

**Abstract**—Maternal effects on the quality of progeny can have direct impacts on population productivity. Rockfish are viviparous and the oil globule size of larvae at parturition has been shown to have direct effects on time until starvation and growth rate. We sampled embryos and prepar-turition larvae opportunistically from 89 gravid quillback rockfish (*Sebastes maliger*) in Southeast Alaska. Because the developmental stage and sampling period were correlated with oil globule size, they were treated as covariates in an analysis of maternal age, length, and weight effects on oil globule size. Maternal factors were related to developmental timing for almost all sampling periods, indicating that older, longer, and heavier females develop embryos earlier than younger, shorter, or lighter ones. Oil globule diameter and maternal length and weight were statistically linked, but the relationships may not be biologically significant. Weight-specific fecundity did not increase with maternal size or age, suggesting that reproductive output does not increase more quickly as fish age and grow. Age or size truncation of a rockfish population, in which timing of parturition is related to age and size, could result in a shorter parturition season. This shortening of the parturition season could make the population vulnerable to fluctuating environmental conditions.

Manuscript submitted 24 March 2011.  
Manuscript accepted 19 September 2011.  
Fish.Bull.: 110:35–45 (2012).

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

## Effects of maternal age and size on embryonic energy reserves, developmental timing, and fecundity in quillback rockfish (*Sebastes maliger*)

**Cara J. Rodgveller (contact author)**

**Chris R. Lunsford**

**Jeffrey T. Fujioka\***

Email address for contact author: [cara.rodgveller@noaa.gov](mailto:cara.rodgveller@noaa.gov)

National Oceanic and Atmospheric Administration  
National Marine Fisheries Service  
Alaska Fisheries Science Center, Alaska Biological Laboratory  
17109 Point Lena Loop Rd.  
Juneau, Alaska 99801

\*retired.

Because fisheries often target older, larger fish, population productivity may be affected more dramatically by fishing than is currently accounted for by population models where equal reproductive success is assumed for all sizes and ages of mature fish (Berkeley et al., 2004b; Berkeley, 2006; O'Farrell and Botsford, 2006; Spencer et al., 2007). Maternal effects on egg and larval energy reserves, larval size and growth, and fecundity have been documented in several taxa of marine fishes, including rockfish (*Sebastes* spp., [Berkeley et al., 2004a; Sogard et al., 2008; Dick, 2009]), Atlantic tomcod (*Microgadus tomcod* [e.g., Green and Chambers, 2007]), Atlantic cod (*Gadus morhua* [e.g., Carr and Kaufman, 2009]), and haddock (*Melanogrammus aeglefinus* [Hislop, 1988]) and can contribute to reproductive success (e.g., Houde, 1987; reviewed in Heath, 1992; Bergenius et al., 2002). The assumption that the reproductive output and success per unit of weight is the same no matter the age or size of the fish, as is common in many population models, may not be the best management practice.

For some rockfishes, larval energy storage, size, and survival are related to maternal age or size. The size of the oil globule is used as a proxy for energy reserves (e.g., Berkeley et al., 2004a; Sogard et al., 2008) because it is highly correlated to

total body lipid content in rockfish larvae (e.g., black rockfish [*Sebastes melanops*, Berkeley et al., 2004a]; quillback rockfish [*Sebastes maliger*, Sewell and Rodgveller, 2009]). These stores are used for sustenance by larvae when they first enter the marine environment. The positive effects of maternal age on larval quality and parturition date are not consistent among all species of rockfish. For example, in black rockfish larvae sampled off Oregon, maternal age was related to oil globule size (Berkeley et al., 2004a). Larvae from older mothers, therefore, may have a better chance of survival. This positive relationship does not hold true for all rockfish. Sogard et al. (2008) found significant maternal age effects on oil globule size in one out of five rockfish species sampled off California and found that maternal weight and length were significantly related to oil globule size for three of the five species. Also, maternal length or weight was related to development timing for three out of five species (i.e., larger females matured more quickly than smaller females). For those species, depletion of larger females would result in a shortened parturition season.

In previous studies, gravid females were held in captivity until parturition; such a period may affect embryonic development. Rearing

gravid females in the laboratory has the potential to introduce laboratory effects on oil globule size at parturition and also on parturition date. For example, some yellowtail rockfish (*S. flavidus*) resorbed embryos when in the laboratory (Eldridge et al., 2002). Laboratory results may also be skewed because larval performance in the laboratory environment may differ from performance in the natural environment (Marshall and Keough 2008; Marshall et al., 2010). Sampling gravid fish in the field and taking immediate measurements excludes potential effects of laboratory rearing. Because embryos among females will be at different developmental stages, the relationship between the stage of embryos and preparturition larvae (embryos that hatch in the ovary shortly before parturition) and oil globule size must be accounted for when assessing maternal effects on oil globule size.

Our objectives were to assess the effects of maternal size and age on 1) the oil globule size of embryos and preparturition larvae of quillback rockfish sampled opportunistically in Southeast Alaska; 2) the developmental stage of embryos; and 3) fecundity.

