

AN ABSTRACT OF THE THESIS OF

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Title: Recruitment Variability in Black Rockfish (*Sebastes melanops*):
Effects of Maternal Age on Offspring Quality.

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Abstract Approved _____

Steven A. Berkeley ✓

Black rockfish (*Sebastes melanops*) is an important marine recreational species throughout the Pacific Northwest. Recent catch data indicate a trend of age-truncation in the black rockfish population off the Oregon coast, with older females rapidly disappearing from the population. In populations with broad age distributions, older fish may contribute disproportionately to larval production through a variety of mechanisms. Thus, the removal of older age classes through fishing may impact the population far beyond the simple loss of biomass. We tested the hypothesis that older females produce higher quality offspring, or offspring otherwise more capable of survival, than those from younger females. Mature female black rockfish of various ages were captured live and held until parturition. Larvae were then reared under identical conditions to compare performance in terms of growth, starvation, and mortality. Results indicate that older females produce offspring that grow faster in both length and weight, survive longer in the absence of an exogenous food supply, and exhibit lower mortality rates than offspring from younger mothers. This difference in larval performance may be explained by the relatively greater

amount of endogenous energy reserves present in the oil globules of offspring from older mothers. Larval oil globule volume at parturition was significantly related to all larval performance factors and was strongly correlated with maternal age. Given the difference in larval quality, it is critical for the management of black rockfish, and possibly other species as well, 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.

Recruitment Variability in Black Rockfish (*Sebastes melanops*):
Effects of Maternal Age on Offspring Quality

By
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Recruitment Variability in Black Rockfish (*Sebastes melanops*): Effects of Maternal Age on Offspring Quality

INTRODUCTION

Many fish species in the North Pacific exhibit longevity with extreme iteroparity, a trait which partitions reproductive output over many years. This is presumed to be an adaptation that increases the likelihood that larvae will encounter periods of favorable environmental conditions, despite long periods between such favorable conditions. (Leaman and Beamish 1984, Goodman 1984, Schultz 1989). For species that exhibit age-structured spawning schedules, a broad distribution of spawning age classes in the population will extend the length of the spawning season, thus increasing the likelihood that larvae encounter favorable environmental conditions. In addition, older/larger fish may contribute disproportionately to reproductive success via the production of higher quality offspring, or offspring otherwise more capable of survival than the offspring from younger/smaller fish.

Spawning potential and reproductive success can increase with age if the amount of energy devoted to embryogenesis is age-specific. The means by which increased reproductive effort is manifested in older fish are complex and may occur through two primary mechanisms: increased relative fecundity, and/or the production of higher quality eggs and larvae.

Fecundity generally increases with the age/size of the female, while *relative* fecundity increases only with the production of more eggs per unit of somatic weight. Increases in relative fecundity with age have been observed in a diverse group of fishes, including queenfish, *Seriphus politus* (DeMartini 1991) haddock, *Melanogrammus aeglefinus* (Hislop 1998), and northern anchovy, *Engraulis mordax* (Parrish et al., 1986). Boehlert et al. (1982) report increases in relative fecundity in widow rockfish, *Sebastes entomelas*, from 254.0 eggs per gram of somatic weight at age six to 476.8 eggs per gram at age 13, an average increase in relative egg production of 12.5% per year. However, some data suggest that for many species, including yellowtail rockfish (*Sebastes flavidus*), variation in fecundity does not appear to be great enough to account for the variation seen in fishery recruitment (Eldridge and Jarvis, 1995; Shephard and Cushing, 1980). This suggests that recruitment is not tightly coupled to total number of eggs produced, and is likely influenced by other factors such as the environment and/or maternal effects. Maternal processes contributing to the health or fitness of embryos or early larvae may significantly influence survival and year class strength.

Maternal effects comprise a class of effects that parents have on phenotypes of their offspring that are unrelated to the offspring's own genotype. Mather and Jinks (1971, p. 293) offered this definition of maternal effects: "Maternal effects arise where the mother makes a

contribution to the phenotype of her progeny over and above that which results from the genes she contributes to the zygote.” Thus, a maternal effect is a part of an offspring’s phenotype not resulting from the effects of its own genes and the interactions of those genes with the environment (Bernardo, 1996).

These maternal contributions may take many forms, some of which are: (1) cytoplasmic inheritance, (2) nutritional inheritance, (3) transmission of pathogens and antibodies, (4) imitative behavior, (5) oviposition site choice, (6) offspring and/or nest defense, and (7) sibling interaction either directly or through the mother.

Maternal effects have been observed and documented in a diverse group of taxa (overview: Bernardo, 1996; *empirical reviews*, *plants*: Roach and Wulff, 1987; McGinley et al., 1987; Haig and Westoby, 1988; Lacey, 1991; *insects*: Lees, 1979; Mousseau and Dingle, 1991a,b; *fish*: Reznick, 1991; *mammals*: Cowley, 1991). In fish, the most common maternal effects involve egg and/or offspring size. However, as Reznick (1991) points out, this probably has more to do with where investigators have looked than with where maternal effects are most likely to be found.

A maternal effect in which older/larger females produce larger or higher quality eggs and larvae has been demonstrated in a number of studies. In Baltic Sea cod (*Gadus morhua*) both egg size and recruitment were positively related to the proportion of total eggs that were produced by

older females (Vallin and Nissling, 2000). In winter flounder (*Pleuronectes americanus*) egg size and viability were positively correlated with female size (Buckley et al., 1991). In striped bass (*Morone saxatilis*), females <4.54 kg produced eggs that had 21% lower hatchability, weighed 32% less, and resulted in larvae 33% smaller than those produced by larger females (Zastrow et al., 1989). Subsequent experiments by Monteleone and Houde (1990) demonstrated that these relative differences are maintained even 25 days post hatch.

Egg size increases with maternal size and/or age in a number of additional fish species (*Chinook Salmon*- Heath et al., 1999; *Haddock*- Hislop, 1998), and large eggs tend to produce large larvae (Reznick, 1991; Blaxter and Hempel, 1963; Knutsen and Tilseth, 1985; Monteleone and Houde, 1990). Initial larval size can be an important determinant of larval survival because large larvae tend to survive longer without food (Reznick, 1991; Blaxter and Hempel, 1963; Hislop, 1998), can feed more effectively and utilize a wider range of prey sizes (Blaxter and Hempel, 1963; Knutsen and Tilseth, 1985; Hislop, 1998), exhibit better swimming performance and can avoid predators more effectively (Miller et al., 1988; Bams, 1967; Ojanguren et al., 1996), and may require less time to metamorphose out of the high mortality larval stage (Reznick, 1991; Monteleone and Houde, 1990; Gall, 1974; Pitman, 1979; Wallace and Aasjord, 1984). Furthermore, as demonstrated by Houde (1987), even small differences in larval growth

rates or stage duration can have a highly significant effect on survival and subsequent recruitment levels.

The nutritional status of newly extruded eggs and larvae has an important relationship to growth and survival. The amount of metabolically available energy establishes the duration of survival in the environment until adequate food becomes available. Starvation during the time in which an organism must rely on its endogenous energy stores has been considered a major source of mortality or reduced fitness, may contribute to fluctuations in year-class strength, (May 1974; Shepherd and Cushing, 1980; Rissik and Suthers, 1996), and may be a key factor in recruitment variability in rockfish species (Moser and Boehlert 1991).

The variable provisioning of energy reserves to offspring is a mechanism that could generate variability in initial size, growth potential, ability to withstand starvation, and ultimately survival and recruitment. A maternal effect on energy provisioning has been demonstrated in capelin (*Mallotus villosus*), where both female condition and female lipid content were positively correlated with initial egg yolk volume (Chambers et al., 1989). Thus, there is ample evidence in the literature suggesting that offspring produced by older/larger females may have a greater probability of survival than those produced by younger/smaller females.

Black rockfish (Figure 1) are ideal subjects for studying age-related variability in reproductive success. They are widely distributed along the

west coast of North America, inhabiting nearshore rocky reefs from Baja California to the Aleutian Islands (Hart 1973). They are relatively sedentary and long-lived, with fish reaching a maximum age of 38 years (Stewart 1993). Off Oregon, all females are mature at an age of 9 years and a length of approximately 43 cm (McClure, 1982). In black rockfish, as with many species of *Sebastes*, there is evidence of sperm storage, with insemination occurring many weeks to months prior to fertilization and subsequent parturition (Boehlert and Yoklavich 1984; Sorokin, 1961; Moser, 1967; Love et al. 1990). Once fertilized, gestation is estimated to be 37 days at 10°C (Boehlert and Yoklavich 1984). Female black rockfish give birth to live larvae predominantly during January through March (Laroche and Richardson, 1980). Larvae average 4.0-4.5 mm at birth (Figure 2), and are pelagic for the first few months, eventually emigrating to nearshore, intertidal, and estuarine areas at ages from 4 to 6 months (Boehlert and Yoklavich 1983). Although rockfish are sometimes reported as being ovoviviparous, recent studies have confirmed that they are a primitive viviparous group and supply nutrients to developing embryos (Boehlert and Yoklavich 1984). The ability of embryos from female black rockfish to actively take up nutrients from an exogenous substrate was demonstrated by Yoklavich and Boehlert (1991), possibly providing a mechanism by which age-specific reproductive energy expenditure could result in offspring of variable quality.

Black rockfish have experienced a rapid increase in popularity in the Oregon sport fishery. In Oregon, because of the decline of salmon stocks and restrictive regulations on other species, such as halibut and lingcod, black rockfish have become the single most important groundfish species in the marine sport fishery, comprising as much as 80% of all landed groundfish in most ports (Stewart 1993). The adult population of black rockfish off the Oregon coast has been fished at moderate but sufficiently high levels to have already reduced the number of age classes in the population. The burden of reproduction is thus being progressively shifted to younger fish. Berkeley and Markle (1999) showed that older black rockfish release larvae earlier in the season followed by progressively younger fish, and that successful recruitment may come from a relatively restricted time period towards the earlier part of the spawning season. This suggests that older females may be more successful spawners than younger females.

The continued decline in the proportion of mature adults and average age in the population (Figure 3), even if not the principal causal factor, is likely to exacerbate recruitment problems. It is thus important to understand whether the underlying mechanism is simply the reduction in spawning stock or the selective removal of older age classes. If there is any difference in offspring quality and subsequent reproductive success between older and younger fish, then the fished population will be impacted

far beyond the loss of biomass.

The goal of this research was to determine if the apparently greater reproductive success of older female black rockfish could be attributed to the production of higher quality offspring, compared to offspring from younger female black rockfish. Specific objectives of this research were: (1) to determine if larval performance (i.e. growth, starvation, and mortality) is related to maternal age; (2) determine which larval characteristics might account for any observed differences in larval performance, and (3) determine if the larval characteristics affecting larval performance are related to maternal age.

METHODOLOGY

We tested the null hypothesis that larval performance is unrelated maternal age, by rearing larvae from different age mothers. From the rearing experiments, data were collected on larval growth rates (in both length and weight), time to starvation, and mortality rate. These larval performance data were then compared to maternal age to determine if a relationship existed between larval performance and maternal age. Since maternal age alone does not directly affect the larvae, additional data were collected from each mother and her respective offspring. Data collected from each mother included length, weight, age, liver weight, and gonad weight. Data collected from each larval cohort included total lipid concentration, initial length, initial weight, and oil globule volume. These larval/ maternal trait data were then compared to the larval performance data to determine what traits might account for any observed differences in larval performance.

