50% maturity, we then solved the equation to determine the corresponding age at 50% maturity.

We estimated the timing of parturition by microscopically determining embryo development stages for all females collected with fertilized eggs following Yamada and Kusakari's (1991) stages of embryonic development for kurisoi, *Sebastes schlegeli*, modified to reflect the gestation period of 37 days for black rockfish reported by Boehlert and Yoklavich (1984). We modified Boehlert and Yoklavich's (1984) regression model of stage duration (D, days/stage) and stage (S) of $D = 0.0452 * S^{1.090}$ to describe the relationship between the time until parturition and

stage using polynomial linear regression (Figure 2.2). Estimated parturition dates were grouped into weekly intervals by age group: 6-8; 9-11; 12-14; and ≥ 15 . These data were adjusted to reflect fertilized absolute fecundity and the observed proportion of mature fish belonging to each age group calculated from data pooled for all years (Table 2.3).

Results

Ovarian development

Black rockfish off Oregon exhibited group-synchronous oocyte development with individuals extruding one brood of larvae per year. Based on our observations of ovarian development from all three years of this study, parturition took place from mid-January through mid-March, with February the peak month. 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 were comprised of oogonial nests and slightly larger oocytes with a basophilic cytoplasm and a maximum diameter of 50 μ . Also present at this time were various sized developing oocytes between 50-150 μ in diameter with small lipid vacuoles surrounding the nuclear membrane. Yolk formation, vitellogenesis, began in late August and was observed through the third week of February. In the latest stages of vitellogenesis, the largest oocytes were approximately 700 μ in diameter with oil

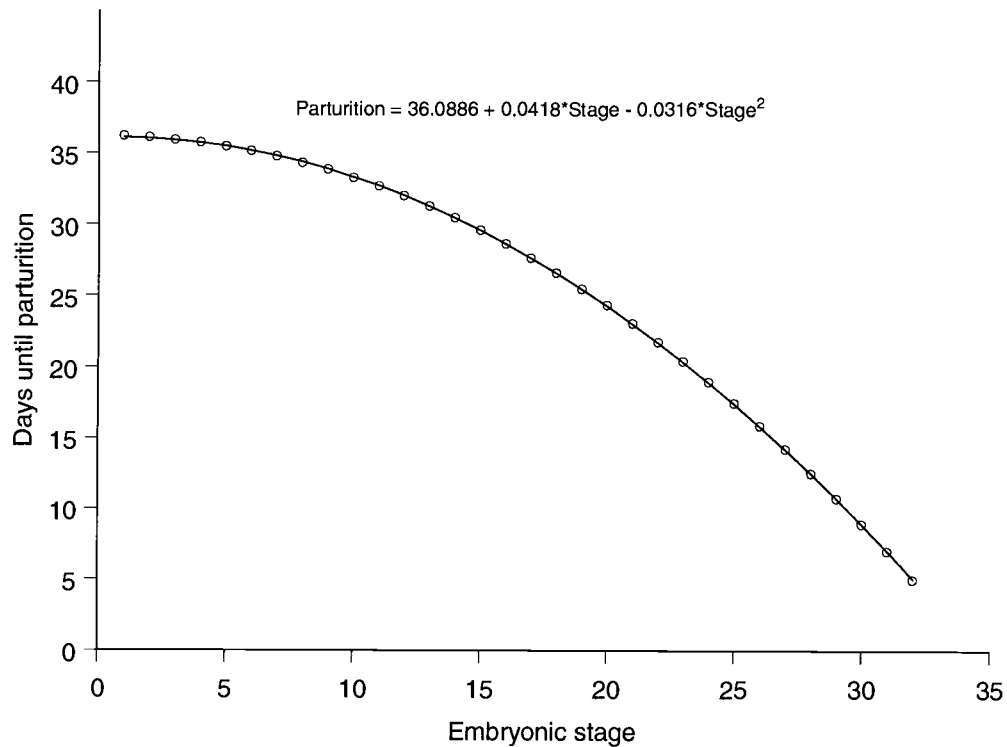


Figure 2.2. Estimated time until parturition as a function of Yamada and Kusakari's (1991) stages of embryonic development based on Boehlert and Yoklavich's (1984) relation between stage duration and stage for embryonic *Sebastes melanops*.

Table 2.3. Age group-specific fertilized absolute fecundity and percent of all observed mature females in each age group used to correct raw estimates of larval production to accurately reflect population levels. Calculated from data pooled from the years 1996 - 1998.

Age Group	Fertilized Absolute Fecundity	Percent of mature females in 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%

vacuoles and yolk globules occupying the entire developing oocytes' cytoplasm. The first female with fertilized eggs (stage 3) was observed during the second week of January, with stage 3 females observed until the third week of February. Recently fertilized eggs were approximately 850 μ in diameter. Female black rockfish with ovaries containing eyed larvae were also first observed during the second week in January and were seen through the second week of March. Recently spent females were first collected during the last week of January and were most frequently collected in late February and early March.

Sexual maturity

The smallest mature female black rockfish we observed was 345 mm; all individuals were mature by 450 mm. Fifty percent of the females were estimated to be mature at 394 mm fork length (Figure 2.3). Based on our length-maturity logistic model, we observed a decreasing trend in the percent maturity for female black rockfish recreational landings from ODFW collections from 1992-2000 (Figure 2.4).

The von Bertalanffy parameter estimates for female black rockfish were $L_{\infty} = 442$ mm, $k = 0.33$, $t_0 = 0.75$. Using these estimates along with the fork length at which 50% maturity, we estimated the age at which 50% of female black rockfish were mature to be 7.5 years. The median age at parturition for mature females decreased in each collection year from age 10 years in 1996 to 9 in 1997 and to age 7

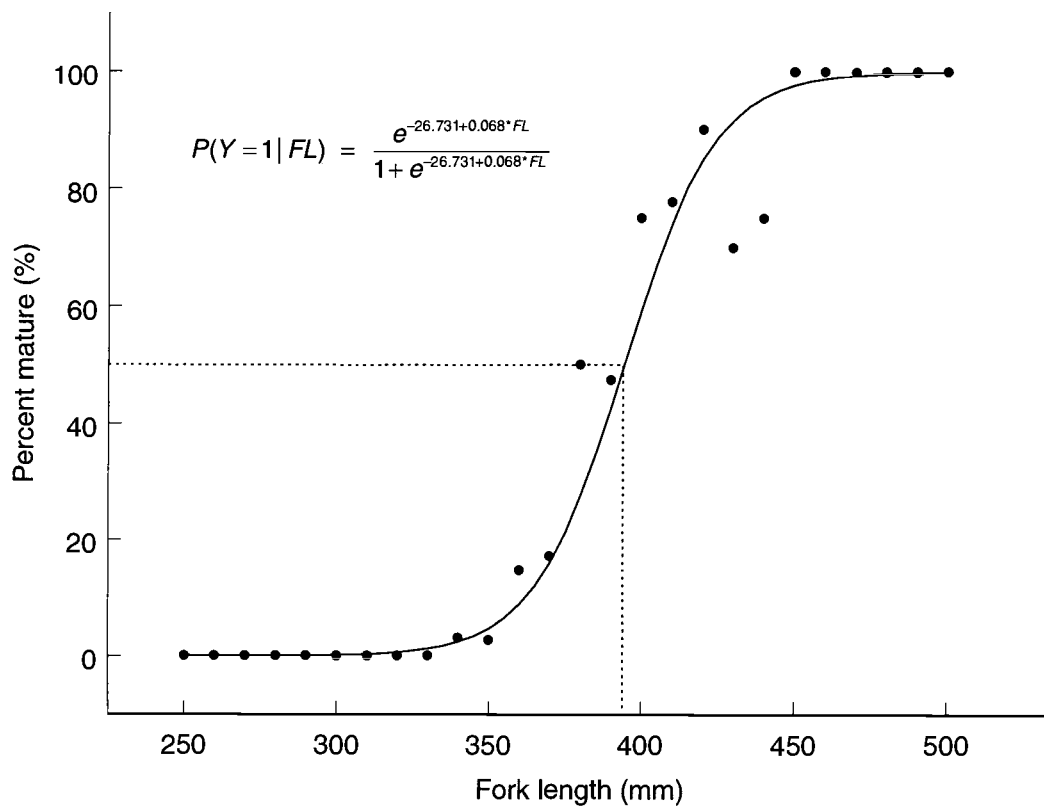


Figure 2.3. Logistic regression model for the estimated percent of sexually mature female black rockfish, *Sebastes melanops*, as a function of fork length with associated percent mature at 10 mm length intervals.

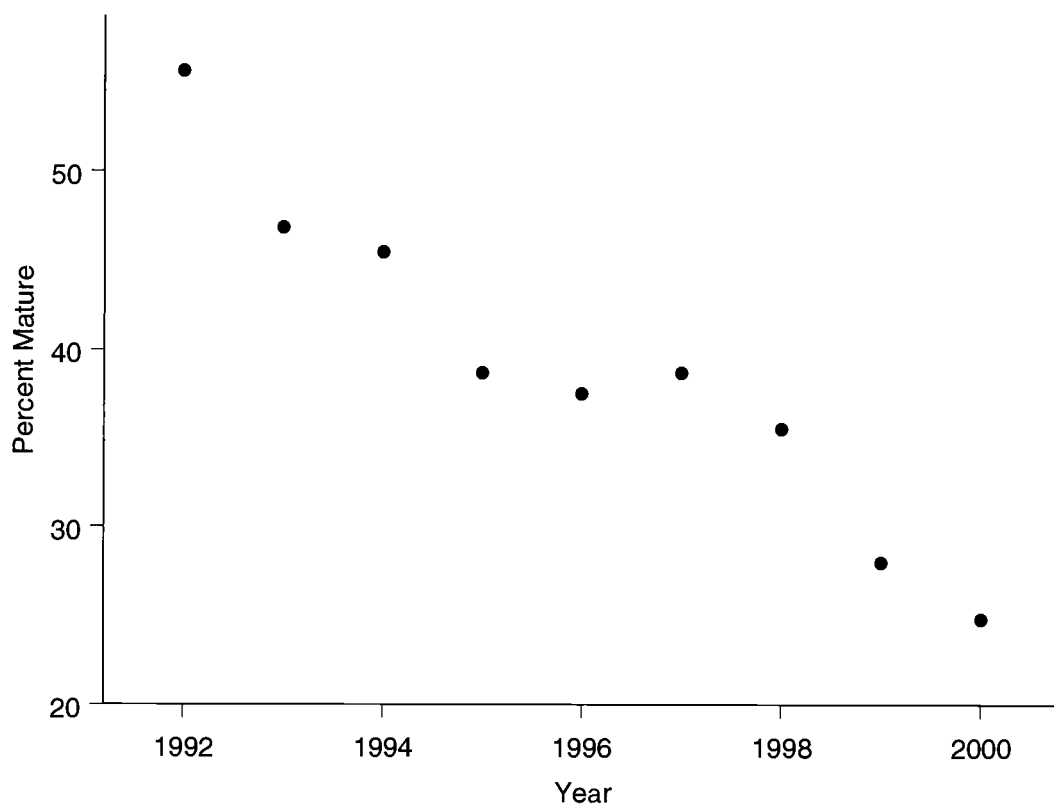


Figure 2.4. Estimated percent maturity for recreationally landed female black rockfish from Newport, Oregon based on our fork length-maturity logistic regression model. Data are from regular summer port sampling conducted by the Oregon Department of Fisheries and Wildlife from 1992-2000.

in 1998. In addition, the percentage of all mature fish age 10 or older also decreased each year, from 51.1% in 1996, to 31.8% in 1997, and 14.5% in 1998.

Fecundity

There was a significant linear relationship ($P < 0.0001$) between absolute fecundity and age over the age range observed for pre-fertilized females in each year (Figure 2.5a). While the results of ANCOVA (Table 2.4a) over a common age range showed marginal evidence of differences in slopes ($P = 0.062$), among the years 1996-98, we proceeded with our analysis assuming a common slope. ANCOVA also showed no significant difference in elevations ($P = 0.615$), indicating no annual effect and allowing one model to be fit to the pooled data (Figure 2.5b). There was also a significant linear relationship between absolute fecundity and age over the age range observed for females with fertilized eggs in each year (Figure 2.6a). Due to the low number of females with developing embryos collected in 1996 and 1998, 19 and 4, respectively, and based on the results of pre-fertilized females, all data were pooled and fit with one model (Figure 2.6b). While we were able to pool the data for all years for both stage-specific fecundities, there was evidence of interaction (i.e., unequal slopes) between stage-specific absolute fecundity and age (2-tailed t-test, $P = 0.048$), requiring the data to be fit to a separate lines model (Figure 2.7).

Similar to the ANCOVA results for absolute fecundity, there were no differences in slopes or elevations for pre-fertilized relative fecundity for the years

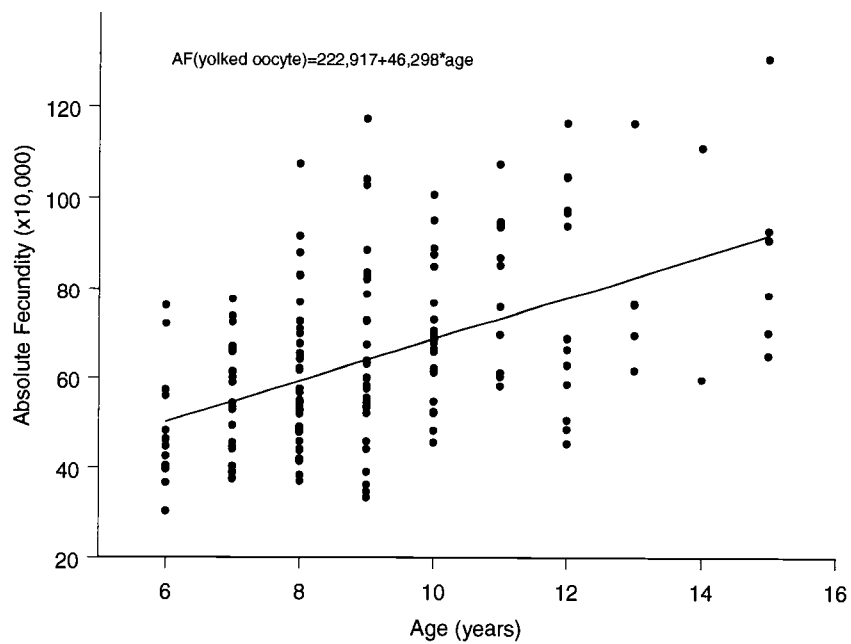
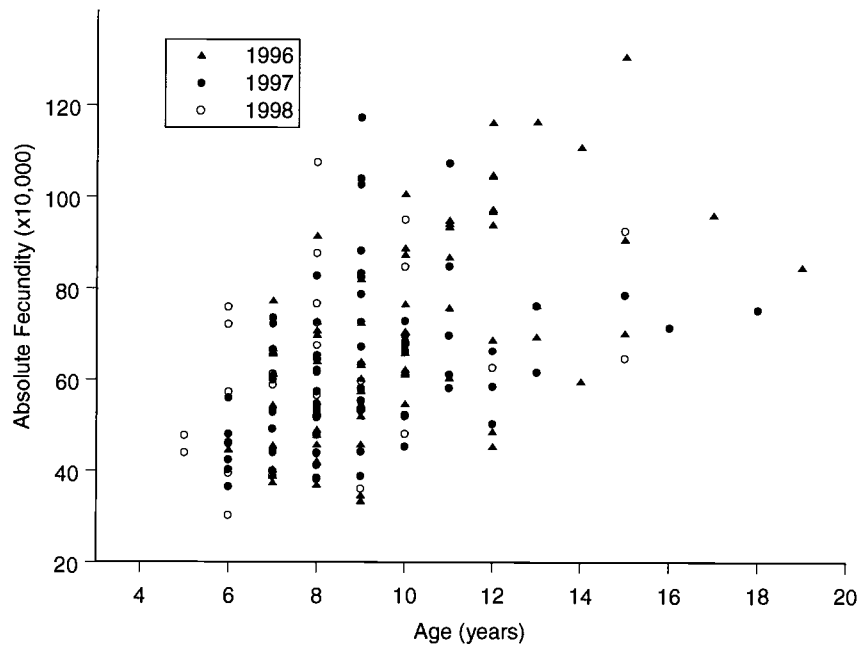


Figure 2.5. a) Scatter plot of black rockfish pre-fertilized absolute fecundity on age by year (1996-98) and b) Best fit pooled curve based on results of ANCOVA over common age range.