## Materials and methods

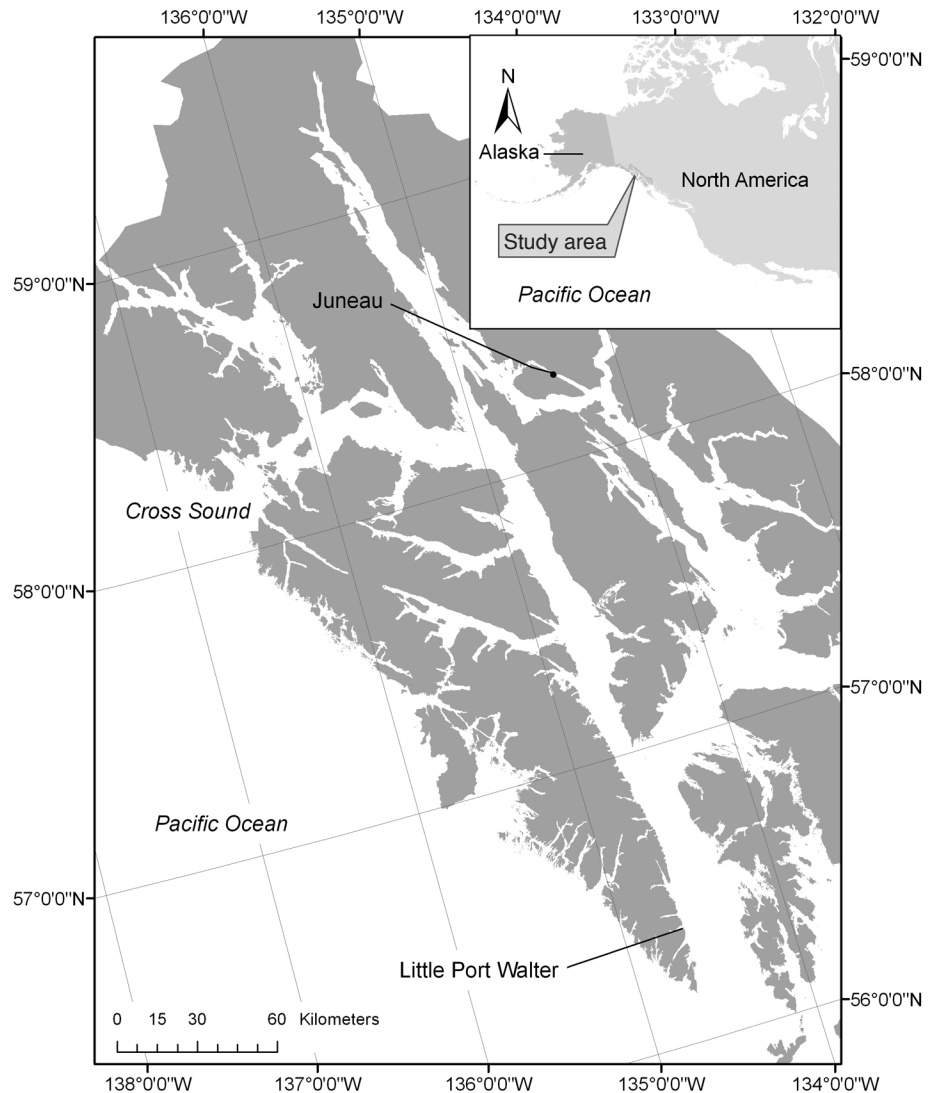
### Field sampling and oil globule measurements

Gravid quillback rockfish were sampled opportunistically with hook-and-line gear in Southeast Alaska during April or May, 2006–2008 (Fig. 1). Fish were sampled in Cross Sound on the northwest side of Chichagof Island during 15–20 April 2006, 14–19 April 2007, and 22–26 April 2008. Additional sampling occurred on the southeast side of Baranof Island near the National Oceanic and Atmospheric Administration's Little Port Walter research station during 31 May 2007 and 2–5 May 2008. Although each sampling trip occurred over several continuous days, for simplicity we will refer to each trip as a "sampling period." At both locations, gravid females were captured at depths ranging from 30 to 75 m (98–246 ft).

Gravid females were weighed (nearest 1.0 g) and measured (total length, nearest 1.0 cm), and otoliths

were collected. Otoliths were aged with the break-and-burn technique (MacLellan, 1997) by scientists within the Alaska Fisheries Science Center's Age and Growth Program. Because oil globule size is closely related to energy stores, the oil globule diameter (OGD) was used as a proxy for the amount of stored energy, which is used by embryos and larvae during early development and after they enter the marine environment before they learn to feed. Twenty embryo or preparturition larva samples were collected from each female by mixing all embryos from an ovary in a dish and randomly subsampling 20 embryos or preparturition larvae for oil globule measurements. Previous analyses showed that a coefficient of variation of less than 5% for average oil globule diameter for a female was possible with a sample size of 20.

All subsampled embryos were photographed by using a dissecting microscope soon after capture in the field.



**Figure 1**

Map of study areas in Southeast Alaska where quillback rockfish (*Sebastes maliger*) were sampled in 2006–08.

To identify structures within embryos and preparturition larvae, the samples were placed in a petri dish with a small amount of fresh water and raised above the microscope stage less than 2.5 cm. An object was placed under the dish to block some light coming from the stage below to provide proper shading for identification of internal structures. Often this procedure worked best when the light was covered under half of the embryo. Oil globule diameter was calculated by measuring two perpendicular bisecting diameters and averaging them.

We followed Yamada and Kusakari's (1991) criteria for developmental staging of *Sebastes schlegeli* embryos and preparturition larvae and added additional characteristics, such as eye and body pigmentation, to further divide late stages (Table 1, Fig. 2). One developmental

code was assigned to each female because for nearly every female all embryos were at the same developmental stage. In the few cases where more than one stage was present, owing to one group of embryos being unhealthy and arrested in development, only healthy embryos were photographed and analyzed.

Fecundity measurements were taken from fish sampled near Little Port Walter in 2008 to examine the relationships between weight-specific fecundity and maternal age, length, and weight. Fecundity estimates were determined by the gravimetric method where subsamples of the ovary are related to ovarian weight (e.g., Jennings et al. 2001).

### Analysis

Because gravid females were sampled at different times and embryos were at varying stages of development, these factors had to be considered when examining the relationship between OGD and maternal age, length, or weight (maternal factor). OGD was related to the developmental stage (i.e., OGD decreases as the embryo develops). This trend was similar among sampling periods. Our data also showed that younger, smaller fish have earlier stage embryos (within a sampling period) than older, larger females. This finding indicated that older, larger females develop larvae earlier than younger, smaller ones. Because developmental stage is confounded with both the maternal factors and OGD, comparisons across fish at different developmental stages can mask any relationship between the maternal factors and OGD. Therefore, it is necessary to remove the stage effect from both the maternal factors and the OGD to reveal the effects of the maternal factors on OGD. Our approach was to develop adjusted measures of OGD and maternal factors that removed the stage effect and to use the adjusted measures to visualize and statistically test the relationships between OGD and a given maternal factor. Alternatively, a general linear model (GLM) with OGD as the dependant variable, and with stage, maternal factor (either age, length, or weight), sampling period, and interaction terms as independent variables could be used to account for these confounding relationships. However, significant interaction terms in a GLM require that separate models be run for each factor (Lehman et al., 2005). With multiple significant interactions, a multitude of models would be required.