To conduct the rearing experiments, mature, inseminated, female black rockfish ranging from 372 mm to 532 mm were collected alive using hook-and-line during December and January of 1997-98, 1998-99, 1999-00 and 2000-01. Collections were made as close to parturition as possible to minimize any laboratory or holding effects on developing larvae. Once brought on board, captured fish were examined to determine sex. We were

able to determine the sex of all mature fish externally. Fish were then placed in a large plastic container with seawater at ambient temperature and salinity. Fish were relieved of excess swim bladder gas using a sterile 18-gauge hypodermic needle inserted laterally just behind the pectoral fin. Males and immature females were released once neutral buoyancy was reestablished. Mature females were transported live to the laboratory (Hatfield Marine Science Center, Newport OR) and held outside in covered, individual, 750-litre, flow-through tanks (Figure 4) at ambient temperature and salinity. All fish were handled following the procedures and guidelines of the Oregon State University institutional animal care and use committee.

In the first year of experiments, efforts were made to provide food (cut squid and live sand shrimp (*Neotrypaea californiensis*)) to the females at a maintenance ration of 1% of body weight per day. However, we were never able to get the fish to feed and efforts to provide food were discontinued. In the first year of experiments, females reaching parturition were allowed to release their offspring in the holding tanks. This made recovery of the larvae extremely difficult, as the larvae were not only difficult to capture in such a large volume of water, but were also suffering high mortality from impingement on the drain screening. Thus, in all subsequent experiments the females were not allowed to release larvae in the holding tanks.

Because the females were not to release larvae in the holding tanks, a set of criteria was established to determine when parturition was imminent, thus allowing us to conduct the experiments on larvae taken at a similar stage of development. Using "naturally" extruded larvae (natural parturition from captive females) from various size females, the average initial length, pigmentation pattern, structural development, and oil-globule diameter were recorded. These data allowed us to compare and stage developing larvae so that they would be removed at or near parturition.

Larval development was monitored through (1) external examination of the female and (2) catheterization (Yoklavich and Boehlert, 1991; Boehlert and Yoklavich, 1984; Kusakari, 1991). When a female was near parturition it exhibited extreme distension of the belly, sedentary behavior, and frequent opercular movements. The presence of small amounts of what we believe to be ovarian fluid or tissue was also released in to the tanks just prior to parturition. As the female approached parturition, we monitored gestation by inserting a catheter into the oviduct and removing a sample of larvae. For catheterization, the water volume in the holding tank was reduced by approximately half and 12.0 grams of MS-222 (Tricaine Methanesulfonate), pre-dissolved in 1.0 liter of saltwater, was emptied into the tanks. When the fish became lethargic (10-15 minutes) it was manually rolled on its side and a flexible, 3 mm diameter catheter was inserted approximately 1 inch into the oviduct. Gentle suction on the catheter easily

removed enough developing larvae for examination and staging. Once catheterization was complete, normal flow of seawater was restored to the holding tank and the fish would regain normal motion and buoyancy within 5 minutes. The developing larvae were then staged according to our criteria. This procedure was repeated approximately every two days until the larvae met our criteria for full development and parturition was deemed imminent, at which time the female was sacrificed, measured, and weighed, and larvae removed manually with gentle pressure. Larvae were delivered into two 5-gallon plastic containers with saltwater at ambient temperature and salinity. After the majority of larvae were extruded the fish was weighed again, liver and gonad weights recorded, and sagittal otoliths removed for subsequent age determination. To determine the age of each female the sagittal otoliths were cleaned in distilled water and aged using the break-and-burn method by an expert age reader.

A sample of approximately 40 viable larvae was immediately removed from the 5-gallon container from which we determined average initial length, weight, and oil globule diameter. All length measurements are presented here as the distance from the snout to the end of the notochord. Initial lengths are the average of approximately 40 individual length measurements, estimated to the nearest 0.01mm, from digital images using the UTHSCSA *Image Tool* program (developed at the University of Texas Health Science Center at San Antonio, <http://ddsdx.uthscsa.edu>) and a

dissecting scope equipped with a digital camera. Initial weights were determined by randomly selecting 10 of the 40 viable larvae, rinsing in distilled water, and drying at 60°C for 24 hours. The 10 larvae were then collectively weighed to the nearest 1.0 μg on a Sartorius microbalance, and the total weight divided by 10. The oil globules present at parturition were approximately spherical and their volumes were estimated from their diameters (volume = $\frac{4}{3}\pi r^3$). Measurements of oil globule diameter were made from digital images using the image analysis system described above. Larval oil globule volume was then estimated for each brood by taking the mean of approximately 40 individual oil globule measurements from newly extruded viable larvae.

A separate, larger sample of viable larvae was then removed, rinsed repeatedly with distilled water, and frozen at -80°C in distilled water for later CHN and ash weight analysis via the Dumas combustion method (Analytical Chemistry Laboratory, U.C. Santa Barbara, CA). From these results protein (N x 6.25) and lipid (dry weight minus protein and ash) concentration was determined, which served as a measure of initial larval condition (Zastrow et al., 1989; Boehlert and Yoklavich, 1984)

Larvae to be used in rearing experiments were carefully removed from the delivery buckets using a large diameter pipette, counted and placed in black, plastic rearing tanks of approximately 50 L (Figure 5).

Larvae were stocked into rearing tanks at an initial density of 10 larvae l⁻¹. Rearing tanks were set up in a temperature controlled cold room at 10°C. The bottom of each rearing tank was painted white with a biologically inert paint to facilitate detection and removal of dead larvae. Water in the rearing tanks consisted of filtered, UV-sterilized seawater with salinity at 33 ppt. Water was gently aerated and water quality maintained by use of individual Penguin Mini Bio-Wheel filters (Marineland, Inc.). Each filter was fitted with a custom pre-filter utilizing 15-micron nylon mesh. The pre-filters were permeable to water but not food items and had a large surface area, thus preventing free-swimming food and larvae from being sucked into the circulating pump. Nitrate and ammonia levels were checked every other day and neither exceeded 0.0 ppm for the duration of the experiments, thus no water changes were necessary. Larvae were reared at a constant temperature of 10°C with a 12-hour light and 12-hour dark photoperiod.

Larvae were reared on a diet of enriched marine rotifers (*Brachionus plicatilis*) for the duration of the rearing experiments. Rotifer cultures were maintained using a combination diet of cultured algae (*Isochrysis galbana*) and Rotimac (Aquqfauna Bio-Marine Inc.). Prior to larval feeding, rotifers were enriched, per manufacturer instructions, with Algamac 3010 Flake Enrichment Medium (Aquqfauna Bio-Marine Inc.). After enrichment, rotifers were strained from the enrichment medium and placed directly into the rearing tanks. Food density in the rearing tanks was set at three treatment

levels: 10 prey items•ml⁻¹ and 1 prey item•ml⁻¹ to simulate high and low food levels, and 0 prey items•ml⁻¹ as a control and to determine time to starvation. Food densities were kept constant through daily sampling of the water in all rearing tanks to determine number of rotifers•ml⁻¹ and adjustments made accordingly. Dead rotifers were siphoned daily from the bottom of each rearing tank to help maintain water quality. Two replicates of each food treatment were run for a total of six rearing tanks per female. Larvae were reared for a period of 30 days or until no larvae remained. A random sample of approximately 6 viable larvae was removed every third day from each tank to determine growth in both length and weight. Length and weight measurements were taken on the six larvae using the protocols described previously. Mortality was monitored by removing and counting all dead larvae from the bottom of each container every other day. Any larvae remaining on day 30 were removed, counted, measured, dried, and weighed.

A linear regression model was used to estimate growth rate in length:

$$L_t = a + bt$$

where L_t is the estimated length (mm) at time t , b is the growth rate (mm•day⁻¹), t is time (days), and a is the y-intercept. Growth rate in weight was also estimated from a linear regression model:

$$W_t = a + bt$$

where W_t is the estimated weight (mg) at time t , b is the growth rate ($\text{mg}\cdot\text{day}^{-1}$), t is time (days), and a is the y-intercept.

Time to starvation was estimated as the number of days until half of the larvae remained in the 0 prey items $\cdot\text{ml}^{-1}$ treatment. Mortality rates of fed larvae were estimated as the number of days to 60% mortality. Both time to starvation (no food treatments) and time to 60% mortality (food treatments) were chosen as the measures of mortality rate for the rearing experiments because larval mortality was not a constant function across all broods. That is, while some groups of larvae exhibited a linear trend in mortality, other groups exhibited an exponential trend in mortality, while still other groups exhibited a sigmoidal trend (Figure 6). This aspect of larval mortality prohibited the use of a single mathematical function, such as linear regression, to accurately quantify mortality rates for all groups of larvae.

Additional data taken on each larval brood at the time of parturition included both length and weight, which was used to develop a general larval condition factor. The condition factor was equal to:

$$(\text{Initial Weight} / \text{Initial Length}^3) * 100$$

From data taken on each mother at the time of parturition, liver and gonad indices were developed to standardize the observed values. The liver index was equal to:

$$(\text{Liver Weight} / \text{Eviscerated Weight}) * 100$$

and the gonad index was equal to:

$$(\text{Gonad Weight} / \text{Eviscerated Weight}) * 100$$

A general condition factor was also estimated for each female. The condition factor was equal to:

$$(\text{Eviscerated Weight} / \text{Fork Length}^3) * 100$$

Both linear and nonlinear regression models were used to examine relationships between larval performance and maternal age. Subsequent stepwise multiple regression analyses were then used as a variable selection tool in relating the larval/ maternal traits to each larval performance factor. These stepwise multiple regression analyses allowed us to examine the set of explanatory variables (larval/ maternal traits) and determine which, if any, of these variables could be modeled to predict, or explain, the pattern of a given larval performance factor. Any larval/ maternal traits associated with larval performance were then examined in relation to maternal age to determine if that trait (or traits) is indeed related to maternal age. All statistical analyses were performed using Sigma Stat statistical software (Jandel Corporation).

RESULTS

EFFECTS OF MATERNAL AGE ON LARVAL PERFORMANCE

The larval performance factors measured in this study were: growth rate in length, growth rate in weight, time to starvation, and mortality rate. There were six significant relationships between seven larval performance traits and maternal age.

For growth in both length and weight, data from the two replicate food treatment tanks were pooled, and growth rate estimated by linear regression. In a small number of cases, larvae in one of the replicate rearing tanks would exhibit little to no growth (usually accompanied by high mortality). In these cases, only data from the replicate tank in which normal growth was observed was used in the analysis. Growth rate in length for the high food treatments was highly variable between broods (Table 1), with a mean growth rate of .0414 mm/day (95% CI from .0325 to .0503). Larval growth rates from the high food treatments were significantly related to maternal age ($p = 0.0003$, $r^2 = 0.71$; Figure 7), with larvae from the oldest mothers growing at approximately 3 times the rate of larvae from the younger mothers. Growth rate in weight for the high food treatments was also variable between broods (Table 2), with a mean growth rate of .0025 mg/day (95% CI from .0020 to .0030). Larval growth rates from the high food treatments were significantly related to maternal age ($p = 0.0006$, $r^2 =$

0.68; Figure 8), with larvae from the oldest mothers growing at approximately 3 times the rate of larvae from the younger mothers.