Table 2.4. Results of analyses of covariance testing for differences in slopes and elevations of a) annual absolute fecundity-age relation and b) annual relative fecundity-age relation. Response variables = AF and RF, treatment factors = year, and covariate = age.

a) absolute fecundity

Source of variation	df	Sum of squares	Mean square	F	p-value
Equality of slopes	2	1618.68	809.34	2.82	0.062
Error	167	47852.22	286.54		
Equality of Elevation	2	285.14	142.57	0.49	0.615
Error	169	49470.90	292.73		

b) relative fecundity

Source of variation	df	Sum of squares	Mean square	F	p-value
Equality of slopes	2	505.43	252.72	1.14	0.323
Error	167	37067.92	221.96		
Equality of Elevation	2	944.90	472.45	2.13	0.123
Error	169	37573.36	222.33		

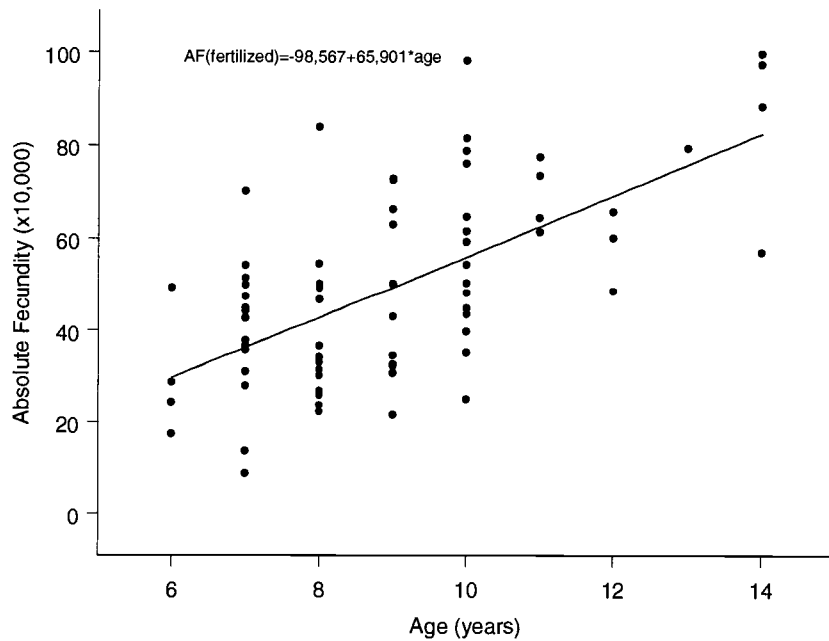
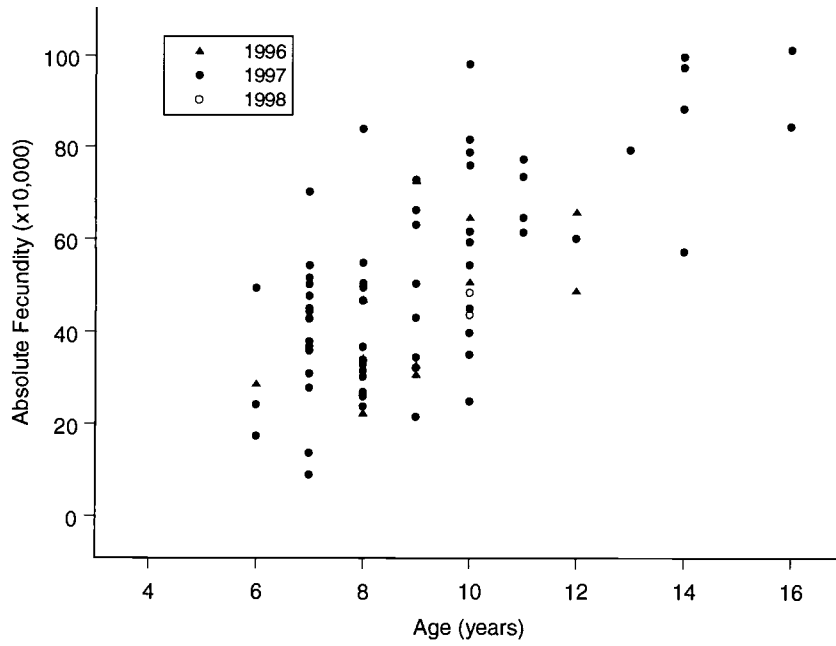


Figure 2.6. a) Scatter plot of black rockfish fertilized egg absolute fecundity on age by year (1996-98) and b) Best fit pooled curve over common age range.

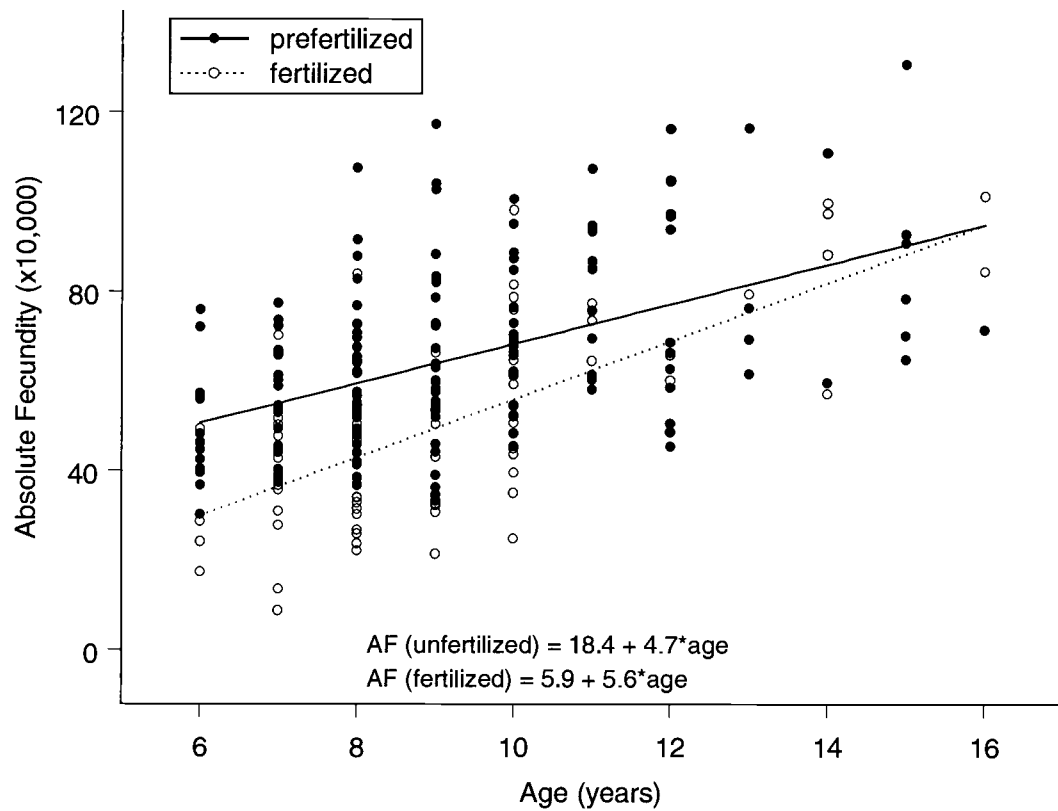


Figure 2.7. Separate lines fit for pre-fertilized and fertilized absolute fecundity on age for black rockfish in Oregon.

1996-98 (Table 2.4b). Again, based on the results of the ANCOVA for pre-fertilized 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 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 $P = 0.113$). There was, however, strong evidence (2-tailed t-test, $P < 0.001$,) of a stage effect (i.e., unequal elevations) requiring the data to be fit with a parallel lines model (Figure 2.8).

Temporal patterns in parturition

From 1996 through 1998 we estimated relative larval production for four age groups, ages 6-8; 9-11; 12-14; and 15 and older (Figure 2.9). In each year parturition took place from the mid-January until mid-March, with older, larger fish extruding larvae earlier than younger fish. In 1996 and 1997, the 9-11 year old fish dominated larval production, responsible for 60% and 46.5% of all larvae extruded, respectively (Table 2.5). In 1998 age 6-8 fish produced the largest number of larvae, while in all years, relative larval production was lowest for the oldest age group.

Discussion

Ovarian development for black rockfish in Oregon was similar to the development cycles reported for other rockfish species (Moser, 1967; Bowers, 1992;

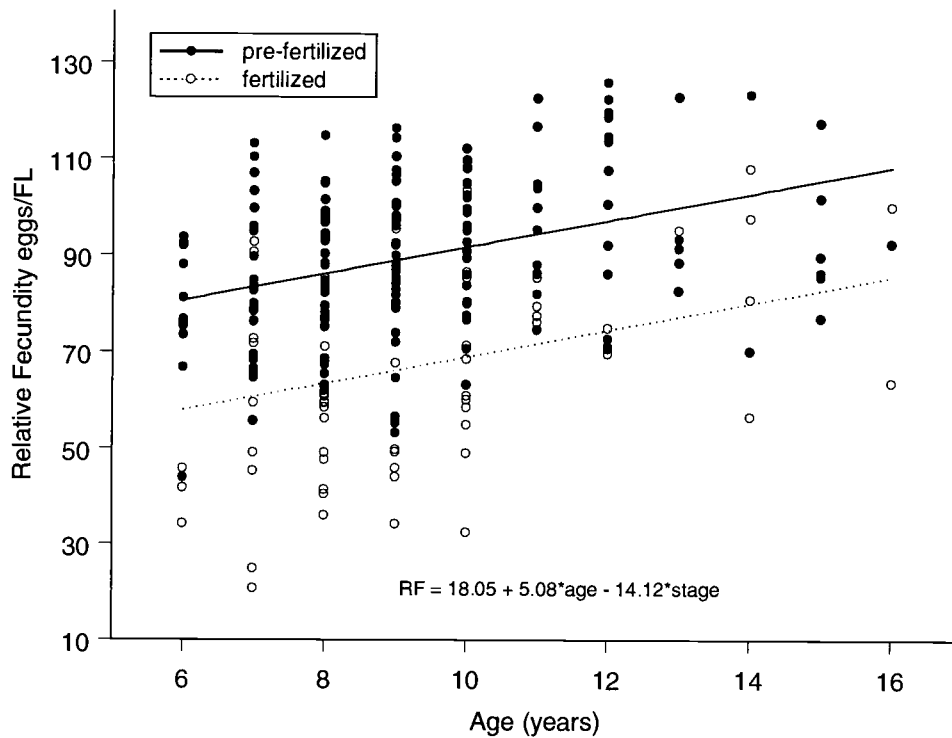


Figure 2.8. Parallel lines model fit for pre-fertilized and fertilized relative fecundity on age for black rockfish in Oregon.

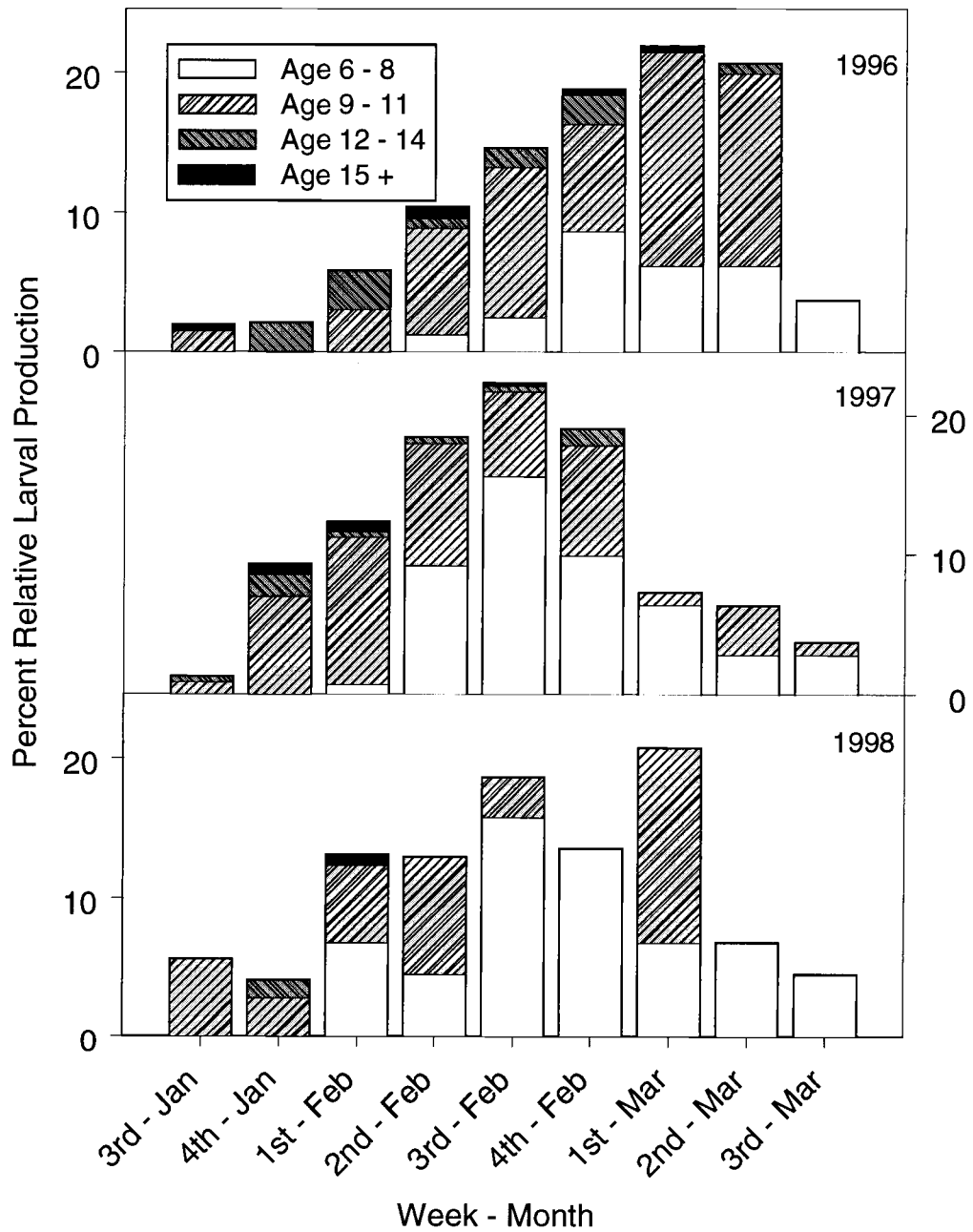


Figure 2.9. Percent relative larval production estimated from observations of larval development, age-group specific fertilized absolute fecundity, and percentages of all mature females belonging to each age-group for black rockfish collected in Oregon during 1996-98.