The OGD observations were adjusted by subtracting the expected OGD based on polynomial expression for stage,

$$OGD = \text{intercept} + \beta_1 S_i + \beta_2 S_i^2, \quad (1)$$

where  $S_i$  = the stage of all embryos and pre-parturition larvae within a female.

The intercept and  $\beta$  parameters were estimated regression coefficients.

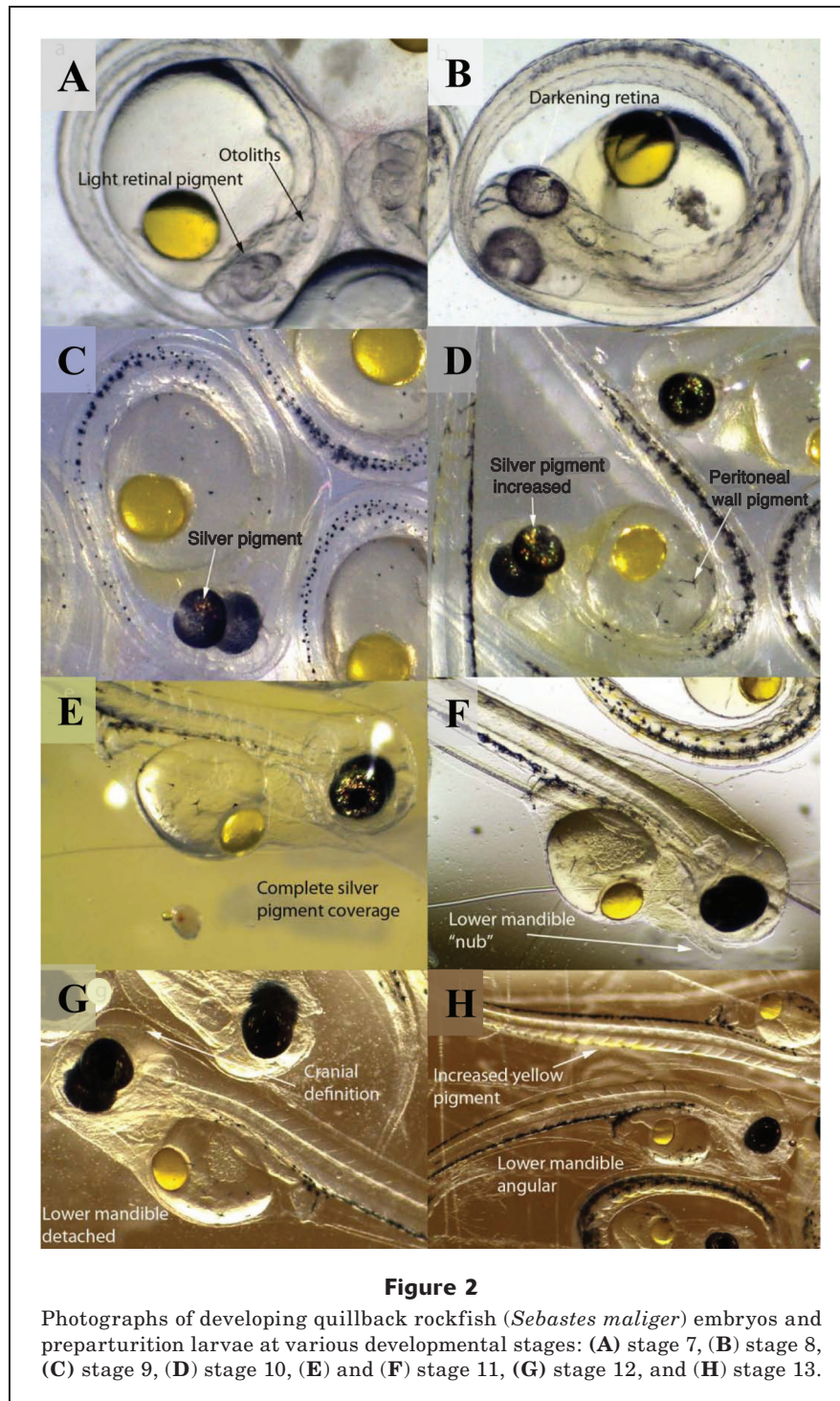
Each maternal factor was also adjusted to eliminate

**Table 1**

Descriptions of developmental stages observed in quill-back rockfish (*Sebastes maliger*) embryos and pre-parturition larvae and the corresponding stages from Yamada and Kusakari (1991) (Y&K).

| Stage | Y&K   | Description   |
|-------|-------|---|
| 1     | 14    | Late gastrula   |
| 2     | 16    | Head fold   |
| 3     | 17    | Optic vesicle   |
| 4     | 20    | Optic cups  |
| 5     | 21    | Auditory placodes   |
| 6     | 22    | Lens  |
| 7     | 23–25 | Otoliths, heartbeat, black pigment in retina and iris is strongest in periphery.  |
| 8     | 25    | Entire retina and iris translucent black, small, black spots of pigment on ventral side of tail.  |
| 9     | 25    | Black retina with scattered silver pigment in iris, spots on ventral side of tail darkened and multiplying.   |
| 10    | 29    | Iris silver but black still visible throughout, dark spots of pigmentation on gut and peritoneal wall, yellow pigment may be present on tail.   |
| 11    | 29    | Iris is completely silver, yellow pigment on tail, dark ventral pigment may have spread to form a line, lower mandible appears as a nub, but is not detached; when mechanically stimulated, will respond with a twitch. |
| 12    | 28    | Lower mandible detached and mouth open, yellow pigment appears on top of the head, embryos hatch easily when disturbed and are able to swim, the top of the cranium is a defined bulb.                                  |
| 13    | 28    | Lower jaw becomes angular and defined, lower mandible opens and closes in a gulping motion. Embryos may be hatched.   |





confounding with stage, within each sampling period, by subtracting the expected values obtained from a GLM. Adjustment of the maternal factors would not be necessary if they were randomly distributed across combinations of stages and sampling periods (i.e., if there was the same distribution of maternal factors in each stage-sampling period cell). Because they were not randomly distributed, the confounding between stage