Growth rate in length for the low food treatments varied substantially between broods (Table 1), with a mean growth rate of .0423 mm/day (95% CI from .0343 to .0502). Larval growth rates from the low food treatments were significantly related to maternal age ($p = 0.004$, $r^2 = 0.57$; Figure 9), with larvae from the older mothers again growing at approximately 3 times the rate of larvae from the younger mothers. Similarly, growth rate in weight for the low food treatments varied between broods (Table 2), with a mean growth rate of .0025 mg/day (95% CI from .0020 to .0029). Larval growth rates from the low food treatments were significantly related to maternal age ($p = 0.0059$, $r^2 = 0.55$; Figure 10), with larvae from older mothers adding weight at approximately 3 times the rate of larvae from younger mothers.

Overall time to starvation for larvae reared under the no food treatments was estimated by taking the average of the time to starvation estimates from the two replicate no food treatment tanks. Time to starvation was highly variable between broods (Table 3), with an overall mean of 8.61 days (95% CI from 7.54 to 9.68). Time to starvation was significantly related to maternal age ($p < 0.0001$, $r^2 = 0.80$; Figure 11), with larvae from older mothers surviving approximately twice as long as larvae from younger mothers in the absence of an exogenous food supply.

Mortality rates (time to 60% mortality) for the high and low food treatments were estimated by taking the average of the mortality rates from the two replicate food treatment tanks. Mortality rates for the high and low food treatments ranged from 8.3 to 22.9 days and from 8.3 to 21.6 days, respectively. Mortality rates varied substantially between broods (Table 4). Overall mean mortality rate for the high food treatments was 14.81 days (95% CI from 12.73 to 16.89), while overall mean mortality rate for the low food treatments was 14.23 days (95% CI from 12.48 to 15.95). Mortality for the high food treatments was significantly related to maternal age ($p=0.001$, $r^2=0.55$; Figure 12). However, mortality for the low food treatments, while highly suggestive, was not significantly related to maternal age ($p=0.094$).

This pattern of relationships between larval performance and maternal age suggest that, all else being equal, offspring from older mothers perform better, in terms of growth, starvation, and mortality, than offspring from younger mothers. That is, offspring from older mothers grow faster in both length and weight, survive longer in the absence of an exogenous food supply, and exhibit lower mortality rates than offspring from younger mothers.

EFFECTS OF LARVAL/ MATERNAL TRAITS ON LARVAL PERFORMANCE

The six larval/ maternal traits measured in this study were: larval condition, total larval lipid concentration, larval oil globule volume, female liver size (as measured by a liver index), female gonad size (as measured by a gonad index), and female condition. Separate stepwise multiple regression analyses were run between these larval/ maternal traits (independent variables) and each larval performance factor (dependent variable) to determine which, if any, of the larval/ maternal traits could be modeled to predict, or explain, the pattern of a given larval performance factor.

In all but one analysis, oil globule volume was the only larval/ maternal trait selected for inclusion in each respective regression model (Table 5). In the one analysis in which oil globule volume was not selected for inclusion in the regression model, none of the variables were selected. Thus, of the six larval/ maternal traits measured in this study, oil globule volume at parturition was consistently selected, with no other accompanying traits, for inclusion in the models relating larval/ maternal characteristics to larval performance.

These results suggest that, all else being equal, oil globule volume at parturition is the primary larval/ maternal trait (of those measured) having a

significant affect on larval performance, as measured by growth, starvation, and mortality rates.

EFFECTS OF LARVAL OIL GLOBULE VOLUME ON LARVAL PERFORMANCE

Larval oil globule volumes were highly variable (Table 6), even within a brood. Oil globule volumes ranged from 0.0022 mm^3 to 0.0138 mm^3 , with a mean of 0.0048 mm^3 (95% CI from 0.0039 to 0.0058). The regression of oil globule volume on each larval performance factor showed larval oil globule volume to be significantly related to six of the seven larval performance factors (Figure 13).

Larval oil globule volume was positively related to growth in length for both the high and low food treatments ($p= 0.0007$ and $p= 0.0061$ respectively). Larval oil globule was also significantly related to growth in weight for both the high and low food treatments ($p= 0.0011$ and $p= 0.0094$ respectively). In terms of survival, both larval time to starvation and larval mortality rate were significantly related to oil globule volume ($p< 0.0001$ and $p= 0.0021$ respectively). The one larval performance factor not significantly related to oil globule volume (although highly suggestive) was mortality rate for the low food treatments ($p= 0.0994$).

Thus, of the six larval/ maternal traits measured in this study, oil globule volume at parturition was the only trait positively associated with larval performance (i.e. time to starvation, growth rate in length, growth rate

in weight, and mortality). This pattern of associations suggests that, all else being equal, larvae with larger oil globules at birth are more capable of withstanding starvation, grow faster in both length and weight, and experience a lower mortality rate than larvae born with smaller oil globules.

EFFECTS OF MATERNAL AGE ON LARVAL OIL GLOBULE VOLUME

Larval oil globule volume at parturition was then examined in conjunction with maternal age to determine if oil globule volume is related to the age of the mother. Oil globule volume was indeed significantly related to maternal age ($p < 0.0001$, $r^2 = 0.79$; Figure 14). Older mothers (ages 12-17) produced offspring with 3 to 4 times the amount of endogenous energy reserves than offspring from younger mothers (ages 4-6).

Collectively, these results suggest that: 1) older females are producing offspring which significantly out perform offspring produced from younger females, in terms of growth rate, ability to withstand starvation and survival rate; 2) the observed difference in performance is attributable to the amount of endogenous energy reserves present in oil globules of newly extruded larvae, with larger oil globules equating to better performance; and 3) that older females are producing offspring with significantly larger oil globules.

DISCUSSION

Black rockfish proved to be an excellent subject for studying age-related variability in reproductive success. Sex could be determined externally with 100% accuracy, and survival of captured females to imminent parturition was 100%.

Our data on time of parturition for the captive females support the age-structured spawning pattern of black rockfish observed by Berkeley and Markle (1999), in which older females reached parturition earlier in the spawning season than younger females (Figure 15).

Initial larval lengths measured in this study ranged from 4.14 mm to 4.65 mm, with an overall mean of 4.43 mm (95% CI from 4.38 to 4.48). These values for initial length are consistent with those reported from other (naturally extruded) reared specimens of *S. melanops* (Boehlert and Yoklavich 1982), suggesting that our criteria for determining imminent parturition were valid. Initial larval weights ranged from 0.011 mg to 0.033 mg, with an overall mean of 0.019 mg (95% CI from 0.017 to 0.022). For newly extruded larvae (i.e. day 0), the length-weight relationship can be described by the equation:

$$\text{Weight} = -0.196 + 0.049 \times \text{Length} \text{ (Figure 16)}$$

Larval growth rates from the high food treatments ranged from 0.015 mm/day to 0.069 mm/day, with a mean of 0.041 mm/day. Growth rates

from the low food treatments ranged from 0.017 mm/day to 0.062 mm/day, with a mean of .042 mm/day. These rates are consistent with those reported from other similarly reared specimens of *Sebastes*. Canino and Francis (1989) report growth rates of 0.056 mm/day for *S. auriculatus* and 0.047 mm/day for *S. nebulosus*. Moreno (1993) reared specimens of both *S. atrovirens* and *S. rastrelliger* and reported growth rates of 0.030 mm/day and 0.036 mm/day respectively. Furthermore, Kendall (1989) references rearing experiments of *S. melanops* in which a growth rate of 0.044 mm/day was observed at 10°C.

For larvae used in the rearing experiments (both high and low food treatments combined), the length-weight relationship through the first 30 days of life can be described by the equation:

$$\text{Weight} = -0.248 + 0.059 \times \text{Length} \text{ (Figure 17)}$$

REARING EXPERIMENTS

The similarity in larval growth rates (for both length and weight) and mortality rates observed between the high and low food treatments (Tables 1, 2, and 4) suggests that the difference in treatment levels (10 prey items•ml⁻¹ and 1 prey item•ml⁻¹) may not be sufficient to produce detectable differences in growth and/ or survival. The larvae appeared to grow and survive equally well under the low food treatment, with 1/10th the amount of prey, as under the high food treatment. Future experiments may reduce the

amount of prey available to the larvae in order to test for differences in performance based on ration.

Larval mortality was very high for both food treatments throughout the experiments, as few larvae ever survived to the end of the experimental period (30 days). Dead larvae were frequently observed to have food present in the gut, perhaps indicating that the diet was nutritionally inadequate to sustain growth and survival over a long period of time. No larvae survived to reach a size in which we were able to switch prey items (to enriched artemia nauplii), thereby possibly offering a more nutritional food item. Boehlert and Yoklavich (1982) report similar growth and survival of reared *S. melanops* while also using marine rotifers (*B. plicatilis*) as prey.

EFFECTS OF MATERNAL AGE ON LARVAL PERFORMANCE

Our results here indicate that maternal age is directly associated with larval performance in terms of growth (in both length and weight), starvation, and mortality. In each case, older females appear to be producing offspring of significantly higher quality than are younger females. Although maternal age, by itself, does not directly affect the offspring, that older female black rockfish are producing offspring of higher quality highlights the importance of the fact that it is this component of the population that is being truncated due to fishing. While there is no evidence to date suggesting that offspring from the older females are, by themselves,

supporting the population of black rockfish off the Oregon Coast, the continued removal of these fish will undoubtedly impact the population in ways we may, or may, not understand.

EFFECTS OF LARVAL/ MATERNAL TRAITS ON LARVAL PERFORMANCE

The fact that oil-globule volume at parturition was consistently the only trait selected for inclusion in each respective regression model relating to larval performance provides some important insights. First, this suggests that of the six larval/ maternal traits measured in this study, larval oil globule volume at parturition was the only trait having a significant affect on larval performance. From the stepwise regressions and table 1, we can see that of the six larval/ maternal traits, oil globule volume at parturition accounted for 74% of the variation in growth rate in length (high food treatments), 41% of the variation in growth rate in length (low food treatments), 72% of the variation in growth rate in weight (high food treatments), 61% of the variation in growth rate in weight (low food treatments), 79% of the variation in time to starvation, and 71% of the variation in mortality rate (high food treatments), suggesting that most of the variation in larval performance is explained by the volume of the oil globule.

Also suggested by these results is that total (i.e. whole body) larval lipid concentration, which is often considered an indicator of initial condition (Ferron and Leggett 1994, MacFarlane and Norton 1998), may not be as

accurate an indicator of initial condition as is oil-globule volume. In this study, total lipid concentration appeared to mask or confound the more descriptive estimate of oil-globule volume, as total lipid concentration was not significantly related to any of the larval performance factors.