Table 2.5. Age group-specific relative larval production for 1996-1998 for female black rockfish off Oregon.

Age Group	Percent 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%

Nichol and Pikitch, 1994) with the exception of seasonal timing and stage duration. Females underwent vitellogenesis for up to five 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 with a peak 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.

As observed by Love and Westphal (1981) for olive rockfish, all but the smallest immature female black rockfish followed a seasonal cycle in which their ovaries developed an orange coloring during those months of reproductive activity for mature fish. 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. Since 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 staged as immature.

Our estimate of fork length at 50% maturity for female black rockfish off Oregon was only slightly lower than the 400 mm estimate reported off north-central California (Wyllie Echeverria, 1987), but much lower than the 422 mm estimate 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 his use of whole otoliths to age fish, thereby possibly underestimating age, and 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. While the increase in absolute fecundity with age was observed in both pre-fertilized and fertilized females, they occurred at different rates. 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. We feel that fecundity in black rockfish is best described using those females with fertilized eggs. When care is taken to ensure that embryo loss is minimized when collecting mature female, estimating fecundity from those females closest to parturition should provide the most accurate estimates of larval production.

We observed a recurring trend of older, larger fish extruding larvae earlier in the reproductive season with subsequent parturition dominated by younger and younger fish. Both Eldridge et al. (1991) and Nichol and Pikitch (1994) observed size-specific patterns of larger, and most likely older, fish spawning earlier in the

season than smaller fish in yellowtail rockfish, *Sebastes flavidus*, and darkblotched rockfish, *S. crameri*, respectively. Reduced food availability was 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.

While age-specific fecundity is often utilized in fisheries stock assessment models, changes in a population's age composition through the removal of older age classes are not considered beyond reducing the estimate of total potential egg/larval production. The decreasing representation of mature female black rockfish aged 10 and older in the three years of this study indicates age truncation is occurring in black rockfish in Oregon. This is detrimental to this long-lived species by not only removing biomass and potential larval production, but also by truncating the upper end of the age distribution of mature females with higher fecundity per individual, a greater success in carrying eggs through to the larval stage, and that help extend the overall spawning season. Further research is necessary to explore differential reproductive success with age, determine their controlling mechanisms, and how to incorporate these findings into stock assessment models.

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CHAPTER 3

GROWTH AND MORTALITY RATES OF YOUNG-OF-THE-YEAR
BLACK ROCKFISH, *SEBASTES MELANOPS*, FROM FLOATING
DOCKS AND EELGRASS BEDS
IN NEWPORT AND COOS BAY, OREGON

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May 2, 2002

Abstract

During the summers of 1997 and 1998 we made biweekly collections of young-of-the-year (YOY) black rockfish, *Sebastes melanops*, from eelgrass beds, *Zoostera* sp., and floating docks in Newport and Coos Bay, Oregon. Captured fish were measured and marked with unique batch Visible Implant Fluorescent Elastomer (VIE) tags and released. Instantaneous daily mortality rates calculated with Program MARK ranged from 0.0051 to 0.0693 day⁻¹, with mortality rates consistently lower in eelgrass beds than floating docks. Daily growth rates calculated from size-at-capture data ranged from 0.31 to 0.35 mm*day⁻¹. There were no significant differences in growth rates between habitats or estuaries. In 1998 YOY black rockfish recruited at smaller sizes than observed in 1997, but fish in both years grew at the similar rates.

Introduction

Since the Sustainable Fisheries Act became law in 1996 and effectively amended the habitat provisions of the Magnuson Act, there has been a marked increase in the amount of research focusing on essential fish habitat (Benaka 1999). Much of the activity has been directed towards estuaries and nearshore coastal habitats, areas important as nursery areas and for their high rates of production, but also the areas most heavily impacted by anthropogenic effects (Nichols et al., 1986; Johnson et al., 1998; Fourqurean and Robblee, 1999).

Benthic young-of-the-year (YOY) black rockfish, *Sebastes melanops*, are unique among North Pacific rockfish in their choice of shallow water nearshore and estuarine settlement habitats, including eelgrass beds, *Zoostera* sp., floating docks, tidepools, and shallow water reefs. These habitats are particularly vulnerable to alteration caused by coastal development and human activity. In addition, we currently have little information regarding the quality of these different habitats for juvenile fish.

The purpose of our research was to determine 1) if mortality and growth rates of benthic YOY black rockfish differed between eelgrass beds and floating docks; 2) if these rates differed between Newport and Coos Bay estuaries; and 3) if any differences in mortality and/or growth were observed between years. Differences in growth and mortality rates were used to determine the relative value of different habitat types to the growth and survival of YOY black rockfish

Materials and methods

During the summers of 1997 and 1998 we made biweekly collections of young-of-the-year black rockfish from eelgrass beds, *Zoostera* sp., and floating docks in Newport and Coos Bay, Oregon (Figure 3.1). The eelgrass bed site in Coos Bay was approximately 2,760 m² in size in both years, while the eelgrass site in Newport was 30 m² in 1997 but only 20 m² in 1998. The floating docks were approximately 870 m² in size in Coos Bay and 2,147 m² in Newport.

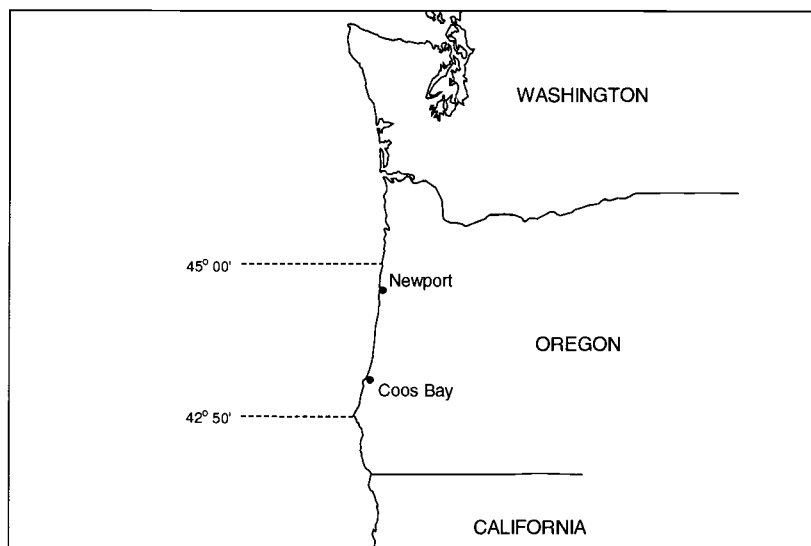


Figure 3.1. Map of the Oregon coast showing the study area where benthic young-of-the-year (YOY) black rockfish were collected.

We used a 6 m long by 1.1 m high beach seine with 3.2 mm mesh to sample our eelgrass bed site in Newport. At the larger Coos Bay eelgrass bed site, we used a 42.5 m by 3 m high beach seine equipped with a 3 m X 1.2 m X 1.2 m bag. To collect YOY black rockfish at both floating docks locations, we used standard fingerling nets with 300 mm deep, 3.2 mm mesh bags. Captured fish were held in covered 68 liter plastic tubs containing seawater and given frequent water changes. We anesthetized fish in seawater containing 75 mg/l of FINQUEL MS-222 buffered with 1.5 g/l of sodium bicarbonate. Once immobilized, each fish was measured for fork length, and injected with a batch-specific Visible Implant Fluorescent Elastomer (VIE) tag using a hand-held injector. Injector needles were wiped with 95% ethanol between applications to maintain antiseptic conditions. Batch marks were placed in lightly pigmented patches on the left and right sides of the fish at the base of the spinous and soft-rayed elements of the dorsal fin (Figure 3.2). In each estuary, fish collected in grass beds and docks were marked with different colored VIE tags to allow us to detect straying between the sampling sites. After tagging, fish were held between 45 minutes and 1 hour in recovery tanks containing fresh seawater before being released.

In May 1997 we collected 41 YOY black rockfish from Newport to evaluate tagging induced mortality, tag retention, and any tagging effects on growth. Twenty of the fish were randomly selected and tagged with VIE tags following the above described method, with the remaining 21 fish left untagged. All 41 fish were held at



Figure 3.2. Picture of a benthic young-of-the-year (YOY) black rockfish tagged with Visible Implant Fluorescent Elastomer (VIE).

the Hatfield Marine Science Center in a single 2500 liter circular tank with a constant flow of unfiltered seawater until mid-August. While juveniles primarily fed on material in the unfiltered seawater, feeding was supplemented twice a week with finely cut squid.

Daily survival rates estimated from our tag-recapture data were calculated with the Cormack-Jolly-Seber open population model (recaptures only model) using Program MARK-version 2.0 (White and Burnham, 1999). The basic assumptions of this model are: 1) every individual present at the time of sampling has the same probability of capture; 2) every individual has the same probability of survival between sampling occasions; 3) tags are not overlooked or lost; 4) sampling time is negligible (Pollock et al., 1990). Mortality rates were calculated from the estimated survival rates by the equation

$$M = -\ln(S),$$

where M = instantaneous natural mortality; and

S = survival rate.

We calculated growth rates by regressing FL (mm) on the day of year date of capture. Analysis of covariance (ANCOVA) was used to test for differences in regression growth rates (i.e., slopes) and adjusted "treatment" means (i.e., elevations) within and between estuaries, habitats, and years. All statistical analyses of growth were performed with S-Plus 2000 (S-Plus 1999).

Results

Our mark and recapture sampling took place from approximately late May through August of 1997 and 1998 when settled YOY black rockfish were approximately three to six months of age (Bobko and Berkeley, 2002a; Bobko and Berkeley, 2002b). Fish ranged in fork length from 36 to 94 mm and 36 to 75 mm in 1997 and 1998, respectively. A summary of the observed capture-recapture histories is presented in Table 3.1.

Estimates of instantaneous daily mortality rates and 95% confidence intervals are presented in Table 3.2. Goodness of Fit (GOF) tests run with Program MARK's parametric bootstrap method showed lack of fit for all our analyses. While we were able to tag, and ultimately recapture, a large proportion of the populations, our overall population sizes were small and resulted in data that inadequately fit our most general models. As a result of the lack of fit, our mortality estimates should be used with caution.

There was no evidence of any tag effect on survival for juvenile black rockfish, with all 41 fish in our tagging experiment surviving the entire summer. Upon completion of the experiment, VIE tags were visible to the naked eye and bright in color for all 20 tagged fish. There were no differences in fork length between those fish receiving tags and those not tagged (2-sided t-test, $t = -0.56$, 39 df, $P = 0.58$).

Table 3.1 Number of demersal young-of-the-year black rockfish marked and recaptured in Newport and Coos Bay, Oregon during biweekly sampling trips conducted during the summers of 1997 and 1998 (notation follows Table 4.1 in Pollock et al. (1990)).

Tagging Event	Date	Number captured (n_i)	Number marked and released (R_i)	Number recaptured (m_i), by tagging event			
				1	2	3	4
1997							
Newport Docks							
1	27-May	143	141				
2	10-Jun	93	92	2			
3	23-Jun	56	56	2	5		
4	15-Jul	43	43	3	2	2	
	29-Jul	36	0	0	3	1	1
	12-Aug	5	0	0	0	0	1
Newport Grassbed							
	22-May	16	0				
1	7-Jun	43	43				
2	21-Jun	12	12	3			
3	3-Jul	4	4	2	1		
	23-Jul	5	0	1 ^a	2		
	18-Sep	3	0	1 ^a	1		
Coos Bay Docks							
1	11-Jun	115	115				
2	23-Jun	60	60	10			
3	16-Jul	40	40	1	1		
	28-Jul	25	0	2	2 ^b	3	
	13-Aug	14	0		2		
Coos Bay Grassbed							
1	12-Jun	91	90				
2	24-Jun	67	67	4			
3	17-Jul	31	31	3	2		
	28-Jul	22	0	2	2		
1998							
Newport Docks							
1	3-Jun	250	250				
2	19-Jun	115	115	12			
3	2-Jul	63	63	9	0		
4	15-Jul	32	31	3	0	1	
	29-Jul	33	0	4	2	3	0
	12-Aug	5	0	1 ^b	0	0	1

Table 3.1 (Continued)

Tagging Event	Date	Number captured (n_i)	Number marked and released (R_i)	Number recaptured (m_i), by tagging event			
				1	2	3	4
1998							
Newport Grassbed							
1	10-Jun	14	14				
2	24-Jun	5	5	0			
	13-Jul	3	3	0	1		
Coos Bay Docks							
1	12-Jun	141	141				
2	23-Jun	114	114	6			
3	8-Jul	44	44	2	6		
	21-Jul	17	0	0	3 ^b	1	
	5-Aug	7	0	1	0	0	
Coos Bay Grassbed							
1	12-Jun	27	27				
2	23-Jun	104	104	4			
3	7-Jul	44	42	2	16		
	21-Jul	7	0	0	0	2	
	5-Aug	25	0	1 ^b	6 ^c	13	

^a one fish also recaptured at tagging event 2

^b one fish also recaptured at tagging event 3

^c four fish also recapture at tagging event 3

Table 3.2. Instantaneous natural mortality rate estimates with 95% confidence intervals for young-of-the-year black rockfish, *Sebastes melanops*, from Newport and Coos Bay, Oregon.

Year	Estuary	Habitat	Daily Mortality	95% confidence interval	
			Rate	Lower	Upper
1997	Newport	Docks	0.0305	0.0147	0.0626
	Newport	Grassbeds	0.0082	0.0006	0.1018
	Coos Bay	Docks	0.0413	0.0214	0.0792
	CoosBay	Grassbeds	0.0051	0.0000	2.7648
1998	Newport	Docks	0.0266	0.0130	0.0540
	Newport	Grassbeds	0.0558	0.0006	1.8710
	Coos Bay	Docks	0.0693	0.0377	0.1257
	CoosBay	Grassbeds	0.0412	0.0241	0.0703

There were no differences in within-habitat growth rates or adjusted treatment means between Newport and Coos Bay estuaries in either 1997 or 1998 (Table 3.3). Consequently, habitat-specific data from both estuaries were pooled and are presented in Figure 3.3 with best-fit linear regression models. We also observed no differences in growth rates of juvenile black rockfish between habitats, although we did observe a slight difference in adjusted treatment means between docks and eelgrass beds in 1998 (Table 3.4). In Figure 3.4 we plot habitat-specific data with a pooled linear growth model for 1997 fish and a best fit parallel lines model for 1998. Finally, juvenile growth rates were the same in both habitats in 1997 and 1998, while adjusted treatment means were significantly higher in 1997 (Table 3.5). Size-at-capture data are plotted for each year, by habitat, with best fit parallel lines linear models in Figure 3.5.