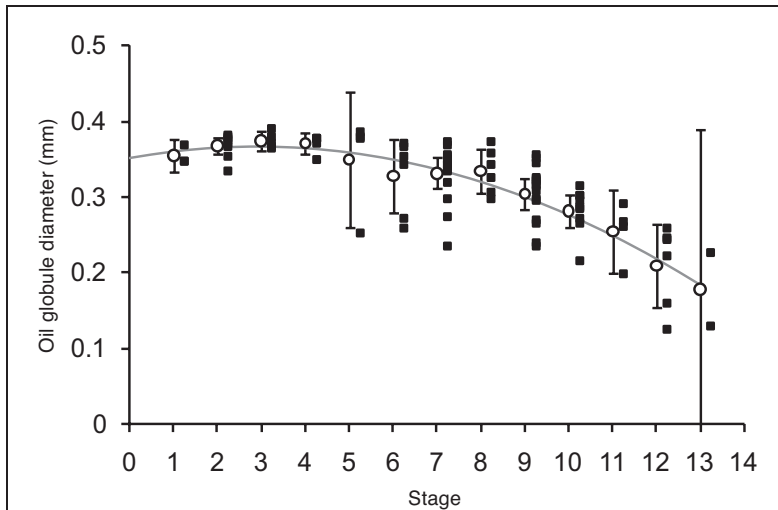
and the maternal factors necessitates the removal of stage effect. The GLM used was

$$A_{ij} = \text{intercept} + \beta_1 S_i + \beta_2 D_j + \beta_3 (S_i \times D_j) + e_{ij} \quad (2)$$

where  $A_{ij}$  = the predicted, i.e., the expected age, length, or weight for the  $i^{\text{th}}$  stage and the  $j^{\text{th}}$  sampling period;

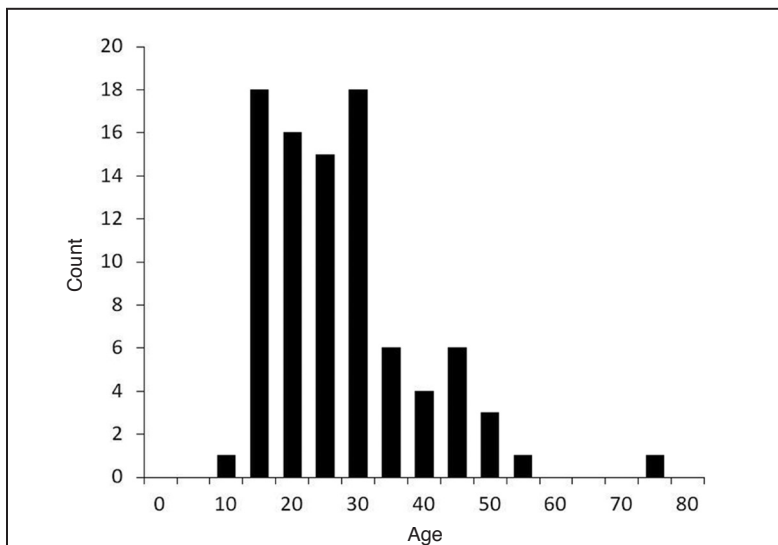
the  $\beta$  parameters = estimated regression coefficients;  
and the intercept

- $S_i$  = the developmental stage;
- $D_j$  = the sampling period;
- $S_i \times D_j$  = the interaction of stage and sampling period; and
- $e_{ij}$  = the normal error.



**Figure 3**

Average oil globule diameters (OGD) of embryos from 89 gravid female quillback rockfish (*Sebastes maliger*) (black squares) versus the developmental stage. Average OGD and 95% confidence intervals from embryos at each developmental stage are denoted by open circles. The solid line is a polynomial fitted to the average OGD, where each female's embryos or larvae are all from one stage.



**Figure 4**

Distribution of ages of gravid quillback rockfish (*Sebastes maliger*) binned by 5-year increments ( $n=89$ ).

One model was run where each maternal factor was the response variable: age, length, or weight. Length and weight met the assumptions of normality and age was log transformed.

The relationship between developmental stage and the maternal factors was evaluated with nine linear regressions, one for each sampling period that had adequate sample sizes ( $n=24-28$ ). Length and weight met the assumptions of normality and age was log-transformed. A significant, positive relationship would indicate that older or larger fish have more developed larvae than younger, smaller females sampled at the same time.

Three linear regressions were used to quantify the relationship between weight-specific fecundity (eggs per gram of ovary-free body weight) and the three maternal factors.

## Results

Oil globule diameter increased, then decreased curvilinearly through stage (Fig. 3) ( $n=89$  females; age range=10–74 years, Fig. 4). A polynomial fitted the data better than other methods (e.g., linear or squared) and was used to predict OGD (intercept= $3.51 \times 10^{-1}$ ,  $\beta_1=1.04 \times 10^{-2}$ ,  $\beta_2=-1.79 \times 10^{-3}$ ,  $r^2=0.65$ ,  $P < 0.05$ ). We defined 13 developmental stages based on physical characteristics associated with development (Table 1, Fig. 2). The range of OGDs within a stage increased after stage 4 (Fig. 3).

Regressions of lengths and weights and OGDs, adjusted for their confounding with stage, were both statistically significant at  $\alpha=0.05$ , but correlations were low. The strongest, positive correlation was between weight and OGD (Fig. 5). Age and OGD were not significantly related (Fig. 5), but the linear fit had a positive slope. The interaction of sampling period and stage was not significant and was excluded from all three models. Sampling period and stage were significant in all three models.