EFFECTS OF LARVAL OIL GLOBULE VOLUME ON LARVAL PERFORMANCE

Our results here not only highlight the relative importance of oil globule volume in larval black rockfish, but also suggest that oil globule volume at parturition may provide a very simple indicator of survival potential.

All else being equal, *S. melanops* larvae born with larger oil globules grow faster in both length and weight, are better able to withstand starvation, and survive longer than larvae born with smaller oil globules. These findings are consistent with other published literature regarding the affects of oil globule volume on larval performance. In a study examining early life history traits of Capelin (*Mallotus villosus*), Chambers et al. (1989) found that the only correlate to post hatching lifespan (among eight measured characteristics) was a direct relationship with oil globule volume at hatching.

The relative importance of lipids, whether located in the oil globule or throughout the body, as sources of nutrition during embryonic and larval

development in oviparous fishes is well understood. However, not all types, or classes, of lipids are equivalent with respect to metabolic availability or energy yield (MacFarlane and Norton 1998). It is this distinction in lipid class that supports the notion of oil globule volume being a better indicator of initial larval condition than is total lipid concentration, as the primary lipid class present in oil globules is triacylglycerols (MacFarlane and Norton, 1998).

The use of triacylglycerols (TAG) as a primary source for energy storage and fuel during embryonic and larval development is well known in fishes (Boulekbache, 1981; Vetter et al., 1983; Tocher and Sargent, 1984; Fraser, 1989). Triacylglycerol was shown to be the predominant lipid class for embryonic and larval development in shortbelly rockfish (MacFarlane and Norton, 1998) and is regarded as the critical variable in condition for herring (Fraser et al., 1987) and anchovies (Hakanson, 1989). The presence of an oil globule in larval rockfish suggests the importance of lipids for energy. The results of this study, although limited to black rockfish, support the hypothesis put forth by MacFarlane and Norton (1998) which stated that "For rockfish, the amount of TAG at birth should be related to survival potential because this lipid class is the predominant component in oil-globules of most fishes (Henderson and Tocher, 1987; Heming and Buddington, 1988) and has consistently been shown to correlate with physiological condition (Fraser, 1989)." Thus, the use of oil

globule volume as a predictor of performance and survival potential may extend to other species, as oil globules are present in nearly all embryonic or larval fishes.

EFFECTS OF MATERNAL AGE ON LARVAL OIL GLOBULE VOLUME

That older females are producing offspring with larger oil globules, and that larger oil globules result in better larval performance, suggests the presence of an important maternal effect in black rockfish. This maternal effect not only influences critical early life history traits, but also alters the survival pattern otherwise exhibited if provisioning of endogenous reserves were equal throughout the population. Larvae with larger oil globules appear to be somewhat buffered against mortality in the critical early stages of life. This buffer likely has significant residual effects later on (i.e. increased fitness).

From the results of this study it is clear that older female black rockfish are endowing their offspring with significantly larger oil globules. However, what remains unclear, and a focus for future investigation, is the mechanism by which older females are able to do so. One possible explanation is that older females are capable of storing greater amounts of lipids in their body tissue than are younger females. These body stores may then be transferred to the developing embryos, resulting in larger oil globules. Such a mechanism was demonstrated when Chambers et al.

(1989) showed a direct relationship between female lipid concentration and initial egg yolk volume in capelin (*Mallotus villosus*). Furthermore, as stated previously, the ability of black rockfish embryos to take up nutrients from an exogenous substrate was demonstrated by Yoklavich and Boehlert (1991).

Another possible mechanism may be that the livers of older females are better able to store lipids, or store a greater amount of lipids, than are the livers of younger females. Again, this greater store of lipids may be transferred to the developing embryos, resulting in larger oil globules.

Regardless of the mechanism by which older females provide their offspring with relatively larger oil globules, our results show that older females are indeed producing offspring of a higher quality than are younger females. As a direct consequence, the offspring from older mothers are better able to withstand starvation, grow faster in both length and weight, and experience a lower mortality rate. Each of these traits individually would likely have a dramatic effect on overall fitness. It is this difference in quality that may explain the disproportionate survival of young-of-the-year black rockfish born early in the spawning season (when the older females spawn) observed by Berkeley and Markle (1999).

Given the results of these experiments, it is quite clear that efforts need to be made and policies established to protect the older component of the black rockfish population off the Oregon coast. While longevity may

compensate for varying environmental conditions, it also makes the fish more susceptible to over-exploitation as many long-lived species become susceptible to fishing gear before they reach sexual maturity. The removal of older age classes through fishing can be detrimental to a long-lived fish species not only by removing biomass and lowering egg or larval 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). As this research has shown, 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 the reduction in total potential egg production. If eggs/ offspring produced by younger age spawners have a lower chance of survival but are regarded equally as eggs/ offspring from older spawners, management decisions will greatly overweight the contribution of young spawners. This is a critical mistake for black rockfish, and perhaps other species. As fishing mortality truncates older fish from the range of spawning age classes, it results in a higher proportion of larvae

coming from the youngest spawners, and as this research has shown, at least for black rockfish, these larvae have a much lower likelihood of survival compared to larvae of older fish. Leaman (1987 and 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. As demonstrated in this study, this can result in greatly underestimating the true impact of fishing on reproductive potential.

The disproportionately greater contribution to recruitment by older fish should be considered in managing rockfish populations. 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. Once a population is severely age-truncated, and the most successful spawners eliminated, recovery may prove difficult until fishing mortality is sufficiently reduced for a long enough period to allow old fish to accumulate.



Figure 1. Black rockfish (*Sebastes melanops*)

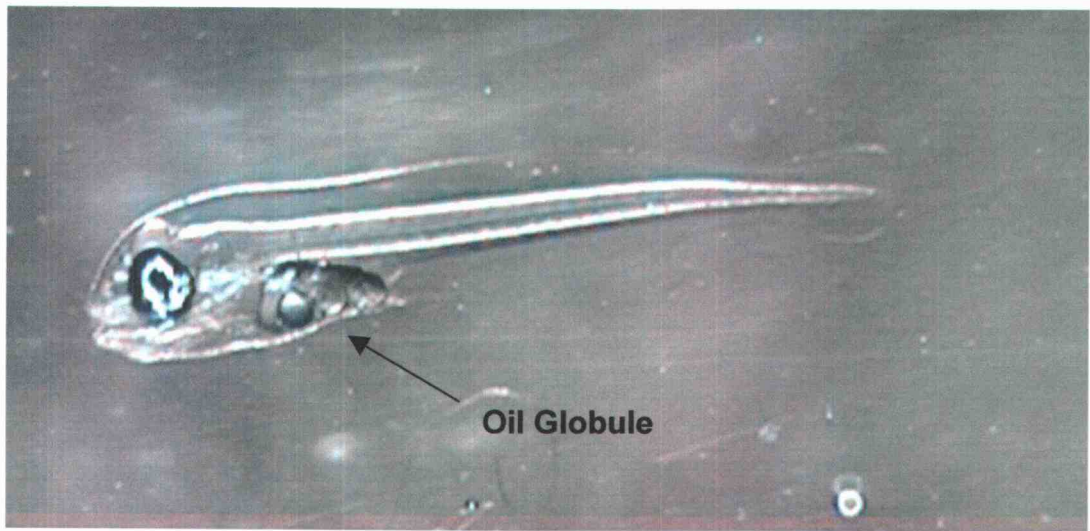


Figure 2. Newly extruded larval *S. melanops* with oil globule clearly visible; 4.3mm.

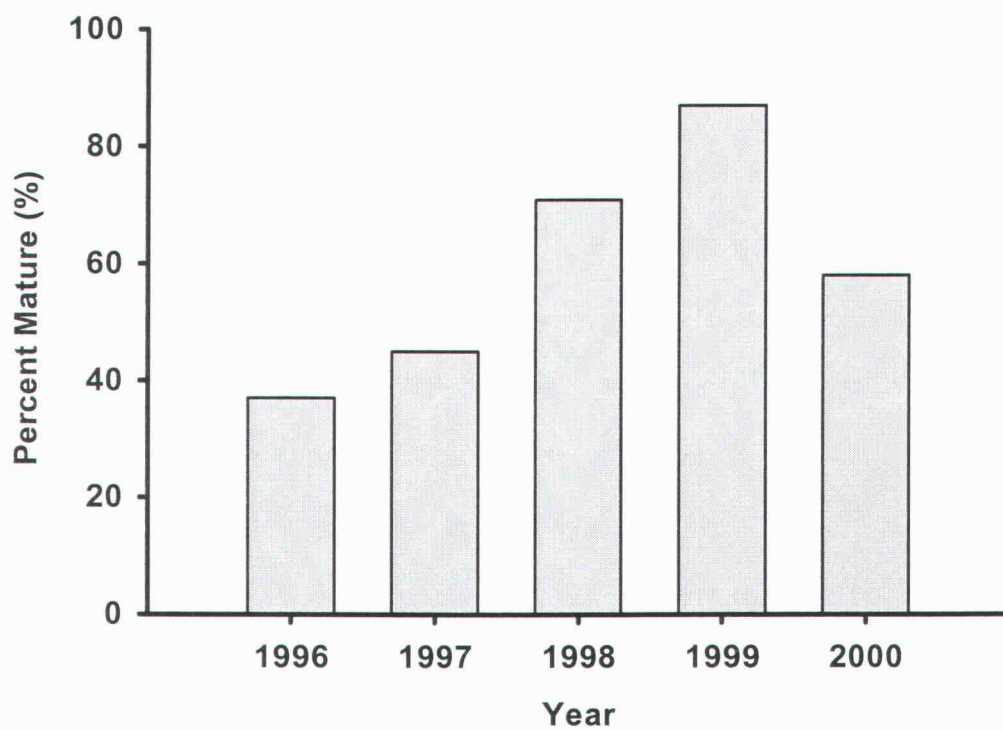


Figure 3. Percentage of mature females less than or equal to age 8, 1996- 2000. Samples obtained throughout spawning season from local charter boat catches.



Figure 4. Individual adult holding tanks with flow through system.