Discussion

Young-of-the-year black rockfish recruit to shallow water estuarine and near-coastal habitats approximately three months after peak parturition (Bobko and Berkeley, 2002a). They remain in these habitats for approximately three months (May – August) at which time they migrate out to slightly deeper coastal waters, although in water usually less than 20m in depth. Over this three-month period estimated daily mortality rates ranged from 0.0051 to 0.0693 day⁻¹. Reported juvenile-stage daily mortality rates cover the period from metamorphosis to one year

Table 3.3. Analysis of covariance (ANCOVA) for differences in growth rates (slopes) and adjusted treatment means (elevations) of YOY black rockfish, *Sebastes melanops*, between Newport and Coos Bay estuaries. All fish were collected in 1997 and 1998 from eelgrass beds and floating docks in Coos Bay and Newport, Oregon. FL = response variable, day of year = regressor, and estuary = covariate.

Year	Comparison	Test	t-stat	df	P
1997	Newport vs. Coos Bay Docks	Equality of slopes	0.16	482	0.88
		Equality of elevation	-0.77	483	0.44
1997	Newport vs. Coos Bay Grassbeds	Equality of slopes	-0.06	136	0.95
		Equality of elevation	-0.49	137	0.63
1998	Newport vs. Coos Bay Docks	Equality of slopes	-0.31	816	0.76
		Equality of elevation	1.71	817	0.09
1998	Newport vs. Coos Bay Grassbeds	Equality of slopes	-1.93	225	0.06
		Equality of elevation	-1.19	226	0.23

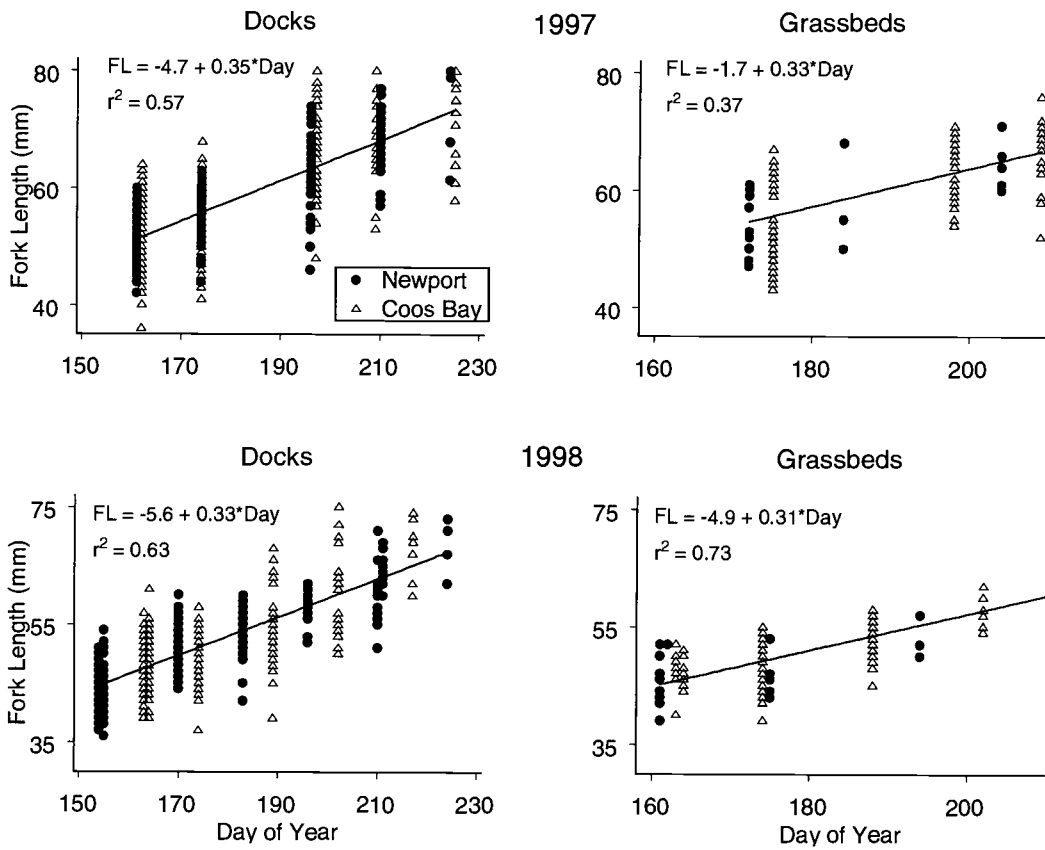


Figure 3.3. Scatter plots and best-fit linear regression models of young-of-the-year black rockfish, *Sebastes melanops*, FL on day of year by year (1997 and 1998) and habitat (floating dock and eelgrass bed). Coos Bay and Newport, Oregon data are pooled based on ANCOVA results listed in Table 3.3.

Table 3.4. Analysis of covariance (ANCOVA) for differences in growth rates (slopes) and adjusted treatment means (elevations) of YOY black rockfish, *Sebastes melanops*, between eelgrass bed and floating dock habitats. All fish were collected in 1997 and 1998 from eelgrass beds and floating docks in Coos Bay and Newport, Oregon. FL = response variable, day of year = regressor, and habitat = covariate.

Year	Comparison	Test	t-stat	df	P
1997	Grassbeds vs. Docks	Equality of slopes	0.4	649	0.69
		Equality of elevation	1.36	650	0.17
1998	Grassbeds vs. Docks	Equality of slopes	0.61	790	0.54
		Equality of elevation	6.26	791	<0.01

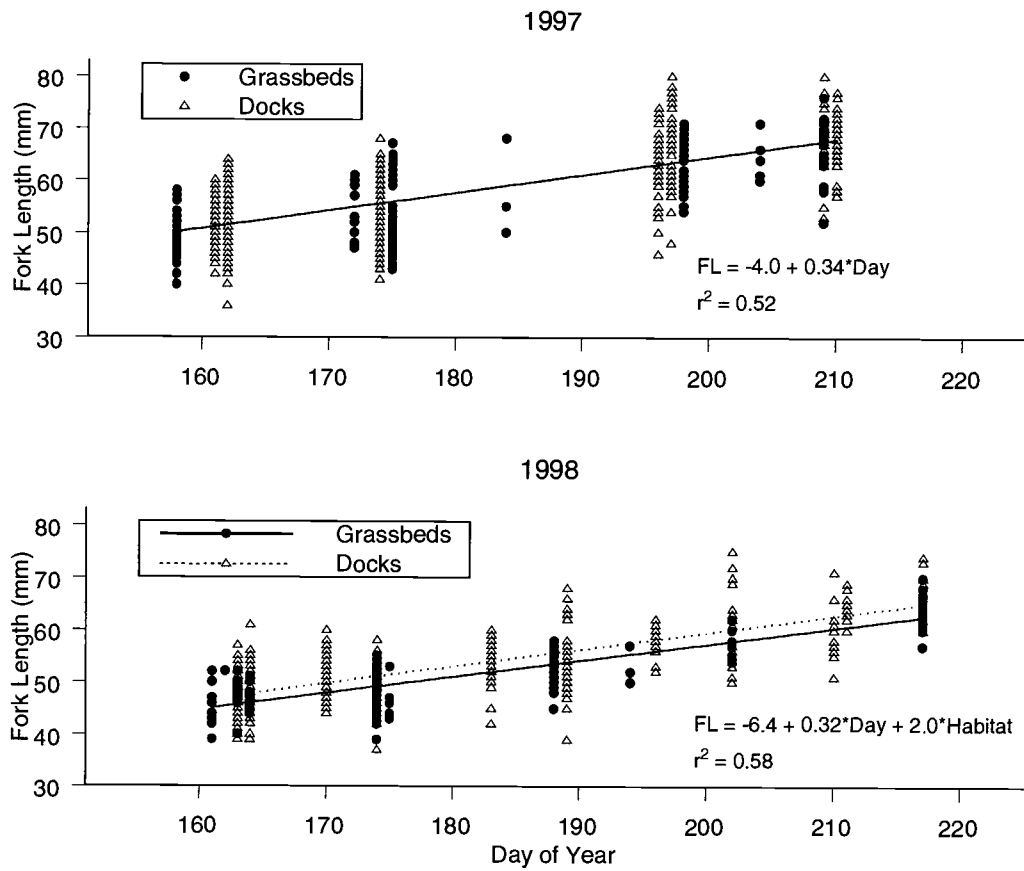


Figure 3.4. Scatter plots and best-fit linear regression models of young-of-the-year black rockfish, *Sebastes melanops*, FL on day of year by year (1997 and 1998). Coos Bay and Newport, Oregon data are pooled based on ANCOVA results listed in Table 3.3. 1997 grassbed and dock data are pooled based on ANCOVA results listed in Table 3.4.

Table 3.5. Analysis of covariance (ANCOVA) for differences in growth rates (slopes) and adjusted treatment means (elevations) of YOY black rockfish, *Sebastes melanops*, between year of collection. All fish were collected in 1997 and 1998 from eelgrass beds and floating docks in Coos Bay and Newport, Oregon. FL = response variable, day of year = regressor, and year = covariate.

Habitat	Comparison	Test	t-stat	df	P
Docks	1997 vs. 1998	Equality of slopes	-0.45	1443	0.65
		Equality of elevation	-19.88	1444	<0.01
Grassbeds	1997 vs. 1998	Equality of slopes	-0.92	411	0.36
		Equality of elevation	-13.96	412	<0.01

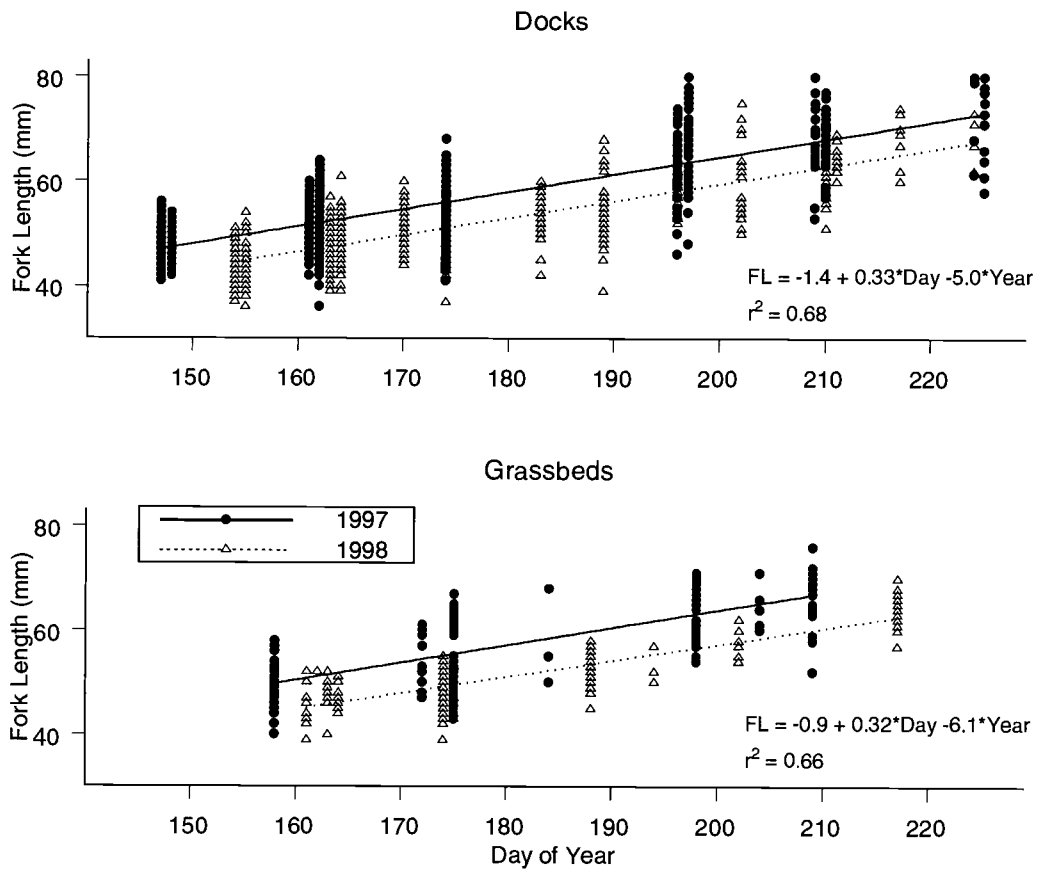


Figure 3.5. Scatter plots and best-fit linear regression models of young-of-the-year black rockfish, *Sebastes melanops*, FL on day of year by habitat (eelgrass beds and floating docks). Coos Bay and Newport, Oregon data are pooled based on ANCOVA results listed in Table 3.3.

of age, which can be as long as 350 days (Houde 1987). Consequently, most of our mortality estimates are higher due to our sampling only covering the early part of the juvenile period (Table 3.6).

Love et al. (1991) commented on possible causes of mortality in substrate-associated juvenile rockfish, such as food and habitat limitation and predation. While little experimental work has been done on determining the relative importance of predation, piscivorous fishes have been reported to heavily prey upon YOY rockfish. Mortality rate estimates were higher for YOY black rockfish settling on floating docks than for eelgrass bed recruits. The one exception was our 1998 Newport collection sites, but in 1998 the grassbed site in Newport was much smaller in size than in 1997 and held few juvenile black rockfish. While large piscivorous predators were observed in both habitats, it appears that thick eelgrass beds provided greater cover and increased survival.

There were no differences in growth rates of juvenile black rockfish between any habitat, estuary, or collection year. Whether fish settled in Newport or Coos Bay, on docks or eelgrass beds, all fish grew between 0.31 and $0.35 \text{ mm} \cdot \text{day}^{-1}$, which may indicate similar prey-availability, or at least food quality, among estuaries and habitats. Other published growth rates for juvenile YOY black rockfish are presented in Table 3.7. Our growth rates, estimated from size-at-capture data, are similar to growth rates reported by Bayer (1981) and two of Boehlert and Yoklavich's (1983) lab rearing temperature treatments. Growth rates calculated with size-at-age data for

Table 3.6. Published instantaneous daily mortality rates for juvenile fishes with reported stage durations.

Species	Mortality Rate	Stage Duration	Study
Black rockfish	0.0051 - 0.0693	90 days	This study
Blue rockfish	0.001 - 0.008	270 days	Adams and Howard (1996)
Striped bass	0.005	328 days	Houde (1987)
Atlantic cod	0.010	291 days	Houde (1987)

Table 3.7. Growth rates of YOY black rockfish, *Sebastes melanops*, from field and laboratory studies.

Size Range (mm)	Growth Rate (mm/day)	Estimation Method	Source
36-94	0.31-0.35	size-at-capture	This study, chapter 3
36-78	0.36 - 0.51	daily otolith increments	This study, chapter 4
48-60	0.2	size-at-capture	Laroche and Richardson (1980)
70	0.3	mean size at age	Bayer (1981)
35-99	0.09	Lab Rearing @ 7°C	Boehlert & Yoklavich (1983)
39-109	0.3	Lab Rearing @ 12°C	Boehlert & Yoklavich (1983)
38-111	0.31	Lab Rearing @ 18°C	Boehlert & Yoklavich (1983)

YOY black rockfish collected in the same areas and years were much higher (Bobko and Berkeley, 2002b).