The stage of development was positively related to age, length, or weight in eight out of nine linear regressions (Fig. 6). This positive relation indicates that older, larger females have further developed embryos and that parturition larvae within a sampling period and likely will parturite earlier than younger, smaller ones. For every 35 mm increase in length (20% of range in lengths) the predicted increase in stage was 0.8, 1.0, or 1.8 stages (depending on the sampling period). For every 350 g

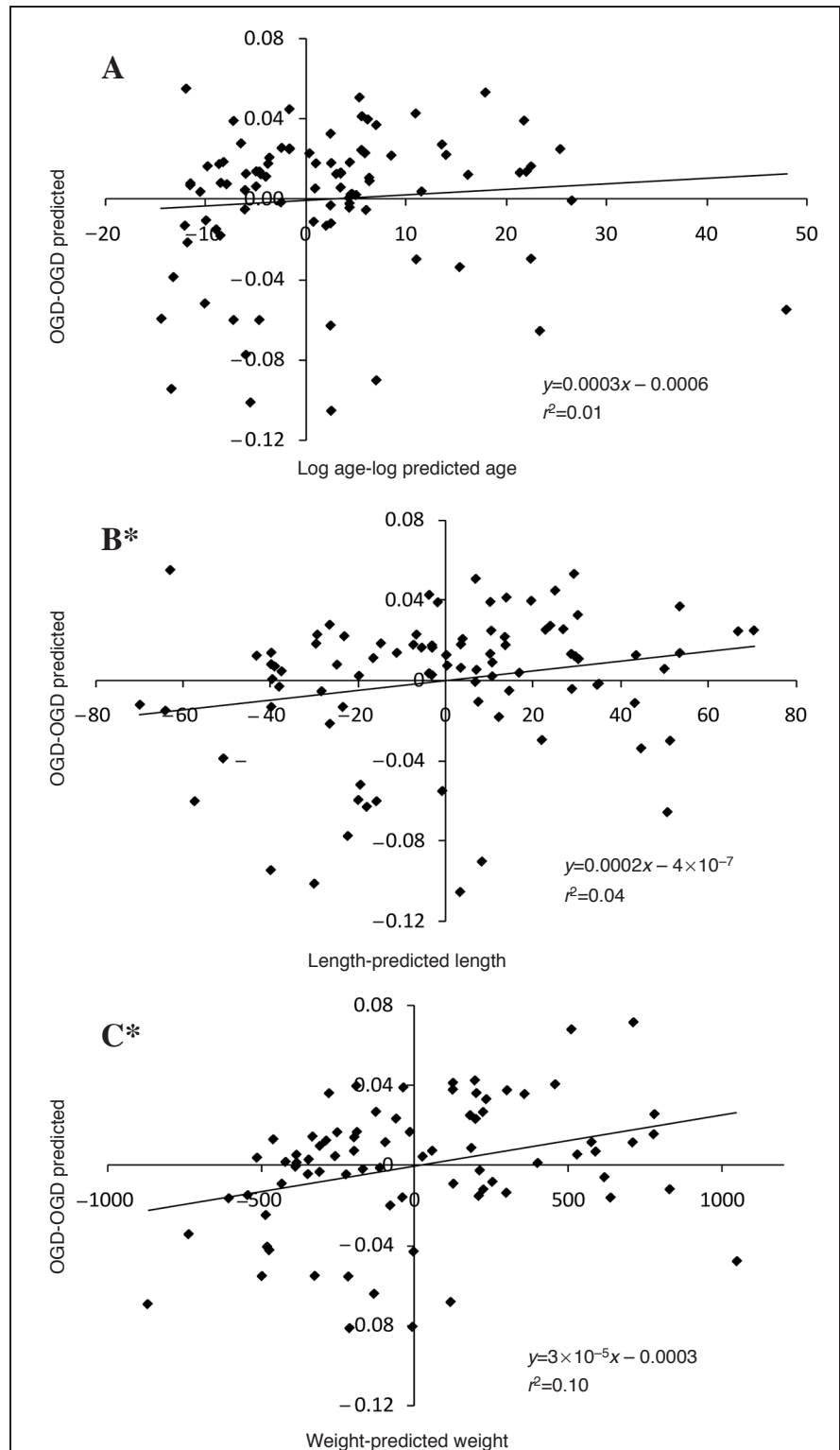
increase in weight (20% of range in weights) the predicted increase in stage was 0.8, 1.1, or 1.4 stages. Age was log normal and therefore the rate of change in stage between ages varied. From age 5–10 years there was a predicted increase in stage of 1.0, 2.0, and 2.4 stages; from age 20–25 there was an increase of 0.3, 0.6, and 0.7 stages; and from age 40–45 there was an increase of 0.2, 0.4, or 0.8 stages.

None of the regressions of weight and weight-specific fecundity were significant (Table 2), indicating that reproductive potential does not increase faster with increasing size or age.