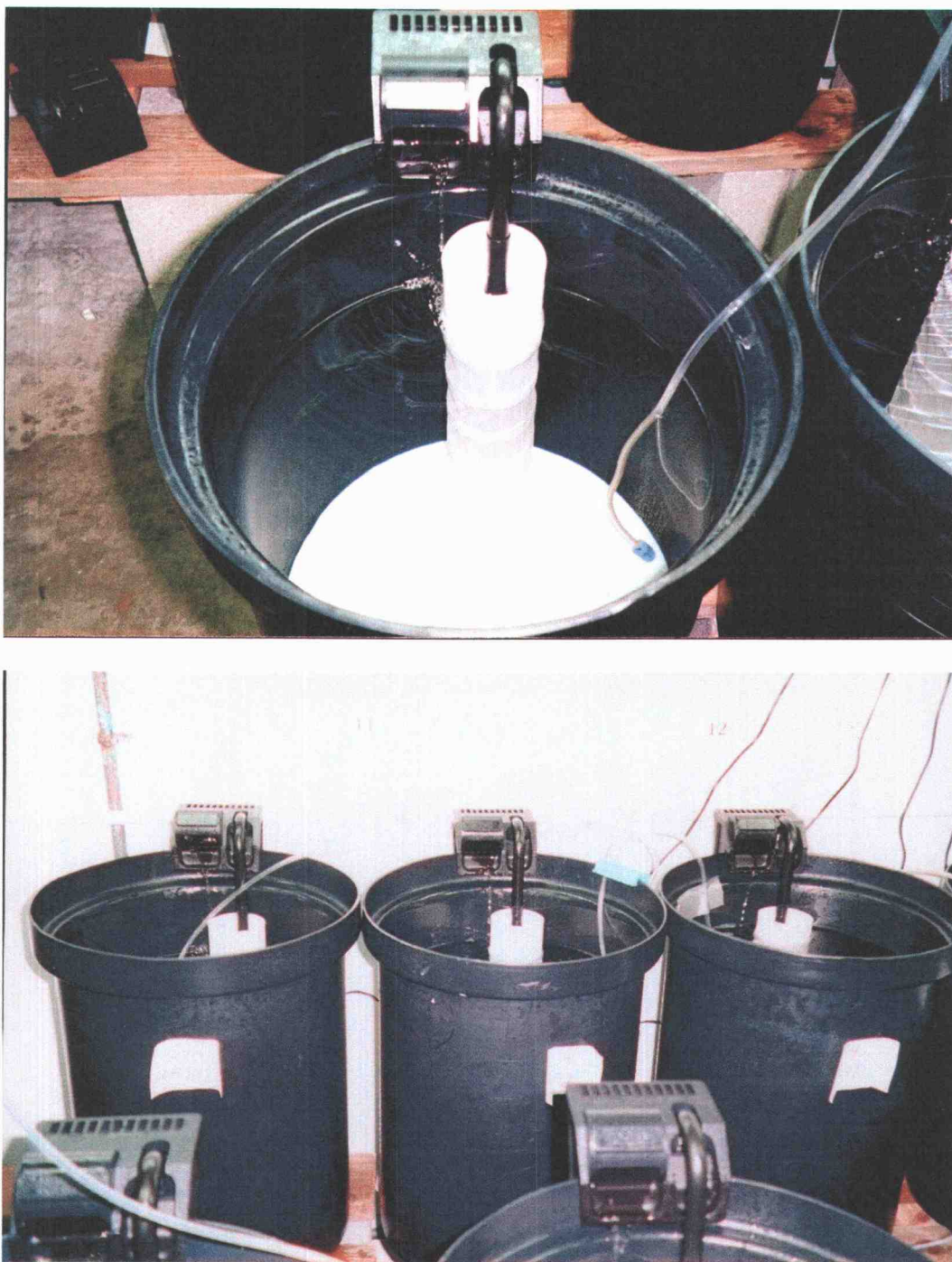


Figure 5. Rearing tanks used in larval rearing experiments.

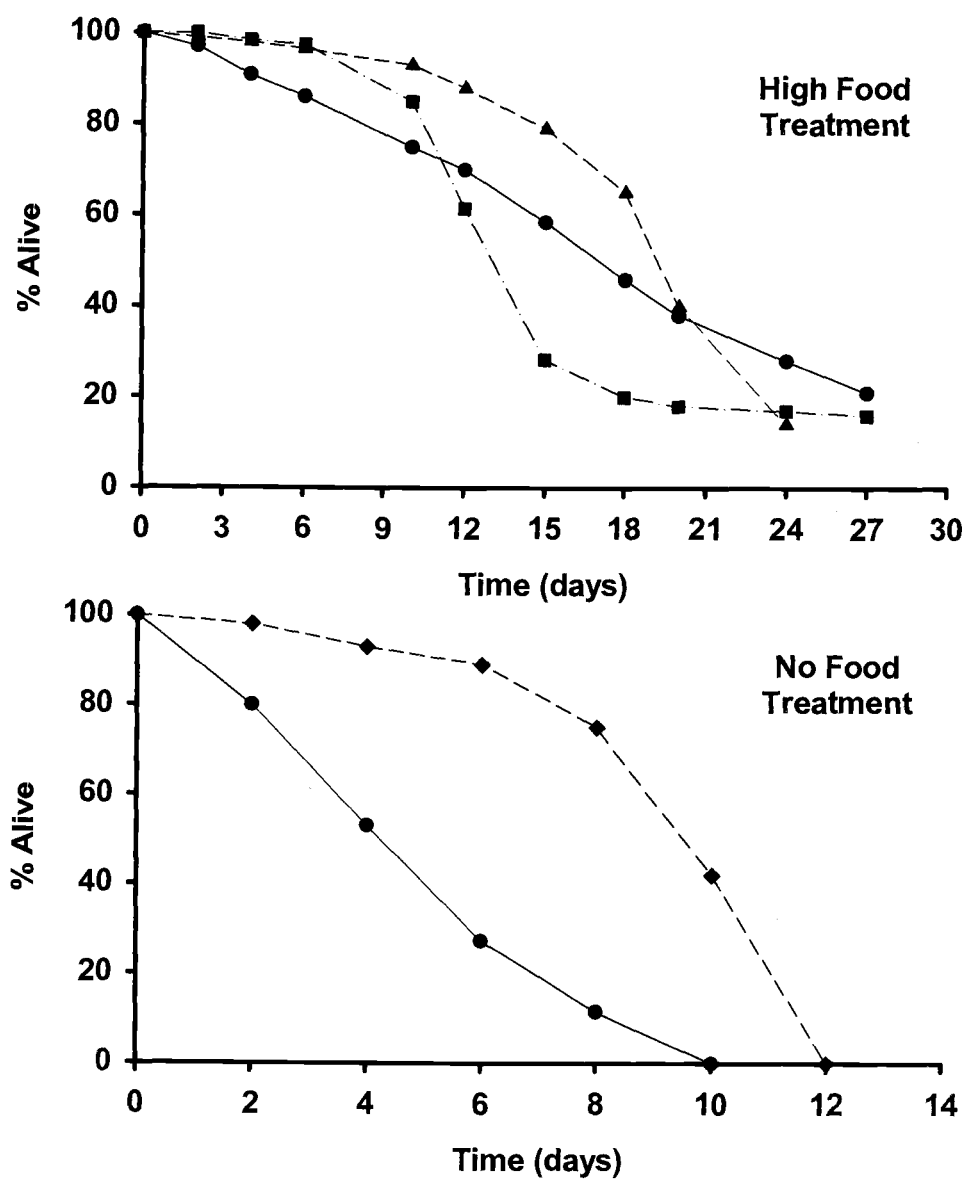


Figure 6. Differential patterns of larval mortality observed in the rearing experiments.

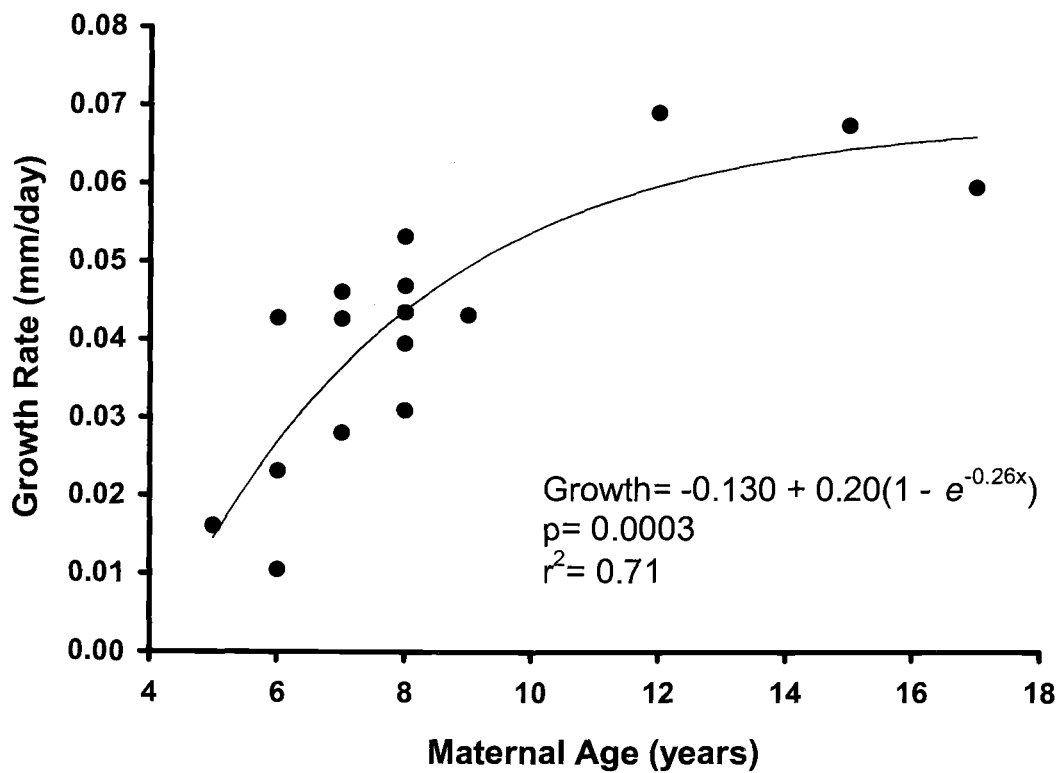


Figure 7. Relationship between larval growth rate in length and maternal age for larvae reared under the high food treatment.

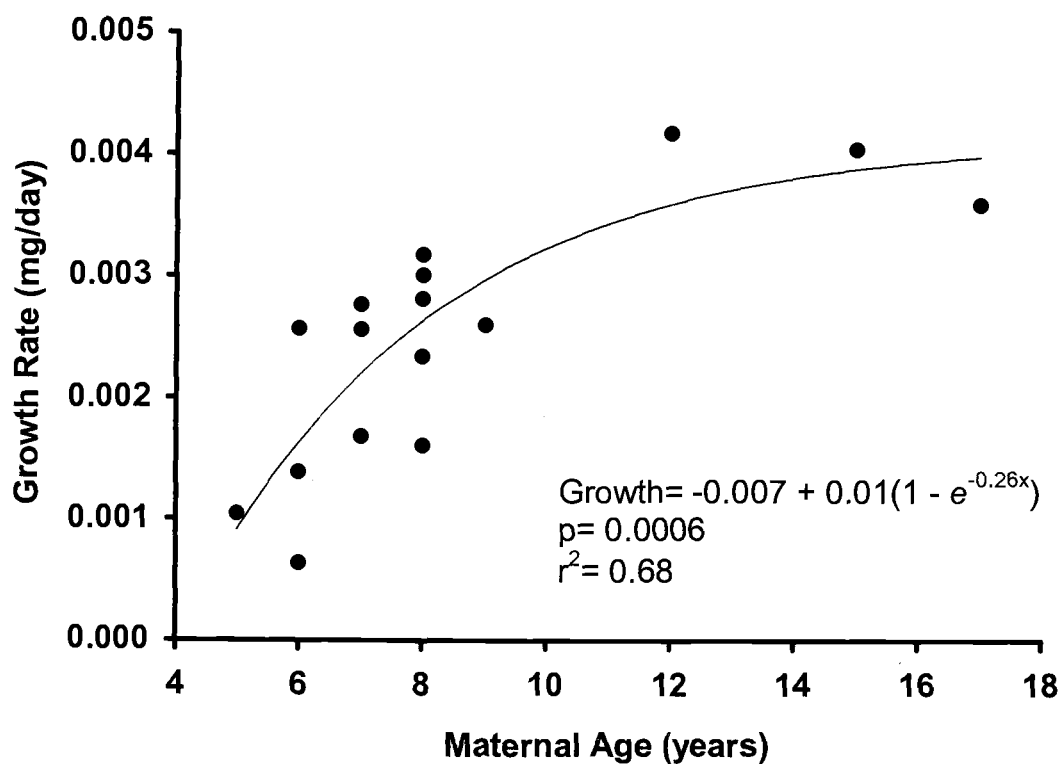


Figure 8. Relationship between larval growth rate in weight and maternal age for larvae reared under the high food treatment.

