Maternal effects in rockfishes *Sebastes* spp.: a comparison among species

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ABSTRACT: In temporally variable environments, longevity is generally considered to be a bet-hedging adaptation in which reproductive effort is spread across many years, increasing the probability that favorable conditions for larvae will be encountered at least some time in a female's life span. A long reproductive life span provides the potential for individual females to exhibit inter-annual differences in energy allocation patterns that may be age- or size-dependent. We examine the effects of maternal age and size on larval quality, fecundity, and timing of parturition in 5 species of live-bearing rockfishes in the genus *Sebastes* (blue, yellowtail, olive, gopher, and kelp rockfish), and compare these maternal effects with previously documented patterns in black rockfish *Sebastes melanops*. Larval quality was indexed by size (notochord length) and condition (lipid storage in the oil globule). Maternal effects were found for oil globule size in blue, yellowtail and gopher rockfish, for weight-specific fecundity in blue and yellowtail rockfish, and for parturition date in blue, yellowtail, and kelp rockfish. In all cases the maternal effects were similar to those reported for black rockfish, with increasing lipid provisioning of larvae, greater weight-specific fecundity, and earlier timing of parturition in the spawning season with increasing maternal age or size. No effect of maternal age or size on larval size was observed. In general, maternal effects were more evident in winter spawning species of the subgenus *Sebastosomus* (black, blue, olive, and yellowtail rockfish) than the spring spawning species of the subgenus *Pteropodus* (gopher and kelp rockfish). These results confirm that older and larger females in rockfish populations may contribute disproportionately to larval recruitment by producing higher quality larvae and more larvae per unit biomass, and releasing them at a different time than younger and smaller females. A shift in timing of parturition with female age may constitute a diversified bet-hedging strategy, providing a temporal spread of spawning effort within a maternal lineage, whereby successive female progeny release larvae at different times within the same year.

KEY WORDS: Larval quality · Lipid provisioning · Spawning timing · *Sebastes* spp.

INTRODUCTION

Maternal effects on offspring fitness are typically ascribed to non-genetic factors influencing offspring phenotypes (Mousseau & Fox 1998). For example, supplemental nutrition provided in the yolk of developing eggs can vary widely across females, with effects on offspring survival independent of offspring genotype. Likewise, maternal behavior in the timing and location of spawning can markedly affect the future success of offspring. Such effects are thought to be either a consequence of physiology, in which offspring quality directly reflects the environment and resources encountered by the mother (e.g. McCormick 2006), or an adaptive strategy, whereby females adjust some traits of offspring, depending on the environment anticipated upon release (Fox et al. 1997). Offspring size has been widely examined for the influence of

maternal effects. In teleost fishes, numerous examples exist in which larger or older females produce larger eggs compared to younger or smaller females (Hislop 1988, Roff 1992, Chambers & Leggett 1996), and larger eggs typically produce offspring with greater likelihood of survival (Marteinsdottir & Steinarsson 1998, Einum & Fleming 1999). Likewise, teleosts often exhibit a maternal effect on spawning seasonality; older or larger females may spawn earlier (Lambert 1987, Ware & Tanasichuk 1989, Schultz et al. 1991, Danylchuk & Fox 1994, Wright & Gibb 2005) or later (Gillet et al. 1995, Morgan 2003) in the season, or for batch spawners, may have a more protracted period of spawning than younger or smaller females (Hutchings & Myers 1993). However, these effects are not likely to be universal and in some cases differences may be largely attributed to experience, with first-time spawners having markedly reduced reproductive success compared to second-time spawners (Trippel 1998).

At the population level, the combined effect of potentially greater larval quality, higher fecundity, and a different temporal period of spawning underscores the importance of retaining old females in a population to ensure resilience. Here we equate resilience with the buffering effect generated by a diversity of reproduction patterns in the face of variable environmental conditions. Several recent studies suggest that the removal of older and larger fish by fishing causes greater fluctuations in recruitment of commercially harvested species compared to pre-harvest conditions (Marteinsdottir & Thorarinsson 1998, Secor 2000, Wieland et al. 2000, Berkeley et al. 2004a, Hsieh et al. 2006). These effects need to be considered in management efforts if the goal is to define sustainable harvest levels.

Rockfishes in the genus *Sebastes* are livebearers with internal fertilization. Females can store sperm for at least several months, controlling the time of fertilization and thereby the time course of development and parturition (Love et al. 2002). At parturition, larvae are 4 to 6 mm in length and the yolk sac is fully absorbed, but endogenous energy is provided in an oil globule comprised of triacylglycerol (TAG) lipids (Norton et al. 2001). The oil globule is essentially an energy-rich package that sustains an individual larva after its release from the mother. In a prior study of black rockfish *Sebastes melanops*, we found that older females produced larvae with larger oil globules than those of larvae from younger mothers (Berkeley et al. 2004b). This relationship appeared to be the functional mechanism underlying faster larval growth rates and greater resistance to starvation with increasing maternal age (Berkeley et al. 2004b). Subsequent analysis of the effect of oil reserves on larval quality has confirmed the dependence of survival in the absence of food on

initial oil globule size (Fisher et al. 2007). In addition to a maternal effect on oil globule size, black rockfish also vary in timing of parturition, with older females releasing larvae earlier in the spawning season than younger females (Bobko & Berkeley 2004). Likewise, older females have a higher weight-specific fecundity and fertilize a greater proportion of developing oocytes compared to younger females (Bobko & Berkeley 2004).