## Discussion

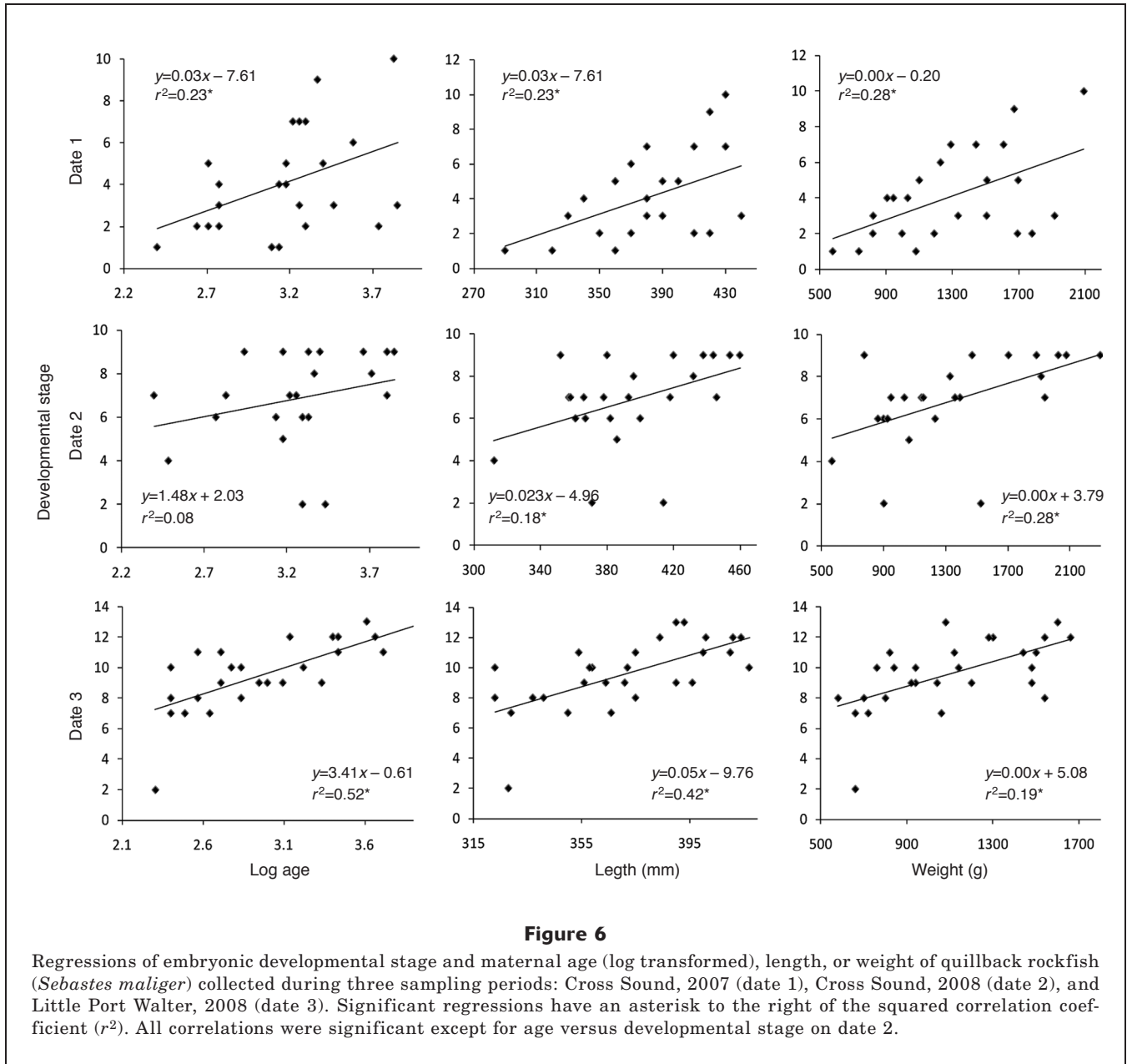
Ours is one of a few studies to relate timing of parturition for rockfish with age and size. Other studies have found that size is related to timing of parturition only for some rockfish; however, few found a relationship with age. Sogard et al. (2008) found that fish size was related to parturition date for three of five species of rockfish. In another study, larger dark-blotched rockfish (*S. crameri*) had reproductive events (e.g., maturation and vitellogenesis) earlier than smaller individuals (Nichol and Pikitch, 1994). There were not many indications of a relationship between parturition date and age in the literature. Pacific ocean perch (*S. alutus*) did not show a trend in embryonic development stage by age or size (Hannah and Parker, 2007). Older black rockfish had earlier parturition dates than younger ones only in some years (Bobko and Berkeley, 2004). Parturition date was not related to age for any of the five species examined by Sogard et al. (2008).

Differences in parturition timing of spring-spawning rockfish, like quillback rockfish in Alaska, could be related to earlier fertilization in older, larger mothers who have more energy available to divert to reproduction (Larson, 1991; Sogard et al., 2008). Small-



**Figure 5**

Linear fit and correlation coefficients squared ( $r^2$ ) of (A) oil globule diameter (OGD) and age, (B) OGD and length, and (C) OGD and weight, which were all adjusted for their confounding with development stage. Data are values adjusted by subtracting predicted values from the observed values. Significant regressions have an asterisk after the section labels B and C.



**Table 2**

Regressions of length- and weight-specific fecundity (dependent variables) and maternal factors (independent variables; age, length, weight) for gravid quillback rockfish (*Sebastes maliger*). The number of samples for all analyses was 28.

| Dependent | Independent | <i>t</i> -ratio | <i>P</i> |
|-----------|-------------|-----------------|----------|
| eggs/g    | age         | 1.52            | 0.14     |
|           | length      | 1.38            | 0.18     |
|           | weight      | 0.90            | 0.38     |

er, younger females may require more time to build energy reserves after winter and therefore delay fertilization, and in turn parturition (Larson, 1991). This scenario is possible because many *Sebastes* species can store sperm for weeks or months (Love et al., 2002). A delay may not be favorable if it results in a narrowed summer growth season, especially at northern latitudes with shorter summers. It is also possible that developmental time is shorter for older, larger females. To test these hypotheses, several measurements of embryonic developmental stage would be required from each gravid female through development and ideally measurements of maternal energy density or another metric of energy reserves. In gravid quillback rockfish



that were held in the laboratory, we found that many females began resorbing embryos. Therefore, for this species progressive sampling may not be possible. Our samples included a wide range of sizes and ages and even though we could not track embryonic development of each female, it is likely that we captured various life stages of female quillback rockfish that likely contributed to the significant relationships we found between development stage and age and size.

Maternal length and weight were statistically related to OGD, but the correlations were not strong. Weight and OGD had the strongest relationship and therefore it is possible that energy stores have more of an effect on OGD than age (e.g., Larson, 1991). In the literature, oil globule size and maternal factors are only sometimes related for rockfish. Sogard et al. (2008) found correlations between oil globule volume and weight, age, and length for one out of five species (a different species for all three factors). However, sample sizes were relatively small ( $n=28-40$  females) and the significant relationship with age was heavily influenced by one sample. Berkeley et al. (2004a) also found that black rockfish oil globule volume was related to age ( $n=20$ ).