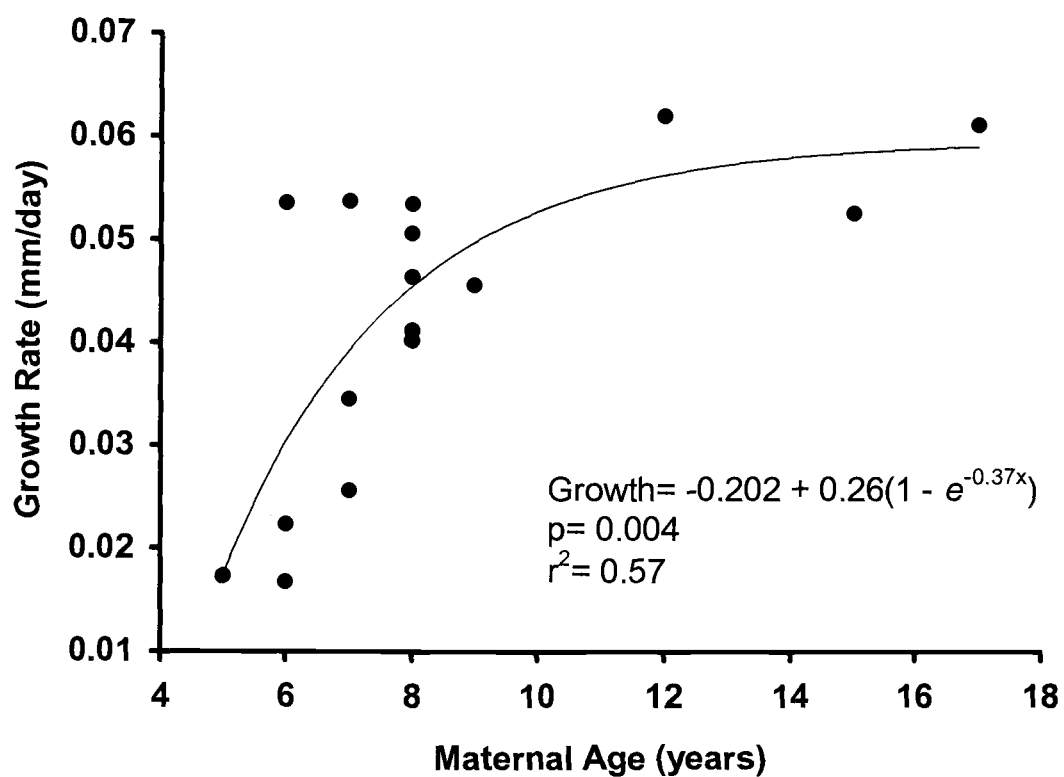


Figure 9. Relationship between larval growth rate in length and maternal age for larvae reared under the low food treatment.

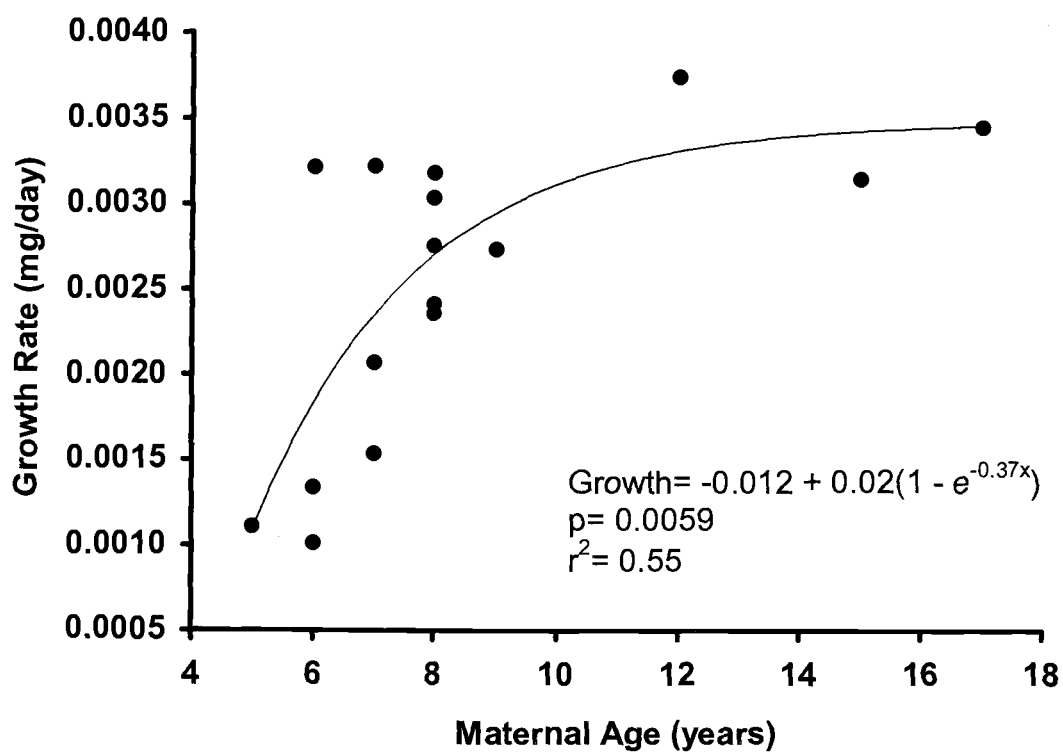


Figure 10. Relationship between larval growth rate in weight and maternal age for larvae reared under the low food treatment.

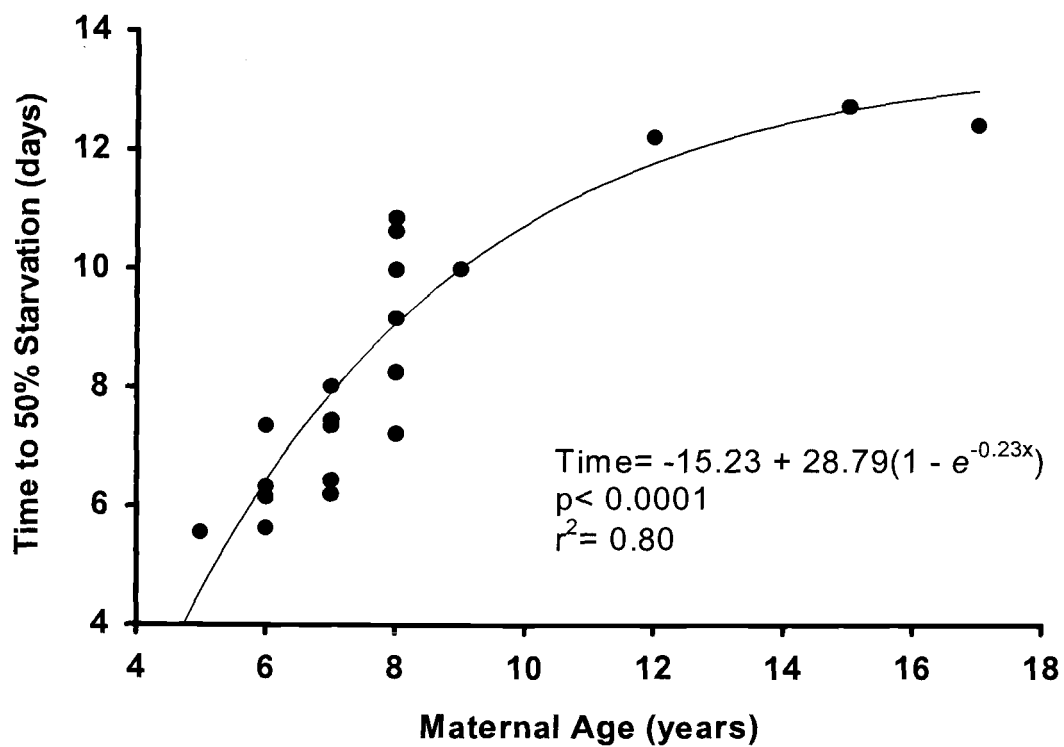


Figure 11. Relationship between larval median time to starvation and maternal age.

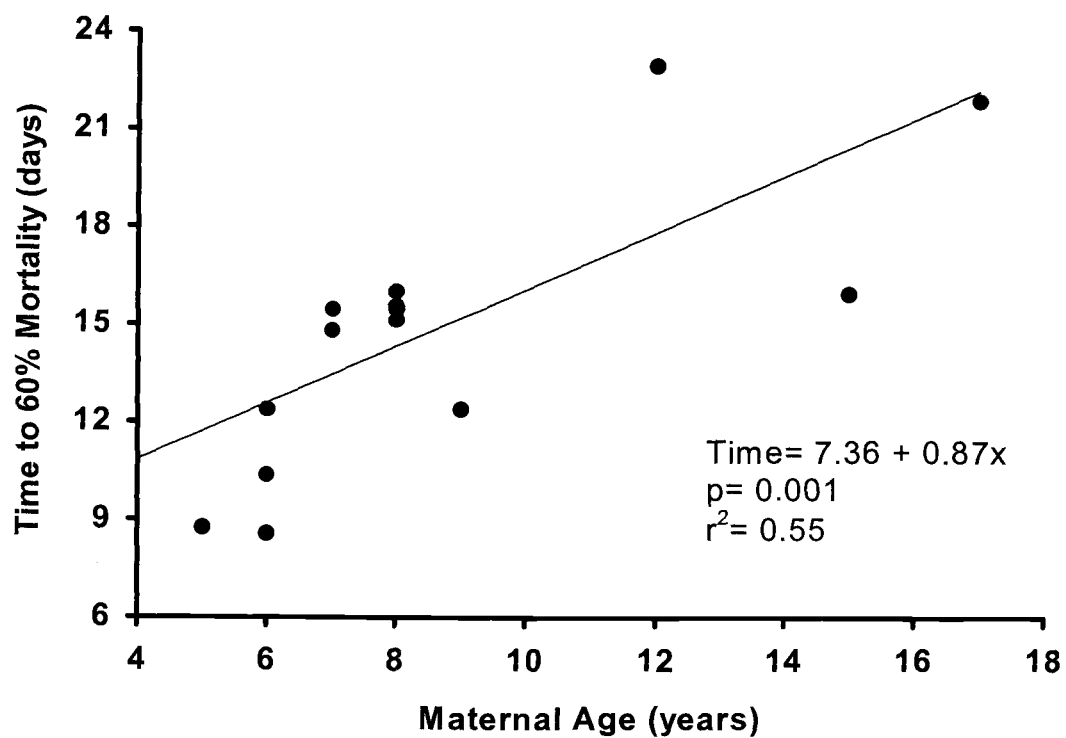


Figure 12. Relationship between time to 60% mortality for the high food treatments and maternal age.