The only observed differences in fish size were the differences in adjusted treatment means between fish recruiting in 1997 and 1998. Fish entered the estuaries at a smaller size in 1998 than 1997 and maintained this size difference throughout the summer. This difference in size can be explained by the difference in the age of YOY black rockfish recruiting to nearshore habitats in 1997 and 1998 (Bobko and Berkeley, 2002b). The median birthdate of fish recruiting in 1997 was 16 February vs. 4 March in 1998.

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CHAPTER 4

BIRTHDATE DISTRIBUTIONS AND GROWTH RATES OF
YOUNG-OF-THE-YEAR BLACK ROCKFISH, *SEBASTES*
MELANOPS,
RECRUITING TO COOS BAY AND NEWPORT, OREGON

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May 2, 2002

Abstract

During the summers of 1996 through 1998 we made biweekly collections of young-of-the-year (YOY) black rockfish, *Sebastes melanops*, from eelgrass beds, *Zoostera* sp., and floating docks, and tide pools along the Oregon coast. Captured fish were measured and otoliths dissected for age determination. We compared lapillus and sagitta age estimates and found no significant differences, enabling us to use lapilli to age collected fish. Birthdate distributions of surviving YOY black rockfish were estimated by back-calculating the date of birth as the difference between the date of capture and the age estimate. Distributions were similar in 1996 and 1997, but 1998 was considerably different. The median birthdate was 19 February in 1996, 16 February in 1997, and 4 March in 1998. Environmental conditions resulting from the El Niño event during early 1998, as evidenced in anomalous coastal downwelling, had a negative effect on survival during larval and pelagic juvenile stages. There were significant differences in growth rates between years, with black rockfish growing 0.371 mm/day, 0.503 mm/day, and 0.414 mm/day in the years 1996-1998, respectively. Faster growth was associated with higher sea surface temperatures after YOY black rockfish recruited to nearshore habitats.

Introduction

Understanding variability in the recruitment of fishes is among the most important objectives in fishery science. Numerous factors, both biotic and

environmental, have been assessed in attempts to explain this variability, with multiple factors contributing in some respect. At what early life history stage recruitment regulation occurs is also uncertain, with many investigators identifying the larval stage (Houde, 1987; Myers and Cadigan, 1993), while others suggest the juvenile stage (Beverton, 1984; Sissenwine 1984). Recruitment regulation for Pacific rockfish (*Sebastes* spp.) is reported to be set during the larval phase by large-scale oceanographic processes (Ralston and Howard, 1995), although natural mortality experienced during the benthic juvenile stage reduces interannual recruitment variability (Adams and Howard, 1996).

Black rockfish, *Sebastes melanops*, parturition occurs from mid January to mid March off the Oregon coast (Bobko and Berkeley, 2002). Larvae and pelagic juveniles remain offshore for approximately three months and at distances of up to 266 km offshore (Laroche and Richardson, 1980). Young-of-the-year (YOY) juveniles recruit to shallow nearshore waters from April through June (Laroche and Richardson, 1980; Bayer, 1981; Bobko et al., 2002).

Although much effort has been directed toward investigating recruitment dynamics and growth of early life history stages of rockfish off California, little work has been done off Oregon coast. As a result, our research focuses on estimating inter-annual variation in birthdate distributions and growth rates of benthic YOY black rockfish off Oregon with the hope of identifying possible factors regulating recruitment success.

Materials and methods

During the summers of 1996-1998 we made biweekly collections of benthic young-of-the-year (YOY) black rockfish from eelgrass beds, *Zostera* sp., tidepools, and floating docks in Newport, Depoe Bay, Seal Rock, and Coos Bay, Oregon. In 1996, collections in Coos Bay and Newport began in late May, as fish entered the estuaries, and continued until fish were no longer observed in large numbers. In 1997 and 1998 our collections in Newport spanned the same time period as in 1996, but our Coos Bay collections were only conducted from late July through early August after the completion of an associated tagging experiment (Bobko et al., 2002). We used standard fingerling nets with 300 mm deep, 3.2 mm mesh bags with wooden handles to collect black rockfish along floating docks. We used a 6 m long by 1.1 m high beach seine with 3.2 mm mesh to sample our grass bed site in Newport and a 42.5 m by 3 m high beach seine equipped with a 3 m X 1.2 m X 1.2 m bag to sample our Coos Bay grass bed site.

Collected fish were anesthetized in 75 mg/l of FINQUEL MS-222 buffered with sodium bicarbonate. Once immobilized, fish were measured for fork length, given a unique gill tag, and placed in 70% ethanol. In the laboratory, we confirmed species identification with pectoral fin ray counts and the ratio of caudal peduncle depth to length (Laroche and Richardson, 1980). For each fish, total weight (g), fork length (mm), and standard length (mm) were recorded and sagittae and lapilli otoliths removed and stored dry.

Boehlert and Yoklavich (1987) validated the formation of daily increments on sagittal otoliths for juvenile black rockfish. To help us identify these daily otolith increments and allow us to compare sagitta and lapillus otolith age estimates, we collected an additional 71 juvenile black rockfish from Yaquina Bay in late May and early June 1996. Live fish were transported to the Hatfield Marine Science Center where they were held in a 2500 liter circular tank with a constant flow of unfiltered seawater. On 20 June 1996, all 71 fish were removed from the tank and placed into a 68 liter plastic tote containing 50 liters of seawater with 0.1 g/l of alizarin complexone buffered with sodium bicarbonate. After 12 hours the fish were removed from the alizarin solution, rinsed in a fresh seawater bath, and returned to the circular holding tank. For each of the following nine weeks between 5 and 10 fish were caught, placed into seawater with MS-222 until respiration ceased, and preserved in 70% ethanol. Laboratory processing of sacrificed fish followed the methods described above for regular biweekly samples.

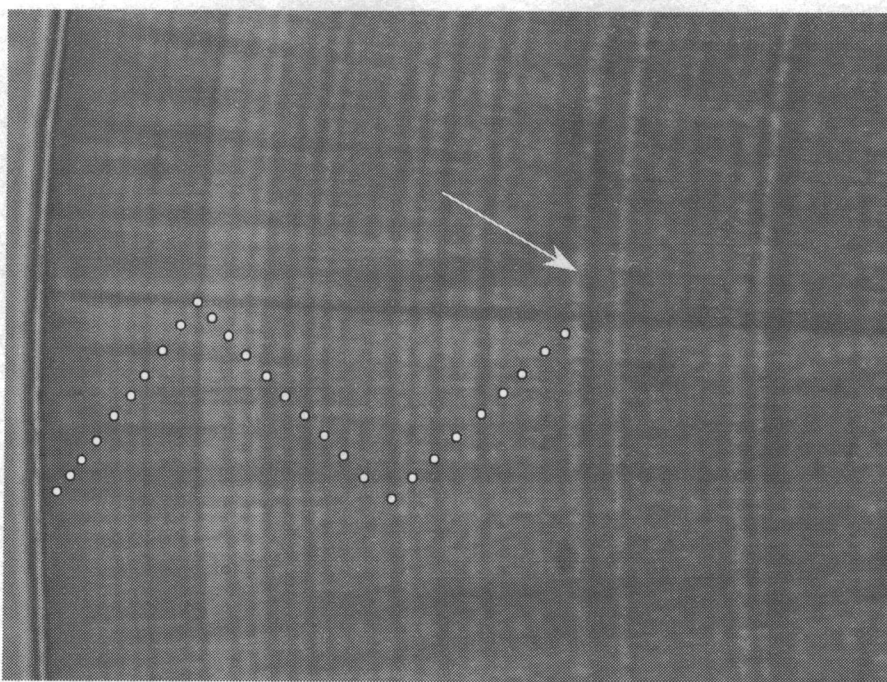
For increment analysis, otoliths were prepared following modified procedures described in Secor et al. (1991). Briefly, sagittae collected from alizarin complexone stained fish only were mounted in Buehler Epoxide Resin and thin sectioned using a Buehler low speed Isomet saw with a diamond wafer blade. Each section was mounted on a slide with Crystalbond thermoplastic and hand polished using 1200 grit wet/dry sandpaper and 1 and 0.3 μ alumina polishing powders. Lapilli from alizarin fish and all regular collections were mounted onto slides with Crystalbond

thermoplastic and hand polished in the same manner as sagittae. Otoliths were aged using a compound microscope at between 200 to 500 times magnification an image analysis system with Optimas 6.1. For our alizarin fish, age estimates from lapilli were plotted against those from sagittae to assess deviation from 1:1 equivalence (Campana et al., 1995). A test for symmetry was used to detect any systematic difference between the age estimates (Hoenig et al., 1995).

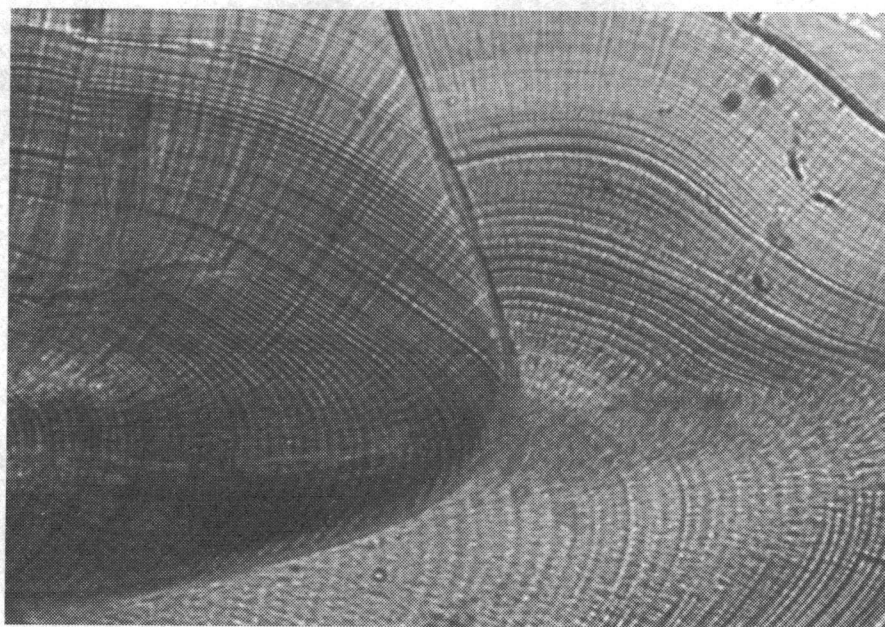
Birthdate frequencies for YOY black rockfish surviving to the benthic juvenile stage were constructed by back-calculating the date of birth as the difference between the date of capture and the age estimate. We calculated growth rates by regressing FL (mm) on age. Analysis of covariance (ANCOVA) was used to test for differences in regression growth rates (i.e., slopes) and adjusted "treatment" means (i.e., elevations) between years. All statistical analyses were performed with S-Plus 2000 (S-Plus, 1999).

Results

All 71 of the black rockfish marked with alizarin survived the immersion process. In Figure 4.1a we show a picture of a black rockfish lapillus sacrificed 28 days after alizarin marking. Sagittae and lapilli from 35 of the fish, with sacrifice dates ranging from 7 to 42 days post-marking, were aged. There was good agreement between age estimates from the different otoliths (Figure 4.2), with no evidence of systematic disagreement between otolith types (test of symmetry, $\chi^2 =$



a)



b)

Figure 4.1. a) Picture of a 28 day post-marking YOY black rockfish lapillus otolith showing alizarin mark (arrow) and daily increments (white circles). b) Picture of a black rockfish sagitta showing seams resulting from growth from accessory primordia.

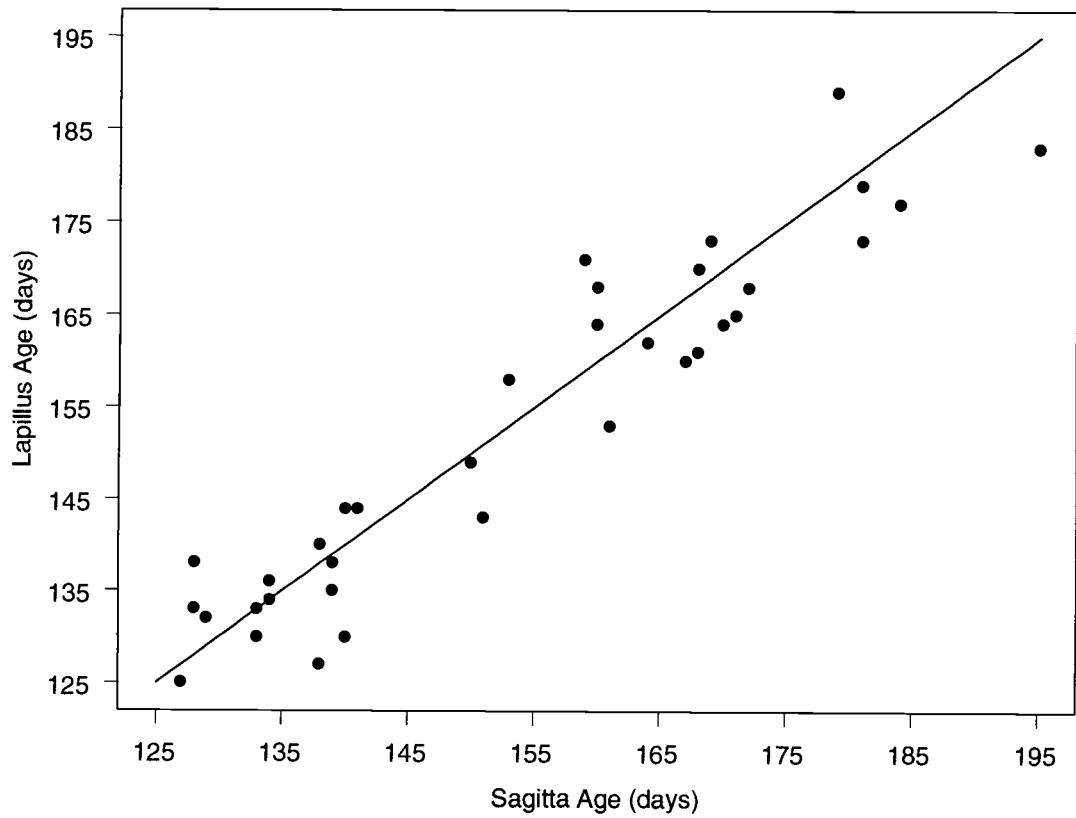


Figure 4.2. Comparison of lapillus and sagitta daily age estimates for YOY black rockfish, *Sebastes melanops*. Solid line represents exact agreement.

33, $df = 33$, $P = 0.47$). Based on the good agreement of age estimates between otoliths, the presence of seams arising from accessory primordia increasing the difficulty of ageing sagittae (Figure 4.1b), and the much shorter processing time for lapilli, all YOY black rockfish from regular collections were aged with lapilli.