In our study, weight-specific fecundity did not increase with size and age. Besides a decrease in fecundity, significant absence of energy stores due to a decreased weight can cause females to skip spawning, where mature fish do not spawn during a spawning season (e.g., Hannah and Parker, 2007). Practically, a skip in spawning would cause a decrease in weight specific fecundity if it was negatively related to weight. Because only gravid females were collected, we did not examine skip spawning.

Because rockfish are matrotrophic (e.g., MacFarlane and Bowers, 1995), effects on larvae of holding gravid females in captivity may be more pronounced than holding other species of fishes. In previous studies pregnant rockfish were held in captivity for 1–14 weeks until parturition or until larvae were fully developed (Berkeley, 2004a; Fisher et al., 2007; Sogard et al., 2008). If embryonic development is minimally compromised in a laboratory setting, there are benefits that cannot be accomplished in a field-based study, such as following embryonic development within a female and measurements of larvae after parturition. However, results of maternal age effects on larval energy stores and growth in the laboratory may not be an accurate predictor of success in the natural environment (Marshall et al., 2010). The laboratory favors the survival of larger larvae. Depending on the environment, bigger may not always be better (Marshall and Keough, 2008). Multiple environmental factors play a role in determining the ideal larval size and parturition date. Larger size does not alleviate pressure from many factors in the environment, such as intra- and interspecific competition, predation, water temperature and chemistry, and food availability (Marshall et al., 2010).

This is the first study where field measurements of OGD were used to avoid effects that laboratory rearing

could have on the energy use and health of developing embryos. The use of field data increased the number of covariates we had to consider in our analyses compared to those based on laboratory studies. However, staging may also be necessary for laboratory studies. It is a likely assumption that larvae from all females that parturied in the laboratory are at the same developmental stage. This may not be accurate; we found that embryos at stages 11–13 often broke out of their egg envelope easily and appeared to have been hatched internally and this activity would imply that they were all at stage 13. With closer investigation of the head and pigment, we classified these hatched larvae into three different developmental stages. Therefore, it is possible that developmental stage may need to be considered even for laboratory experiments.

Staging embryos as accurately as possible and considering developmental stage in analyses excludes variability in OGD that can be attributed to developmental use of the oil globule. We divided late developmental stages, when embryos and preparturition larvae are mobile, into more stages than were used in previous studies of rockfish embryonic development (Yamada and Kusakari, 1991; Eldridge et al., 2002). The polynomial shape of the relationship between OGD and stage, which is typical for rockfish (e.g., Eldridge et al., 2002), illustrates that the oil globule is used more rapidly at later stages of development. Therefore, late stages may require further division to properly account for variation in OGD that is attributable to stage. We also saw increased within-stage variability in OGD between females at later stages of development, possibly because the preparturition larvae and embryos were at different stages of development that we were not able to detect. However, measurements from late-stage embryos are likely a more accurate portrayal of OGD at parturition and the most obvious maternal effects may be detectable at late stages. Therefore, we would expect there to be more variability at later stages. Eldridge et al. (2002) found similar variability at early and late stages; however, sample size was small ( $n=21$ ), especially at middle stages, and therefore their results are inconclusive. Morphometric measurements may be useful for further dividing development because we noticed differences in body and cephalic morphometrics through development.

Studies that examined maternal effects on rockfish larvae have focused on pelagic, relatively shallow-water species sampled off of Oregon and California (Berkeley et al., 2004a; Fisher et al., 2007; Sogard et al., 2008). We studied a relatively long-lived, demersal rockfish in Alaska waters (up to 95 years, depths to 274 m, Love et al., 2002) and had some results that differed from studies of rockfish from southern latitudes. Distributional ranges of many rockfishes extend north to Alaska where the temperature, food availability, and other environmental variables differ substantially. These environmental differences may affect parturition timing and strategies for optimizing larval survival compared to species at lower latitudes. Owing to these environ-



mental differences, the relationship between maternal size and age and larval quality found in rockfish off the U.S. west coast may not be applicable to rockfish species off the coast of Alaska.

Age and size truncation of a population, i.e., a sharp decrease or absence of older, larger fish, is common in an exploited population and should be considered in management of fish stocks. Truncation of a rockfish population, in which parturition timing is related to age or size, could result in a shorter parturition season. Therefore, a size or age truncated population is less resistant to annual environmental fluctuations of larval food availability (Berkeley et al., 2004b). Because summer is shorter in Alaska than on the U.S. west coast, there are likely increased advantages to parturating precisely when larval food is available so that larvae can begin growth as soon as possible. Fish at northern latitudes may therefore be more likely to exhibit effects of age or size on developmental timing. Because quillback rockfish in this study exhibited evidence of age- and size-dependent parturition timing, they are likely vulnerable to potentially deleterious effects of age or size truncation.

## Conclusion

Current management practice is to assume equal reproductive success based on the biomass of mature fish and does not account for variability in success based on maternal age or size. Incorporation of maternal effects on productivity into population models for Alaska Pacific ocean perch causes a decrease in the fishing rate associated with management reference points such as  $F_{msy}$  (the fishing rate associated with maximum sustainable yield) and  $F_{40\%}$  (the fishing rate that conserves 40% of the reproductive output produced per recruit for an unfished population) (Spencer et al., 2007). Further studies of maternal effects on larval quality, parturition timing, fecundity, and population recruitment are recommended for other rockfish species in Alaska. Species subject to higher exploitation rates than those for quillback rockfish may be at greater risk of age or size truncation and potentially a decrease in productivity. In this case, a more conservative harvest would be needed to avoid population declines.

## Acknowledgments

We thank J. Heifetz, P. Rigby, P.-J. Hulson (all from the Alaska Fisheries Science Center, AFSC) for helpful reviews on earlier versions of this manuscript. P. Spencer (AFSC) provided much appreciated reviews and advice throughout writing. We also thank J. Heifetz, K. Shotwell (AFSC), and F. Sewall (University of Alaska Fairbanks) for assistance in the field. We greatly appreciate B. Goetz (AFSC, Age and Growth Laboratory) for reading ages from otoliths. We thank the maintenance and science staff at the AFSC Little Port Walter research

station for assistance with vessels, transportation, and sampling equipment.