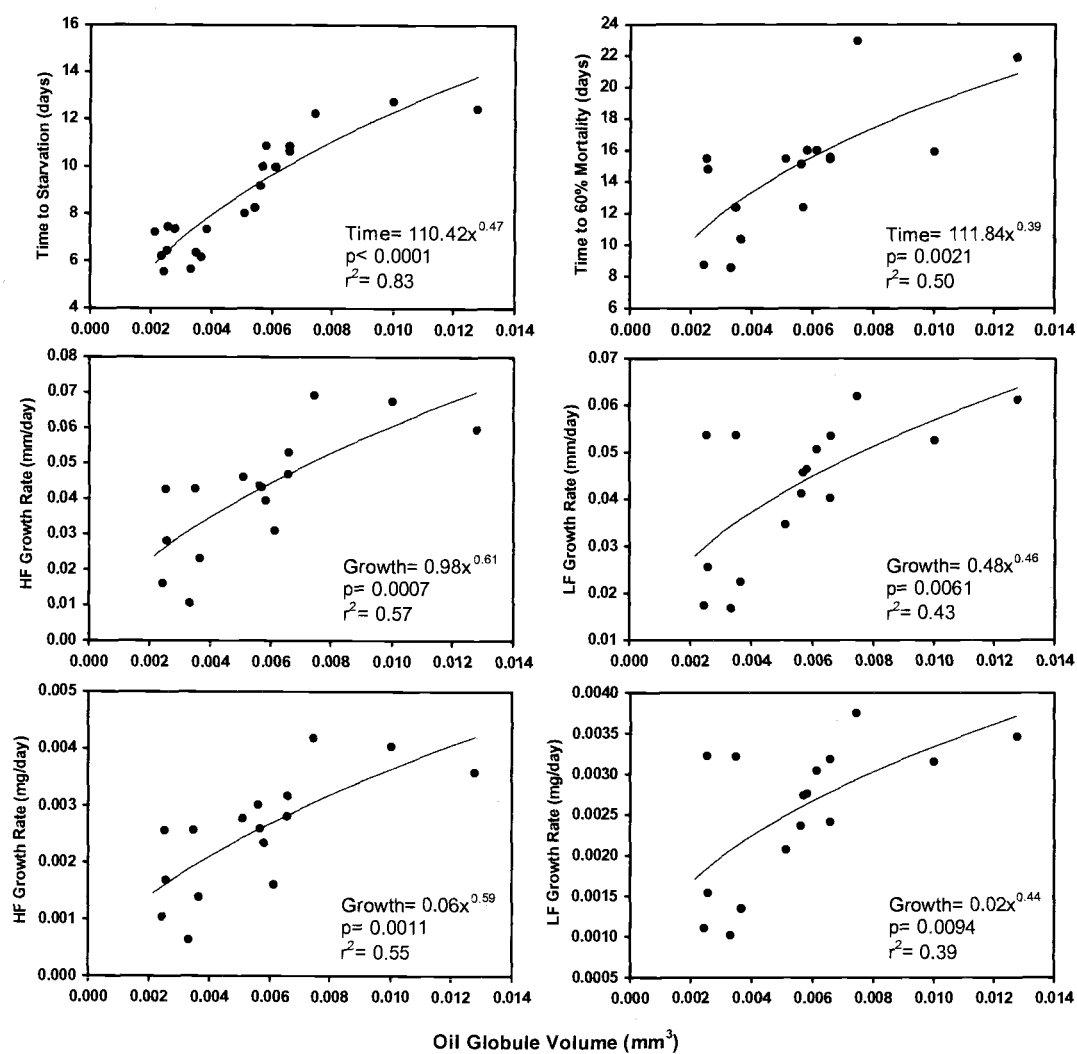


Figure 13. Significant relationships between larval oil globule volume and each larval performance factor as measured from the rearing experiments.

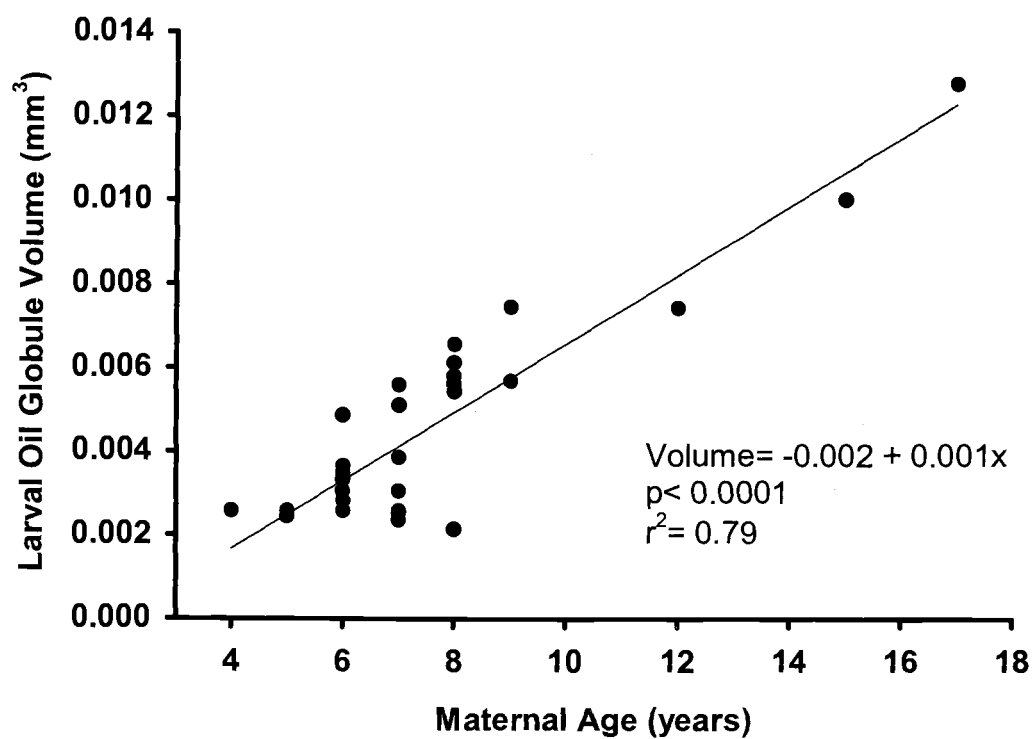


Figure 14. Relationship between larval oil globule volume at parturition and maternal age.

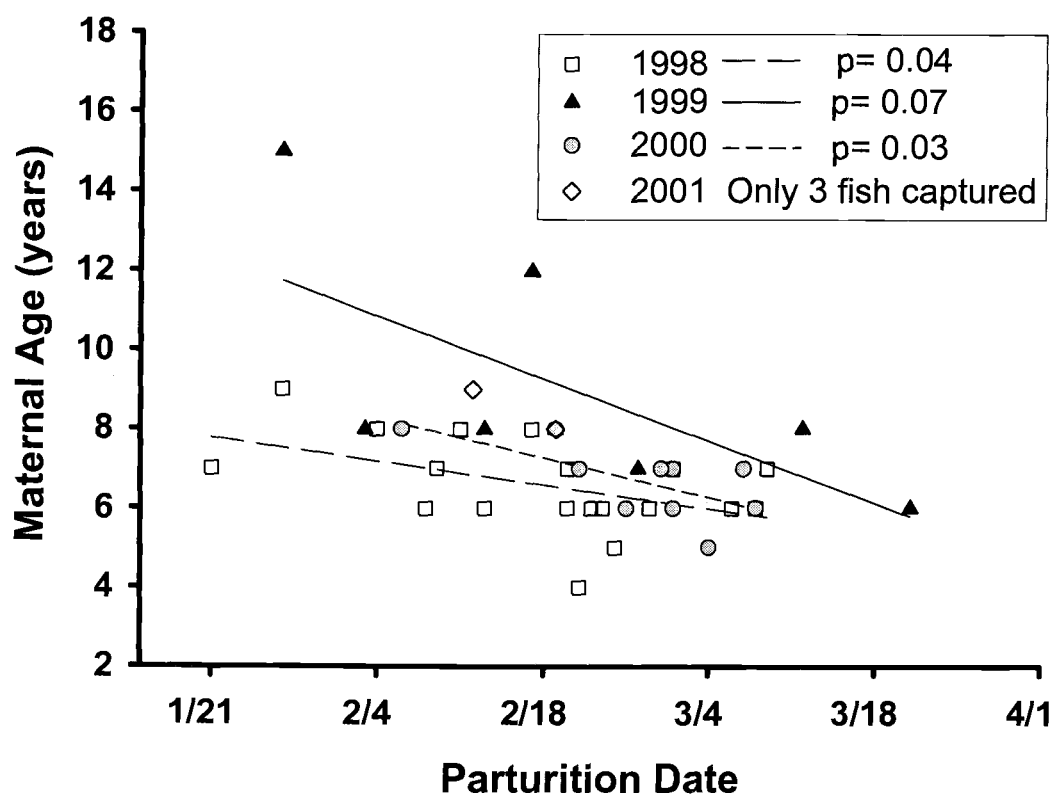


Figure 15. Temporal spawning patterns for black rockfish observed in captivity for years 1998- 2001.

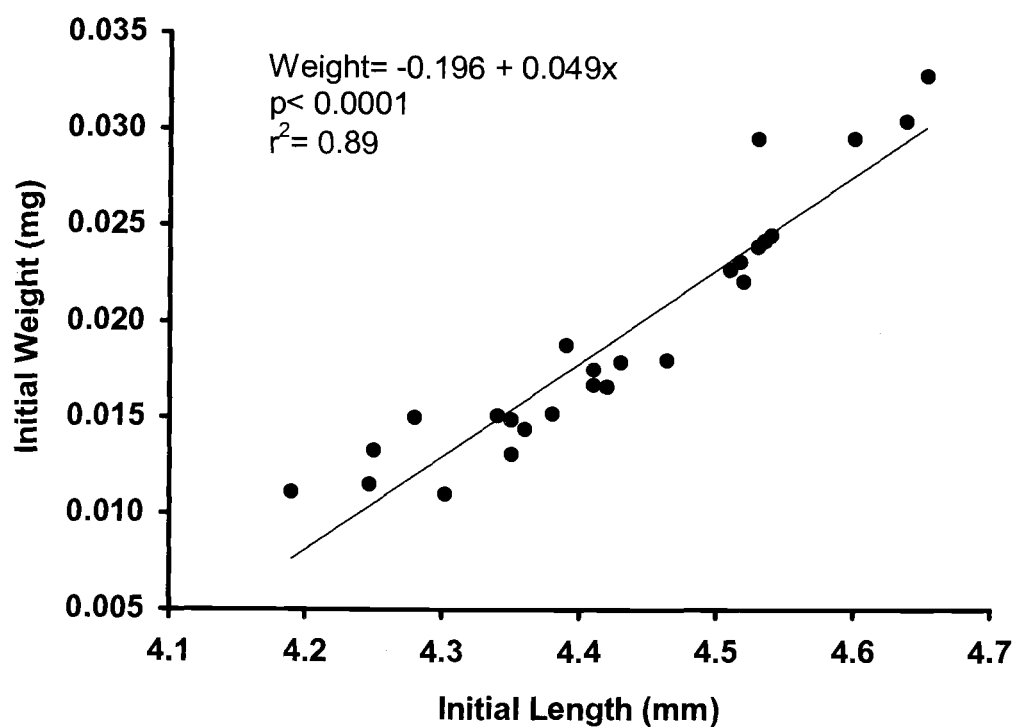


Figure 16. Length- weight relationship for newly extruded larvae.