We collected 1,087 YOY juvenile black rockfish during the summers of 1996-1998 ranging in size from 33.5 – 112 mm in fork length (Table 4.1). Fish started to appear in large numbers at our collection sites in mid to late May of each year. Numbers remained high through early August, and by late August few fish remained. We aged a total of 663 YOY black rockfish with lapilli (Table 4.1). Fish collected in August or later of each year were not aged due to the difficulty in discerning increments near the margin of the otoliths. Age estimates ranged from 96 to 182 days in 1996, 89 to 168 days in 1997, and 88 to 167 days in 1998.

We made biweekly collections to ensure that we would capture cohorts as they settled in nearshore waters. We would then be able to adjust for differential mortality of fish collected on different dates with daily mortality rates from Bobko et al. (2002). Each year as we aged our collections, we determined that we were actually following only one cohort per year (Figure 4.3). Consequently, we were able to pool birthdate estimates from fish collected throughout each summer and not worry about correcting for differential mortality. Birthdate distributions for black rockfish surviving to the benthic juvenile stage in 1996 through 1998 are presented in

Table 4.1 Summary of biweekly collection data of young-of-the-year demersal black rockfish collected in Oregon during the summers of 1996-1998.

Year	Collected <i>n</i>	Aged <i>n</i>	Fork length Range (mm)	Total Weight Range (g)	First Capture Date	Last Capture Date
1996	459	249	43 - 112	0.5 - 12.4	02-Jun-96	28-Aug-96
1997	326	209	36.5 - 91	0.3 - 9.1	22-May-97	18-Sep-97
1998	302	205	33.5 - 74	0.3 - 4.4	22-May-98	18-Aug-98

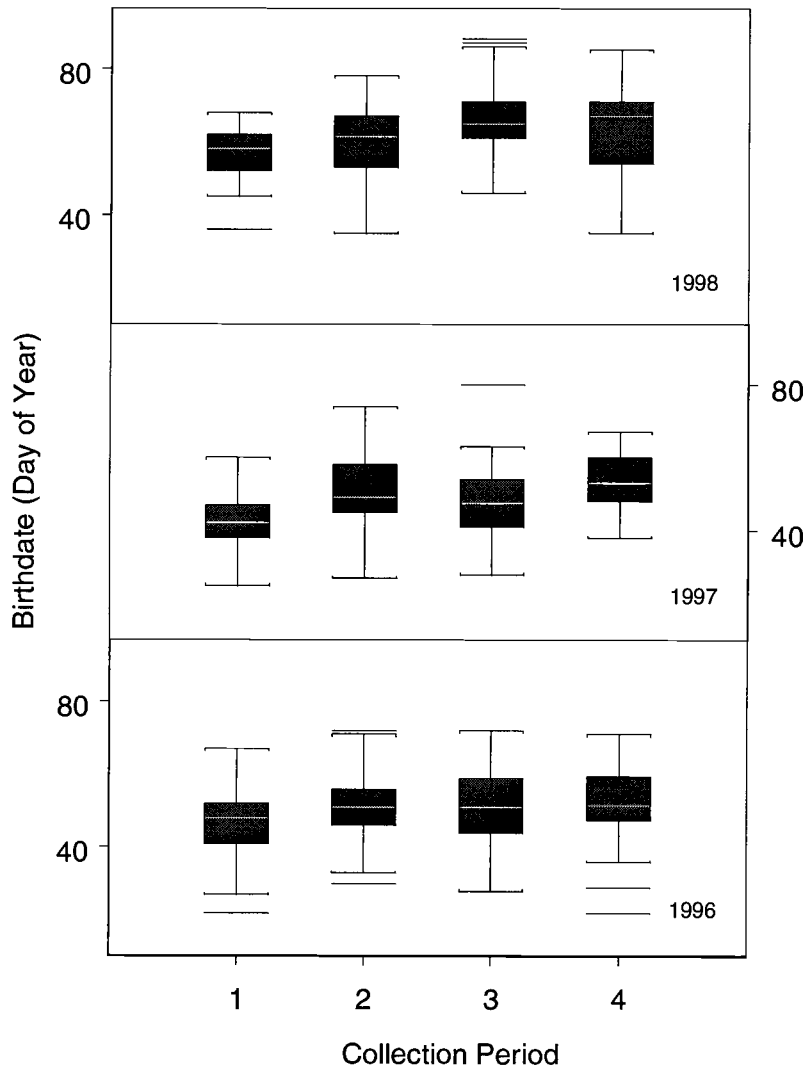


Figure 4.3. Boxplots of birthdates (day-of-the-year) for YOY black rockfish captured during the summers of 1996-1998. Collection period 1 = June 1-15; 2 = June 16-30; 3 = July 1-15; and 4 = July 16-31.

Figure 4.4. The median birthdate was 19 February in 1996, 16 February in 1997, and 4 March in 1998.

Growth was linear for YOY black rockfish collected in each year during 1996-1998 (Figure 4.5). Results from ANCOVA showed significant differences in annual growth rates over a common age range ($F=27.7$, $df=2$ and 632 , $P<0.0001$). Consequently, we fit simple linear growth models to length-at-age data for each year individually (Table 4.2). Growth rates ranged from 0.371 mm/day in 1996 to 0.503 mm/day in 1997.

Discussion

Young-of-the-year black rockfish recruit to shallow water estuarine and nearshore habitats in large numbers in May of each year at approximately 30 to 40 mm fork length (FL). In Yaquina Bay, Bayer (1981) captured one black rockfish of this size in April of 1976, and Laroche and Richardson (1980) started seeing benthic YOY in their June samples. Of interest is that Boehlert and Yoklavich (1983) reported capturing YOY black rockfish 35.4 mm in standard length (SL), which converts to approximately 43 mm FL, as late as October and Laroche and Richardson (1980) saw a smaller group of benthic juveniles in their October samples, something we did not observe in our study.

We found black rockfish lapilli useful in daily age determination for YOY black rockfish. The good agreement between validated black rockfish sagittae

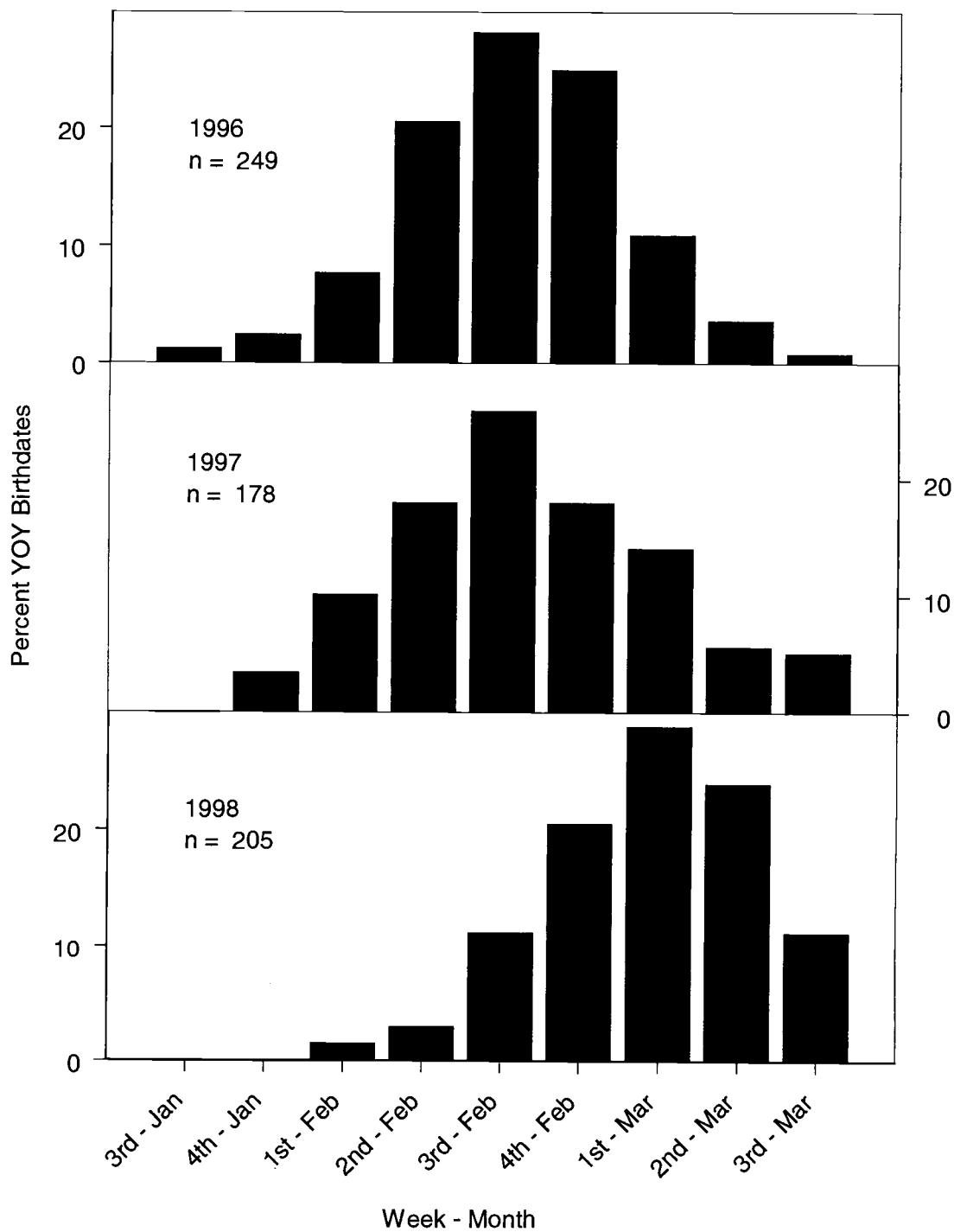


Figure 4.4. Birthdate distributions of YOY benthic black rockfish collected in the summers of 1996 – 1998 from nearshore shallow waters off the Oregon coast.

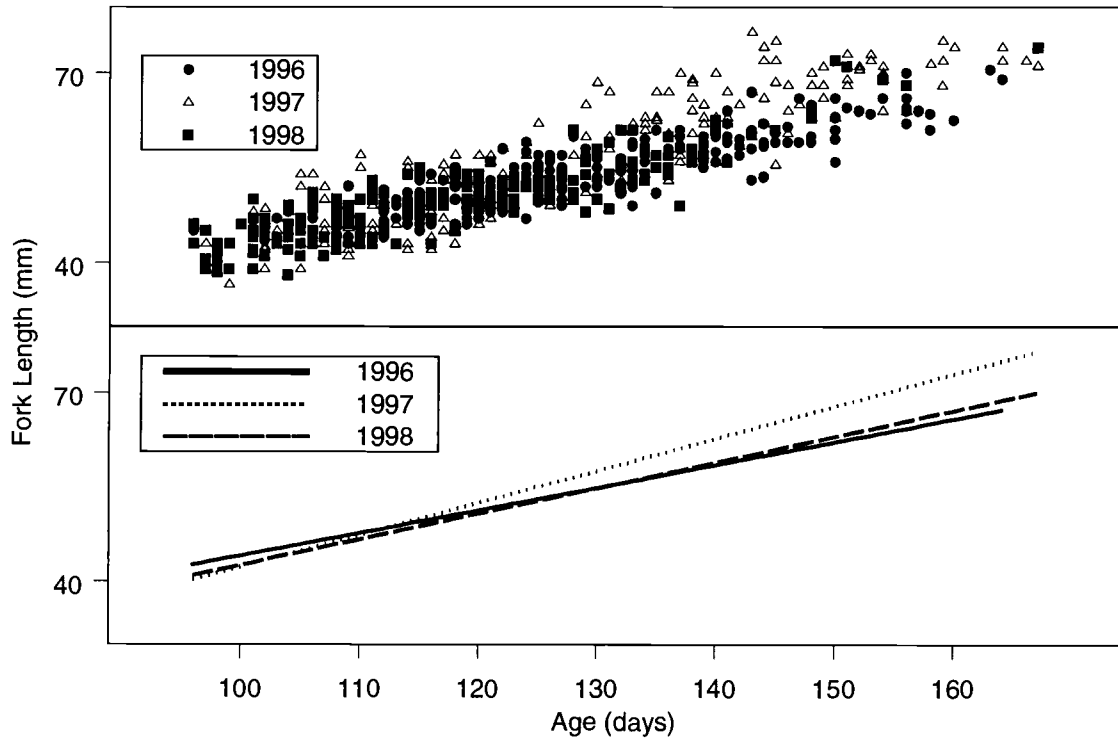


Figure 4.5. Scatterplot and fitted linear regression of fork length on age for YOY benthic black rockfish collected in 1996 – 1998.

Table 4.2. Linear regression coefficients for fork length-at-age growth models for YOY black rockfish collected in Oregon during 1996-1998.

Year	<i>n</i>	Slope (SE) (mm/day)	Intercept (SE) (mm)	r^2
1996	249	0.371 (0.011)	6.812 (1.428)	0.82
1997	209	0.503 (0.016)	-7.752 (2.088)	0.82
1998	204	0.414 (0.014)	1.099 (1.638)	0.81

(Boehlert and Yoklavich, 1987) and lapilli age estimates show that lapilli provide accurate age estimates. Estimated birthdates overlapped the timing of parturition for black rockfish off the Oregon coast (Bobko and Berkeley, 2002).

Birthdate distributions were quite similar in 1996 and 1997, with only small differences observed towards the tails of the distributions. In 1998 we observed a strong shift in birthdates of surviving YOY black rockfish to the later part of the parturition season. Oceanographic conditions resulting from the strong El Nino event during early 1998, as evidenced in strong winter storms and anomalous coastal downwelling, had a negative effect on survival during larval and pelagic juvenile stages. Bakun Upwelling Index values for the Oregon coast in 1996–1998 are shown in Figure 4.6. The onshore flow ceased approximately the third week of February, coinciding with the first week of significant numbers of YOY survivors.

Growth rates of YOY black rockfish were comparable to rates estimated from otolith ages reported for other Pacific Ocean rockfish (Woodbury and Ralston, 1991). The growth rate of YOY black rockfish was the highest in 1997, with the rate in 1996 the lowest. Sea surface temperatures (SST) measured off the Oregon coast show temperatures were the warmest in 1997 and coolest in early 1996 (Figure 4.7). Our data support Boehlert and Yoklavich's (1983) observation that YOY black rockfish grow faster in warmer temperatures, with the linear growth curve from 1997 separating from the 1996 and 1998 curves (Figure 4.5) slightly later than the onset of the high sea surface temperatures observed in the summer of 1997.