## Literature cited

- Bergenius, M. A. J., M. G. Meekan, D. R. Robertson, and M. I. McCormick.  
2002. Larval growth predicts the recruitment success of a coral reef fish. *Oecology* 131:521–525.
- Berkeley, S. A.  
2006. Pacific rockfish management: are we circling the wagons around the wrong paradigm? *Bull. Mar. Sci.* 78:655–668.
- Berkeley, S. A., C. Chapman, and S. M. Sogard.  
2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85:1258–1264.
- Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love.  
2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29(8):23–32.
- Bobko, S. J., and S. A. Berkeley.  
2004. Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). *Fish. Bull.* 102:418–429.
- Carr, J. P., and L. Kaufman.  
2009. Estimating the importance of maternal age, size, and spawning experience to recruitment of Atlantic cod (*Gadus morhua*). *Biol. Cons.* 142:477–487.
- Dick, E. J.  
2009. Modeling the reproductive potential of rockfishes (*Sebastes* spp.). Ph.D. diss., 229 p. Univ. California, Santa Cruz.
- Eldridge, M. B., E. C. Norton, B. M. Jarvis, and R. B. MacFarlane.  
2002. Energetics of early development in the viviparous yellowtail rockfish. *J. Fish Biol.* 61:1122–1134.
- Fisher, R., S. M. Sogard, S. A. Berkeley.  
2007. Trade-offs between size and energy reserves reflect alternate strategies for optimizing larval survival potential in rockfish. *Mar. Ecol. Prog. Ser.* 344:257–270.
- Green, B. S., and R. C. Chambers.  
2007. Maternal effects vary between source populations in the Atlantic tomcod *Microgadus tomcod*. *Mar. Ecol. Prog. Ser.* 344:185–195.
- Hannah, R. W., and S. J. Parker.  
2007. Age-modulated variation in reproductive development of female Pacific ocean perch (*Sebastes alutus*) in waters off Oregon. *In* Biology, assessment, and management of North Pacific rockfishes (J. Heifetz, J. DiCosimo, A. J. Gharrett, M. S. Love, V. M. O'Connell, and R. D. Stanley, eds.), p. 161–180. Alaska Sea Grant Rep. AK-SG-07-01. Alaska Sea Grant Program, Univ. Alaska, Fairbanks, AK.
- Heath, M. R.  
1992. Field investigations of the early life stages of marine fish. *Adv. Mar. Biol.* 28:1–174.
- Hislop, J. R. G.  
1988. The influence of maternal length and age on the size and weight of the eggs and the relative frequency of the haddock, *Melanogrammus aeglefinus*, in British waters. *J. Fish Biol.* 32:923–930.
- Houde, E. D.  
1987. Fish early life dynamics and recruitment variability, 1729 p. *Am. Fish. Soc. Symp.* 2, Bethesda, MD.

- Jennings, S., M. J. Kaiser, and J. D. Reynolds, eds.  
2001. Marine fisheries ecology, 419 p. Blackwell Publ., Malden, MA.
- Larson, R. J.  
1991. Seasonal cycles of reserves in relation to reproduction in *Sebastes*. *Environ. Biol. Fishes* 30:57–70.
- Lehman, A., N. O'Rourke, L. Hatcher, and E. J. Stepanski.  
2005. JMP for basic univariate and multivariate statistics, 481 p. SAS Institute Inc., Cary, NC.
- Love, M. S., M. Yoklavich, and L. Thorsteinson.  
2002. The rockfishes of the northeast Pacific, 405 p. Univ. California Press, Berkeley, CA.
- MacLellan, S. E.  
1997. How to age rockfish (*Sebastes*) using *S. alutus* as an example – the otolith burnt section technique. *Can. Tech. Rep. Fish. Aquat. Sci.* 2146, 39 p.
- Marshall, D. J., S. S. Heppell, S. B. Munch, and R. R. Warner.  
2010. The relationship between maternal phenotype and offspring quality: do older mothers really produce the best offspring? *Ecology* 91:2862–2873.
- Marshall, D. J., and M. J. Keough.  
2008. The evolutionary ecology of offspring size in marine invertebrates. *Adv. Mar. Biol.* 53:1–60.
- MacFarlane, R. B., and M. J. Bowers.  
1995. Matrotrophic viviparity in the yellowtail rockfish *Sebastes flavidus*. *J. Exp. Biol.* 198:1197–1206.
- Nichol, G., and E. K. Pikitch.  
1994. Reproduction of darkblotched rockfish off the Oregon coast. *Trans. Am. Fish. Soc.* 123:469–481.
- O'Farrell, M. R., and L. W. Botsford.  
2006. The fisheries management implications of maternal-age-dependent larval survival. *Can. J. Fish. Aquat. Sci.* 63:2249–2258.
- Sewell F., and C. J. Rodgveller.  
2009. Changes in body composition and fatty acid profile during embryogenesis of quillback rockfish (*Sebastes maliger*). *Fish. Bull.* 107:207–220.
- Spencer, P., D. Hanselman, and M. Dorn.  
2007. The effect of maternal age of spawning on estimation of  $F_{msy}$  for Alaska Pacific Ocean perch. *In* Biology, assessment, and management of North Pacific rockfishes (J. Heifetz, J. DiCosimo, A. J. Gharrett, M. S. Love, V. M. O'Connell, and R. D. Stanley, eds.), p. 513–531. Alaska Sea Grant Rep. AK=SG-07-01. Alaska Sea Grant Program, Univ. Alaska, Fairbanks.
- Sogard, S. M., S. A. Berkeley, and R. Fisher.  
2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. *Mar. Ecol. Prog. Ser.* 360:227–236.
- Yamada, J., and M. Kusakari.  
1991. Staging and the time course of embryonic development in kurosoi, *Sebastes schlegeli*. *Environ. Biol. Fishes* 30:103–110.