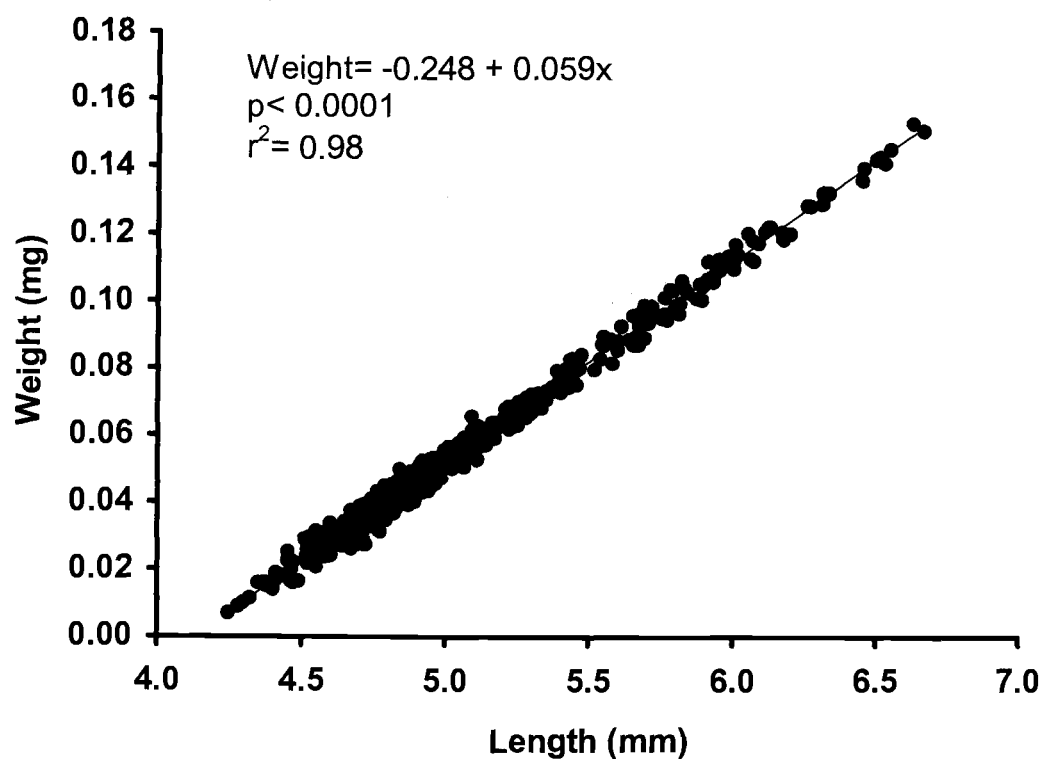


Figure 17. Length- weight relationship for larvae used in the rearing experiments from day 0 through day 30. Represents combined growth under both the high food and low food treatments.

Table 1. Larval growth rates in length for both high food and low food treatments. Growth rate is pooled estimate from two replicate rearing tanks unless otherwise noted in the comments.

Year	Fish ID	Maternal Age	High Food Growth Rate	Low Food Growth Rate	Comments
1999	B2	6	0.0105	0.0167	
	B4	8	0.0532	0.0534	
	C1	15	0.0674	0.0525	HF1 only
	C4	8	0.0435	0.0412	
	D3	7	0.0426	0.0537	HF2 only
	D4	12	0.0691	0.0619	HF2 only
2000	E1	8	0.0395	0.0463	
	F2	7	0.0461	0.0345	
	F3	8	0.0309	0.0506	LF2 only
	F4	6	0.0427	0.0535	LF2 only
	H4	5	0.0161	0.0173	
	I2	6	0.0231	0.0223	
2001	I3	7	0.0280	0.0256	HF1 only; LF1 only
	K1	9	0.0432	0.0456	
	K2	17	0.0595	0.0611	
	K3	8	0.0469	0.0402	
Overall Mean			0.0414	0.0423	
95% CI Lower			0.0325	0.0343	
Upper			0.0503	0.0502	

Table 2. Larval growth rates in weight for both high food and low food treatments. Growth rate is pooled estimate from two replicate rearing tanks unless otherwise noted in the comments.

Year	Fish ID	Maternal Age	High Food Growth Rate	Low Food Growth Rate	Comments
1999	B2	6	0.0006	0.0010	HF1 only
	B4	8	0.0032	0.0032	
	C1	15	0.0040	0.0032	
	C4	8	0.0030	0.0024	
	D3	7	0.0026	0.0032	HF2 only
	D4	12	0.0042	0.0037	HF2 only
2000	E1	8	0.0023	0.0028	LF2 only
	F2	7	0.0028	0.0021	
	F3	8	0.0016	0.0030	
	F4	6	0.0026	0.0032	
	H4	5	0.0010	0.0011	HF1 only; LF1 only
	I2	6	0.0014	0.0013	
2001	I3	7	0.0017	0.0015	HF1 only; LF1 only
	K1	9	0.0026	0.0027	
	K2	17	0.0036	0.0035	
	K3	8	0.0028	0.0024	
Overall Mean			0.0025	0.0025	
95% CI Lower			0.0020	0.0021	
Upper			0.0030	0.0029	

Table 3. Larval time to starvation from the no food treatments. Time to starvation was estimated by taking the average of the time to starvation estimates from the two replicate no food treatment tanks.

Year	Fish ID	Maternal Age	Time to Starvation
1999	B2	6	5.63
	B4	8	10.63
	C1	15	12.74
	C2	8	7.22
	C4	8	9.17
	D3	7	6.43
	D4	12	12.22
	E1	8	10.86
2000	F2	7	8.02
	F3	8	9.97
	F4	6	6.33
	G2	6	7.35
	H2	7	6.2
	H3	8	8.25
	H4	5	5.55
	I1	7	7.35
2001	I2	7	7.45
	K1	9	10
	K2	17	12.43
	K3	8	10.85
Overall Mean			8.61
95% CI Lower			7.54
Upper			9.68

Table 4. Larval mortality rates (time to 60% mortality) for both high food and low food treatments. Mortality rate was estimated by taking the average of the mortality estimates from the two replicate food treatment tanks.

Year	Fish ID	Maternal Age	High Food Mortality Rate (days)	Low Food Mortality Rate (days)
1999	B2	6	8.55	8.30
	B4	8	15.46	15.36
	C1	15	15.92	13.29
	C4	8	15.12	14.79
	D3	7	15.48	17.40
	D4	12	22.92	21.62
	E1	8	16.00	13.20
2000	F2	7	15.46	14.79
	F3	8	16.00	13.29
	F4	6	12.37	13.20
	H4	5	8.75	8.55
	I2	6	10.35	11.06
	I3	7	14.79	15.12
	K1	9	12.37	14.82
2001	K2	17	21.85	15.77
	K3	8	15.57	16.89
Overall Mean			14.81	14.22
95% CI Lower			12.73	12.48
Upper			16.89	15.95

Table 5. P-values (top) and r^2 increment values (bottom) from seven stepwise multiple regression analyses between larval/ maternal traits (independent variables) and each larval performance factor (dependent variable). Bolded p-values are significant at $\alpha = 0.05$. HFGrtL= growth rate in length for the high food treatments, LFGrtL= growth rate in length for the low food treatments, HFGrtW= growth rate in weight for the high food treatments, LFGrtW= growth rate in weight for the low food treatments, Starv= time to starvation, HFMort= mortality rate for the high food treatments, LFMort= mortality rate for the low food treatments.

	1	2	3	4	5	6	7
	HFGrtL	LFGrtL	HFGrtW	LFGrtW	Starv	HFMort	LFMort
Larval Condition	0.335 0.321	0.257 0.058	0.223 0.053	0.285 0.055	0.371 0.009	0.789 0.003	0.875 0.002
Larval Lipid Concentration	0.148 0.069	0.466 0.025	0.127 0.081	0.449 0.029	0.502 0.005	0.299 0.041	0.996 <0.001
Larval Oil Globule Volume	0.001 0.742	0.008 0.407	0.002 0.725	0.013 0.608	<0.001 0.790	0.002 0.711	0.160 0.136
Female Liver Index	0.410 0.024	0.268 0.056	0.449 0.021	0.261 0.061	0.162 0.022	0.385 0.0289	0.234 0.099
Female Gonad Index	0.276 0.041	0.293 0.050	0.321 0.036	0.268 0.059	.0136 0.025	0.750 0.004	0.249 0.094
Female Condition	0.532 0.014	0.757 0.005	0.542 0.014	0.774 0.004	0.985 <0.001	0.995 <0.001	0.502 0.033

Table 6. Mean oil globule volumes from newly extruded larvae.

Year	Fish ID	Maternal Age	Mean Oil Globule Volume (mm ³)	95% CI	
				Lower	Upper
1998	A0	7	0.0058	0.0053	0.0063
	A4	9	0.0083	0.0071	0.0094
	A5	6	0.0049	0.0039	0.0058
	B0	4	0.0027	0.0023	0.0031
	B3	--	0.0037	0.0032	0.0042
	B4	7	0.0025	0.0021	0.0029
	B5	7	0.0037	0.0028	0.0040
	C4	6	0.0025	0.0020	0.0031
	D3	6	0.0033	0.0023	0.0042
	D5	5	0.0026	0.0023	0.0029
	E2	6	0.0033	0.0027	0.0038
1999	B2	6	0.0036	0.0032	0.0040
	B4	8	0.0058	0.0053	0.0064
	C1	15	0.0106	0.0097	0.0116
	C2	8	0.0022	0.0019	0.0024
	C4	8	0.0054	0.0049	0.0060
	D3	7	0.0024	0.0021	0.0028
	D4	12	0.0083	0.0072	0.0094
	E1	8	0.0059	0.0054	0.0064
2000	F2	7	0.0051	0.0046	0.0056
	F3	8	0.0075	0.0059	0.0090
	F4	6	0.0039	0.0034	0.0043
	G2	6	0.0029	0.0026	0.0032
	H2	7	0.0024	0.0021	0.0027
	H3	8	0.0054	0.0051	0.0058
	H4	5	0.0024	0.0021	0.0028
	I1	7	0.0037	0.0032	0.0042
	I2	6	0.0037	0.0032	0.0042
	I3	7	0.0026	0.0022	0.0029
2001	K1	9	0.0057	0.0053	0.0061
	K2	17	0.0138	0.0124	0.0152
	K3	8	0.0077	0.0066	0.0088

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