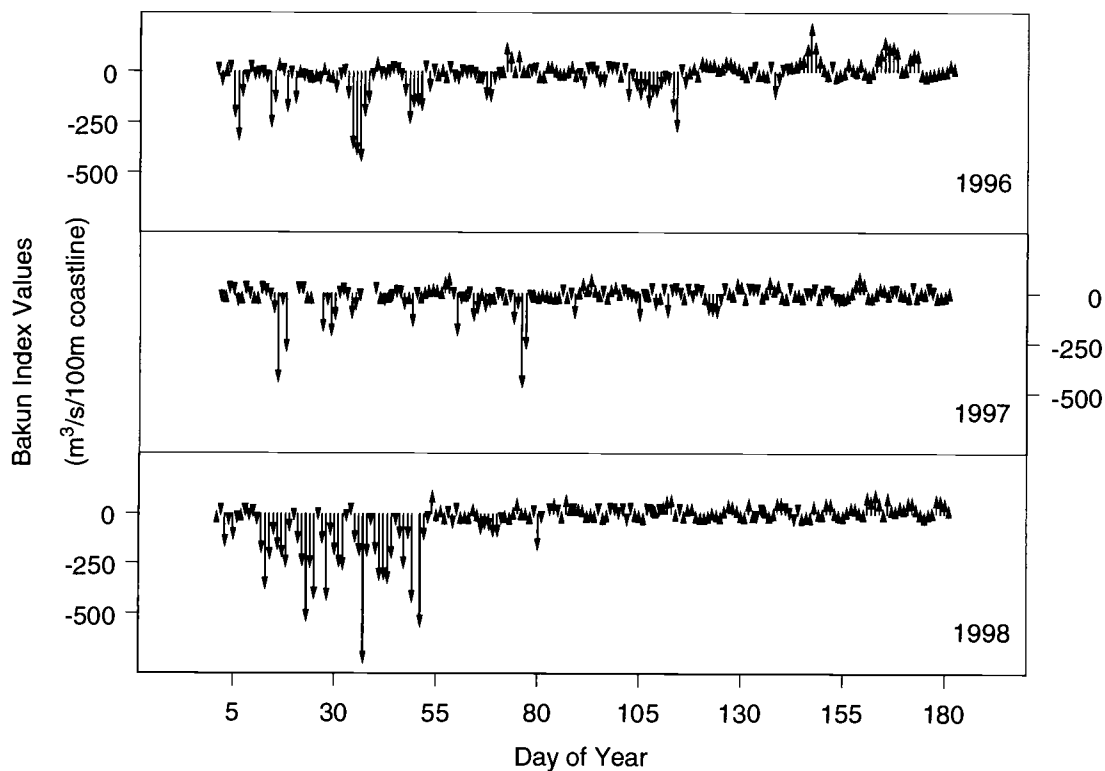


Figure 4.6. Bakun Index Values of upwelling calculated for 45°N 125°W for the years 1996 – 1998. Negative values imply downwelling and the inshore advection of surface waters. Data were obtained from the Pacific Fisheries Environmental Laboratory, National Marine Fisheries Service, Southwest Fisheries Science Center.

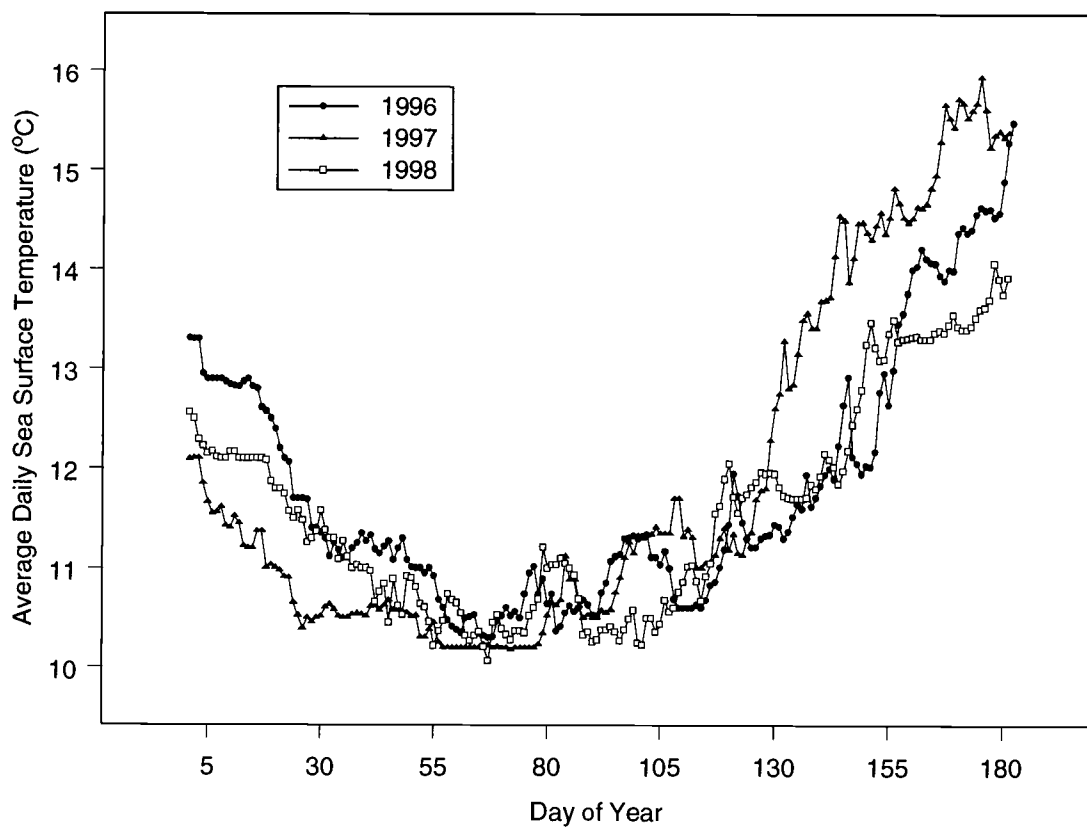


Figure 4.7. Average daily sea surface temperatures (SST) from buoy 46002 (42.5°N 130.3°W) for January through June of 1996 – 1998. Data acquired from the National Data Buoy Center (NDBC), National Weather Service.

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CHAPTER 5

CONCLUSION

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May 2, 2002

Abstract

From December through March of 1995-96 and 1996-97 I collected mature female black rockfish off Newport, Oregon and examined ovaries and otoliths to estimate weekly, age-specific larval production. Over both reproductive seasons, older black rockfish extruded larvae earlier in the season, followed by progressively younger fish. Each of those years, beginning in May, I collected young-of-the-year (YOY) benthic juveniles that settled out in nearshore waters and determined their birthdates from counts of daily rings of lapillar otoliths. I compared the birthdate distribution of juvenile survivors to the age-specific temporal distribution of larval production to estimate the contribution of each adult female age class to juvenile recruitment. The results from 1996 show a disproportionately greater contribution to demersal YOY recruitment by older fish. 1997 results show a relatively even contribution among maternal age groups. In 1998 most of the YOY recruits came from younger fish extruding larvae late in the season. I then examined larvae per recruit (LPR) models to evaluate the effects of fishing mortality on the spawning potential (SPR) of black rockfish. Even at moderate levels of fishing pressure SPR was low. At $F=0.1$, larval production ranged from 26% to 31% of the production from an unfished population. Obviously, changes in black rockfish age composition must be considered beyond simply reducing the estimate of total larval production.

Introduction

Two of the more classical lines of thought on food availability and starvation and their effects on recruitment are Cushing's (1969, 1995) 'match/mismatch' and Hjort's (1926) 'critical period' hypotheses. Both are conceptualized on the premise that starvation is the primary source of variation in recruitment. Hjort's hypothesis is concerned only with starvation at the first feeding, i.e., the critical period, and Cushing's hypothesis focuses on the consequences of starvation at any stage of early development based on larval distribution not coinciding spatially or temporally with peak production. Both hypotheses support the adaptation of spreading reproductive effort over a longer period of time through protracted spawning seasons to increase the probability of a "match" occurring between larvae and adequate prey abundance.

Regardless of age-specific egg production or egg/larval fitness, a broad age distribution will tend to protract a population's spawning season. Differential timing of spawning events within one season has been observed in many fishes, usually with larger, older fish spawning earlier (Simpson, 1959; Bagenal, 1971; Berkeley and Houde, 1978; Shepherd and Grimes, 1984; Lambert, 1987). In contrast, Hutchings and Myers (1993) report that younger Atlantic cod, *Gadus morhua*, began spawning before older individuals, but with the older fish spawning over a longer period of time and effectively extending the overall reproductive season. Fish stocks with age-specific protracted reproductive periods increase the likelihood of spawning occurring while conditions are conducive to maximizing recruitment (Lambert, 1990). Age-

specific egg production is tied to timing of spawning and a mixed-age spawning population leads to protracted spawning which greatly increases the probability of larvae - food match.

While longevity compensates for varying environmental conditions, it also makes the fish more susceptible to over-exploitation. The removal of older age classes through fishing mortality can be detrimental to a long-lived fish species not only by removing biomass and lowering egg production, but by truncating the upper end of the age distribution of spawners and their potentially higher reproductive potential (Borisov, 1978; Beverton, 1986; Leaman and Beamish, 1984). It is critical that these older individuals not be addressed solely in terms of biomass, but their relative reproductive contribution and the repercussions of their removal from the population be considered.

Fisheries stock assessments and catch predictions are typically based upon female spawning stock biomass and/or population egg production. While age-specific fecundity is often utilized in fisheries models, changes in a stock's age composition through the removal of older age classes are not considered beyond reducing the estimate of total potential egg production. This is critical even for a species that spawns over many years. As fishing pressure truncates older fish from the range of age classes spawning it results in a higher proportion of eggs produced in any given year coming from the youngest spawners. Leaman (1987, 1991) discusses the importance of incorporating some measure of reproductive value or potential into

stock monitoring and assessment programs, but unfortunately consideration of the existence of differential reproductive success with age is usually disregarded.

My research is concerned with investigating differing reproductive success, measured here as the proportion of progeny surviving to demersal juvenile stage, as a function of maternal age in black rockfish, *Sebastes melanops*. Black rockfish are ideal subjects for studying age-related variability in reproductive success. They are relatively long-lived, with females reaching a maximum age of 34 years (Wallace and Taggart, 1994). Adult fish usually restrict movements to a small home range, with only 3 % of recoveries of fish tagged off Newport and Garibaldi caught further than 10 nautical miles from their release sites (Butler, 1986; Stewart, 1993). Black rockfish are viviparous, which enables age specific development to be tracked over the entire range of stages, from egg to larva. Juvenile fish are also quite abundant and easily captured in bays and tide pools (Laroche and Richardson, 1980; Bayer, 1981). Black rockfish have also been experiencing an increased popularity in the Oregon sport fishery comprising as much as 80% of all landed groundfish in some ports (Stewart, 1993).

Materials and methods

In this paper I use the results of Bobko and Berkeley (2002a and 2002b) to compare age-specific temporal patterns of larval production to birthdates distributions of black rockfish surviving to the YOY benthic stage. Briefly, for each year from

1996 to 1998, estimated larval production was grouped into weekly intervals by maternal age group: 6-8; 9-11; 12-14; and ≥ 15 . These data were adjusted to reflect fertilized absolute fecundity and the observed proportion of mature fish belonging to each age group calculated from data pooled for the years. For details on methods and procedures of adult black rockfish sampling and analysis, see Bobko and Berkeley (2002a). Estimated annual birthdate frequencies for YOY black rockfish surviving to the benthic juvenile stage were constructed by back-calculating the date of birth as the difference between the date of capture and the lapillus otolith age estimate. For details on YOY collections and analysis, see Bobko and Berkeley (2002b).

I calculated black rockfish spawning potential ratio (SPR) as the number of larvae that would be produced by an average recruit over its lifetime when the population is fished divided by the number of larvae produced by an average recruit over its lifetime when the population is unexploited. The larvae-per-recruit model used was

$$\frac{N_0}{N_r} = \sum_t m_t f_t S_t ,$$

where m_t = proportion of females mature at age t ;

f_t = average absolute fertilized fecundity of a female at age t ;

S_t = survival, which is calculated as $e^{-(M+s_t F)}$,

where M = instantaneous natural mortality;

s_t = selectivity; and

F = instantaneous fishing mortality.

The proportion of females mature at age was calculated using the proportion mature at size and von Bertalanffy growth function (VBGF) parameter estimates for female black rockfish reported by Bobko and Berkeley (2002a). Briefly, size-at-age was calculated with the VBGF and these values were in turn plugged into the proportion mature at size ogive to determine the proportion of female black rockfish mature at age. Average absolute fertilized fecundity at age was calculated with the relationship $AF = 58,789 + 55,634 * age$ (Bobko and Berkeley, 2002a).

Selectivity for black rockfish was calculated using a variation of catch curve analysis of natural log transformed number-at-age data of female fish collected in Newport, Oregon by Oregon Department of Fish and Wildlife during 1992-1995. I used the fully recruited age-classes to produce a catch curve and extrapolated the curve backward to predict the expected number of fish at each partially recruited age-class (Figure 5.1). Selectivity was assumed to be 1.0 for fully recruited age-classes and calculated as the ratio between observed and expected abundance for partially recruited age-classes. For example, if the catch curve estimated that 1,000 age 3 should have been caught, but only 500 were seen, then age 3 fish had a selectivity of 0.5.

Instantaneous natural mortality (M) was estimated with Hoenig's pooled regression equation based on the observed maximum age of black rockfish (Hoenig,

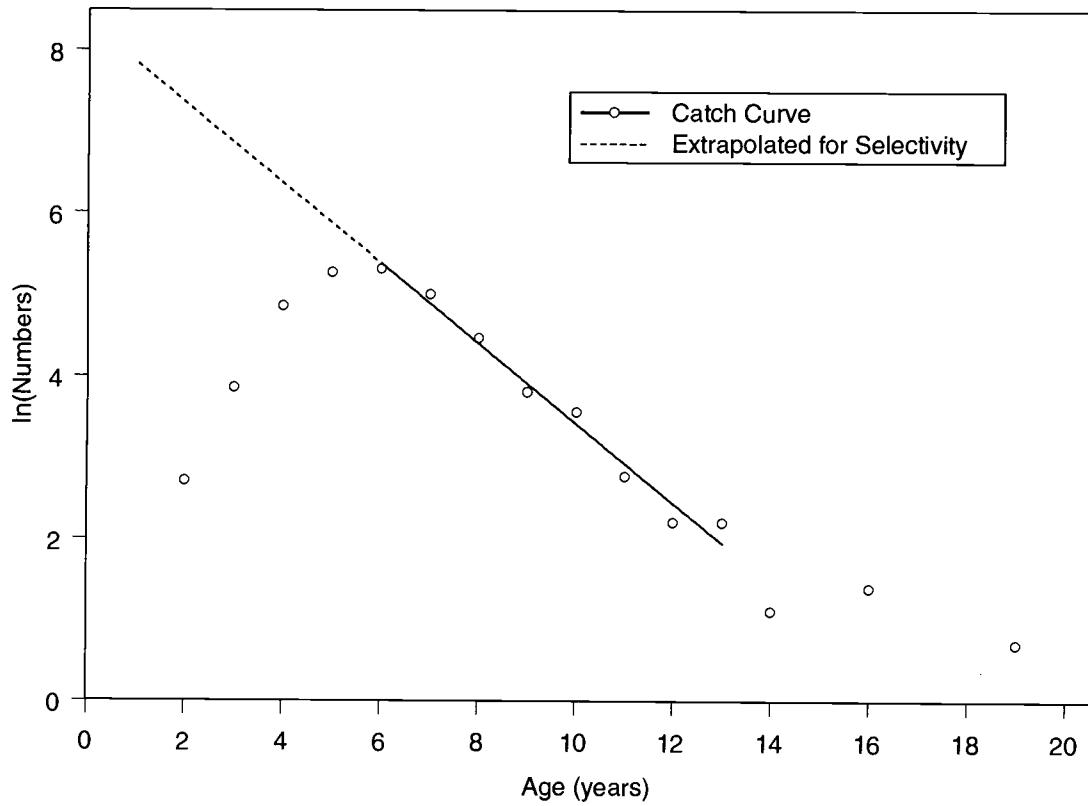


Figure 5.1. Catch curve for black rockfish females landed in Newport Oregon during 1992-1995. Solid line is actual catch curve fit to fully recruited age-classes. Dotted line is catch curve extrapolated backward to estimate selectivity.

1983). Total mortality (Z) was calculated as the mean value of mortality estimates from a catch curve fit to log transformed number-at-age data of mature female black rockfish and from Hoenig's pooled regression equation with sample size correction. Fishing mortality (F) was calculated as the difference between M and Z , with the LPR model run from $F=0.0$ to estimated F .

Results

Graphical comparisons of black rockfish larval production and YOY survivor birthdates distributions for 1996 – 1998 are presented in Figure 5.2. In 1996 32% of the YOY birthdates fell in the first four weeks of the parturition season, while only 20% of the estimated larval production occurred during the same time period. In addition, larval production during this time in 1996 was almost exclusively from females nine years and older. Larval production and YOY birthdate distributions were similar in 1997, with values from the 3rd week of February the highest for both. In 1998 64% of surviving YOY black rockfish were born in the final three weeks of the parturition season, during a period when only 32% of the larval production occurred.

Natural mortality was estimated at 0.166 based on a maximum observed age of 28 years for female black rockfish. The two estimates of total mortality were 0.366 using Heonig's method adjusted for sample size and 0.39 based on catch curve analysis, with an average of 0.378. Catch curve analysis is usually applied to one

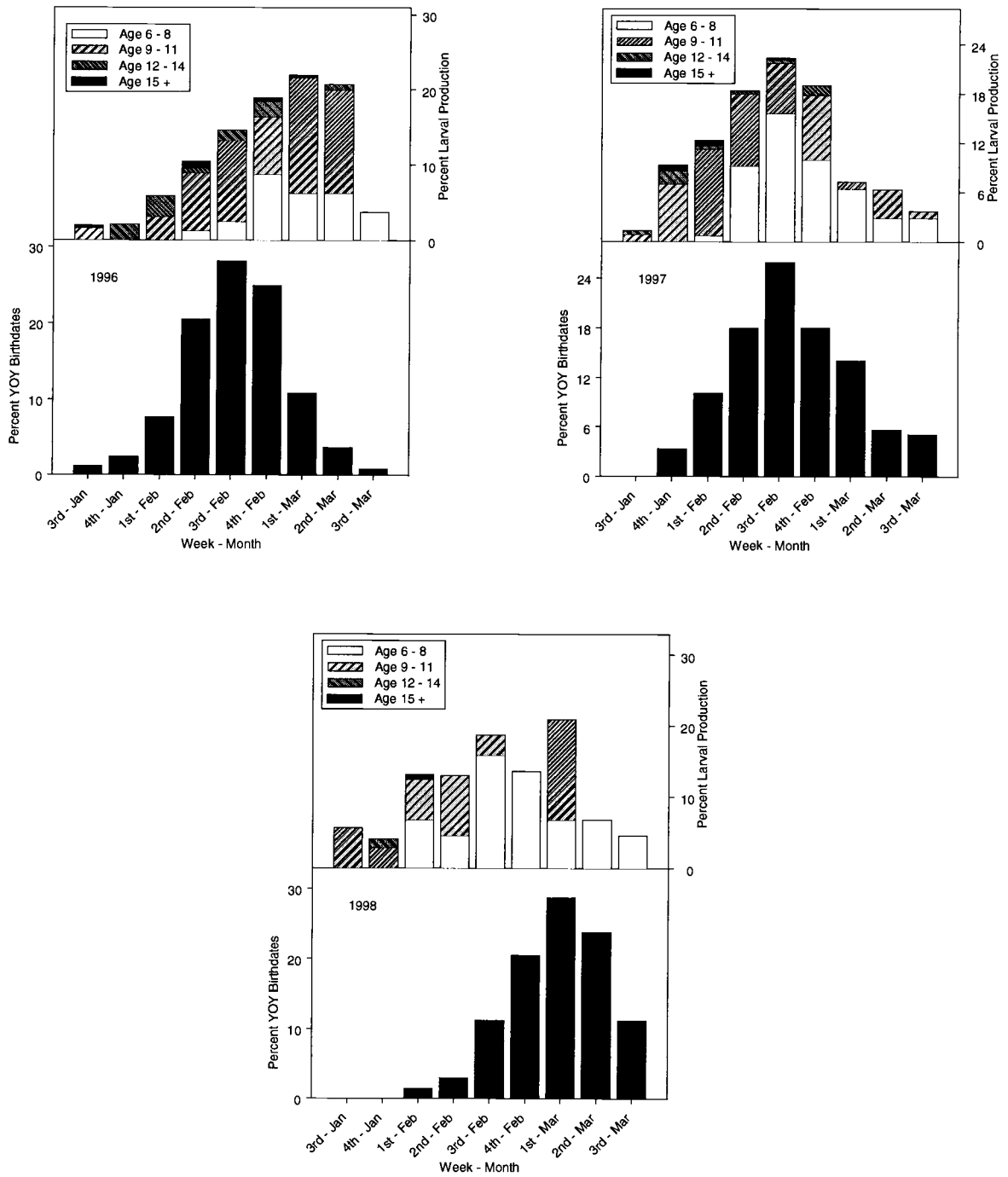


Figure 5.2. Comparisons of black rockfish percent larval production and percent YOY birthdates for 1996-1998.

cohort over time, or to a population with constant recruitment and mortality. I feel its use here for black rockfish is acceptable since it was applied to abundance-at-age data pooled over four years, the data weren't bumpy (i.e., residuals about the fitted line were small), and the Z estimate from the catch curve was very close to the estimate using Hoenig's method.

The LPR model inputs are presented in Table 5.1 with estimates of abundance-at-age at $F=0.0$ and 0.2 . The model was run at varying levels of fishing mortality, 0.0 to 0.212 . Because my estimates of fecundity were based on a maximum age of 18 years, and without any knowledge of how fecundity related to age for older fish, the model was run both with all 28 age-classes and also with only 18 age-classes (Figure 5.3). In both scenarios fishing mortality had dramatic effects of SPR ratios, with the SPR ratio at $F=0.1$ 0.31 and 0.26 for the truncated and full age-class models, respectively (Figure 5.4).

Discussion

The same pattern of maternal age-specific larval production was observed in each year from 1996-1998. Older females extruded larvae over the entire parturition season while the youngest females extruded larvae only in the mid- to late parts of the season. One obvious consequence of only older fish extruding larvae early in the season is that as fishing pressure removes older age-classes from the population, the overall parturition season will be truncated. As observed for black rockfish in 1996, a

Table 5.1 Summary of age-specific data incorporated into larvae-per-recruit modeling of black rockfish, *Sebastes melanops*. $M=0.166$

Age	Proportion Mature (m_t)	Absolute Fecundity (f_t)	Selectivity (s_t)	N_t at $F=0.0$	N_t at $F=0.2$
0	0.00	0	0	1000	1000
1	0.00	0	0	847	847
2	0.00	39761	0.37	717	666
3	0.00	104645	0.56	608	505
4	0.00	169530	0.76	515	367
5	0.01	234414	0.9	436	260
6	0.10	299299	1	369	180
7	0.34	364183	1	313	125
8	0.61	429068	1	265	87
9	0.77	493953	1	224	60
10	0.85	558837	1	190	42
11	0.90	623722	1	161	29
12	0.92	688606	1	136	20
13	0.94	753491	1	116	14
14	0.94	818375	1	98	10
15	0.95	883260	1	83	
16	0.95	948144	1	70	
17	0.96	1013029	1	59	
18	0.96	1077913	1	50	
19	0.96	1142798	1	43	
20	0.96	1207682	1	36	
21	0.96	1272567	1	31	
22	0.96	1337451	1	26	
23	0.96	1402336	1	22	
24	0.96	1467221	1	19	
25	0.96	1532105	1	16	
26	0.96	1596990	1	13	
27	0.96	1661874	1	11	
28	0.96	1726759	1	10	

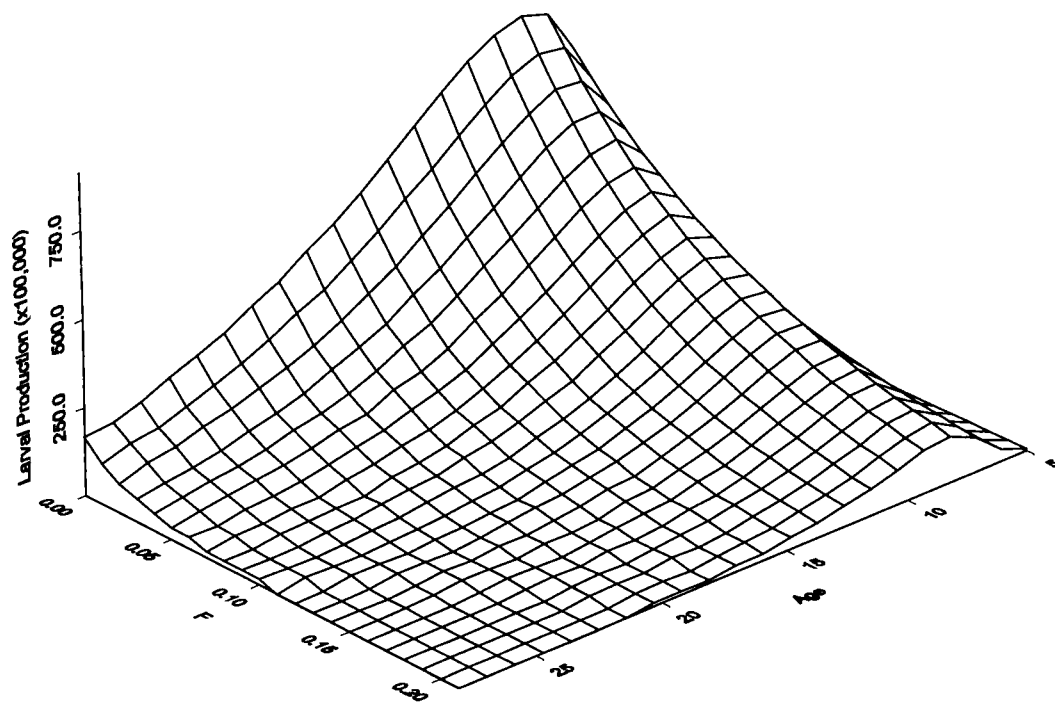


Figure 5.3. Larval production of female black rockfish by age and with varying levels of fishing mortality. $M=0.166$.

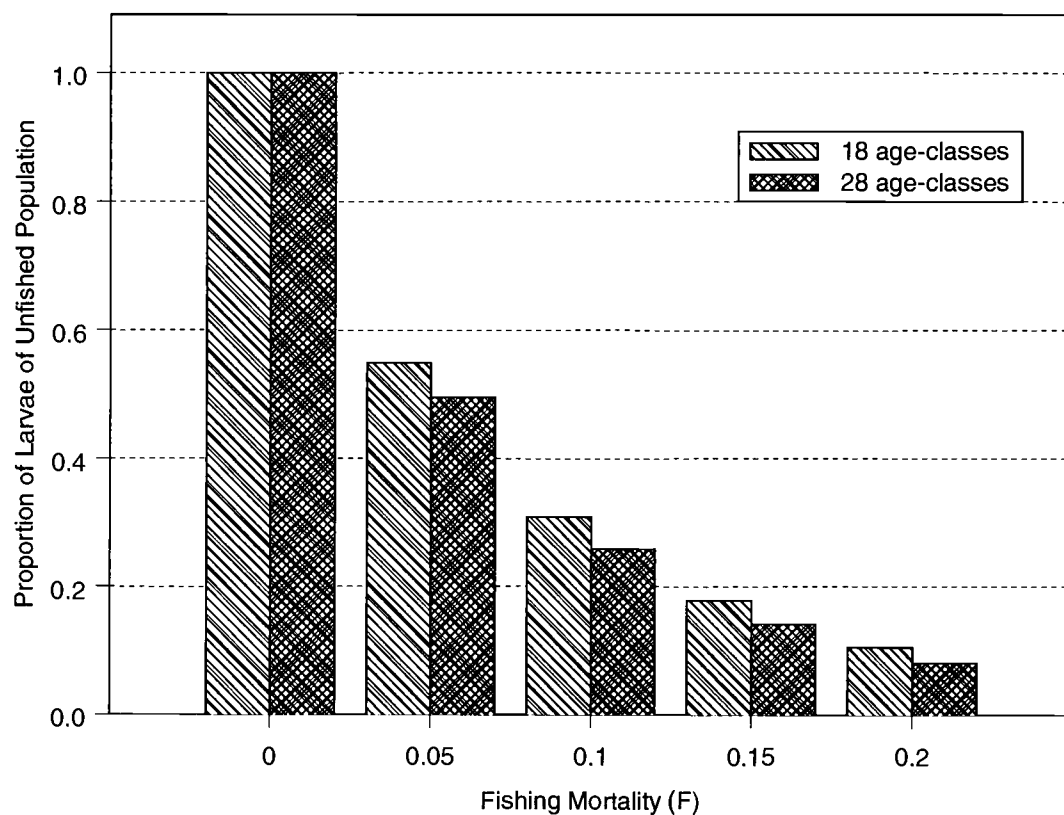


Figure 5.4. Proportion of larval production of an unfished population of black rockfish. $M=0.166$.

disproportionate number of surviving YOY black rockfish came from the early part of the parturition season. Just the opposite was observed in 1998, with most surviving YOY juveniles from late in the parturition season. Given that recruitment regulation for Pacific rockfish (*Sebastes* spp.) is reported to be set during the larval phase by large-scale oceanographic processes (Ralston and Howard, 1995), extending the reproductive season an important bet-hedging strategy to increase the probability of releasing larvae during favorable oceanographic conditions.

The results of the SPR modeling showed that at even moderate levels of fishing mortality, $F=0.1$, larval production was significantly reduced. Age-classes 5 through 28 contributed to the larval production of the unfished population. At $F=0.2$, only age-classes 5 through 14 contributed to larval production. At the current estimate of F , $F=0.212$, larval production is estimated to be only 8% to 10% of the production from the unfished population.

The next logical step in this research is to incorporate maternal age effects into the LPR modeling. One possible method is to incorporate Bakun upwelling indices into larvae- per-recruit simulation models to act as a surrogate for environmental variability. Bobko and Berkeley (2002b) suggested that oceanographic conditions observed during the El Nino event in early 1998 such as prolonged onshore transport causing coastal downwelling might decrease the probability of YOY black rockfish surviving to the benthic juvenile stage. Weighting weekly larval production estimates with weekly running average Bakun values could provide some

insight to trends in overall larval production based on a random environmental index.

One concern with any future exercise with these data is that it appears that black rockfish are already overfished.

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