In comparisons of several rockfish species, we have found a trade-off between larval size and larval condition (as indexed by oil globule volume) that appears to reflect the season of parturition (Fisher et al. 2007). Among the California Current populations we have examined, winter-spawning species of the subgenus *Sebastosomus*, including blue, olive, yellowtail, and black rockfish, produce larvae with relatively large oil globules but small body size, whereas spring-spawning species of the subgenus *Pteropodus* (kelp and gopher rockfish) produce larvae with larger body size but smaller oil globules. Experimental tests of larval performance indicate that the higher energy reserves in large oil globules greatly enhance resistance to starvation, but larger body size has the benefits of improved growth and swimming performance. We propose that the trade-off in larval traits reflects the seasonal oceanographic environment into which larvae are released (Fisher et al. 2007).

Most *Sebastes* release only a single cohort of larvae each year (or 2 in some southern populations, Love et al. 2002). Low natural mortality rates of adults and long life spans ensure that mature females should have multiple years of reproduction during their lifetime (Leaman 1991). However, if the parturition date selected by the female (via her decision of when to fertilize her eggs) results in a poor match with environmental conditions, her full reproductive effort for that year is likely to fail. The dynamic oceanographic conditions experienced by *Sebastes* larvae in the California Current result in a high probability of recruitment failure in any given year, presumably as a consequence of poor larval survival (Hollowed et al. 1987). Thus, factors influencing the timing of parturition play an important role in population dynamics for rockfishes.

In the present study, we test for maternal effects within species for blue *Sebastes mystinus*, olive *S. serranoides*, yellowtail *S. flavidus*, gopher *S. carnatus*, and kelp *S. atrovirens* rockfish. We examine correlations between traits of female length, weight, and age to traits of larval length, larval oil globule volume, timing of parturition, and fecundity. Although not technically a maternal effect because there is no non-genetic influence on offspring phenotype, fecundity also typically increases with female size or age, both on an

absolute basis and often on a weight-specific basis. We include fecundity here to evaluate potential relationships with female age or size. Results previously described for black rockfish are included to examine the generality of the influence of maternal size or age on these larval traits and the relative strength of maternal effects between winter and spring-spawning species.

MATERIALS AND METHODS

Trait estimation. Pregnant female rockfish were collected off central California from 2003 to 2006 (Table 1). They were held singly in 575 l tanks in a flow-through seawater system maintained at 12°C (±1°C) with an ambient photoperiod. Fish were fed to satiation twice weekly with squid. Every morning tanks were checked for evidence of extruded larvae. With a few rare exceptions, parturition occurred at night, with all larvae released on a single date. The exceptions either released a small number of larvae 1 to 4 d prematurely (i.e. prior to complete yolk sac absorption and full parturition) or retained a small number of larvae in the ovaries. Following parturition, adult females were sacrificed and measured for total length and wet weight (wet wt) (ovaries removed). Ages were determined using the break and burn method for sagittal otoliths (Laidig et al. 2003). Otoliths for most of the females were examined by 2 readers and the average age was used in analysis. Across all species, age estimates by the 2 readers differed by 0 (52% of the aged females) to 4 yr (1%), with an average coefficient of variation (CV) of 4.9%. All larvae remaining in the extrusion tank were siphoned through a 200 μm sieve and preserved in 95% ethanol for subsequent fecundity analysis as described in Fisher et al. (2007). Relative or weight-specific fecundity was calculated as total fecundity/wet wt of the female after the ovaries were removed. Fecundities were not available for all females due to overflow and loss of larvae in some tanks.

For estimation of larval traits at parturition, 20 to 30 larvae were randomly selected for each female and digitally photographed under a dissecting microscope. A light anesthetic of MS-222 was used to reduce movement during image collection. Images were subsequently analyzed using the Optimas program to measure notochord length, body depth (immediately behind the gut) and oil globule diameter for individual larvae. The volume of the oil globule (an assumed sphere) was calculated from the diameter. Only images of live larvae were used for measurements to minimize problems associated with shrinkage. Some females released larvae prematurely, with yolk still remaining. Estimates of larval length and oil globule volume could not be obtained for these females. However, we were able to estimate parturition date for premature releases based on the developmental stage of the larvae.

Data analysis. For all analyses, the unit of replication was the adult female, using the mean of measurements for 20 to 30 randomly selected larvae. Larval measurements within a female were consistent, with a mean CV of 2.8% for larval length and 16.4% for oil globule diameter. The influence of maternal traits of age, total length, and gonad-free body weight on larval traits of oil globule volume, notochord length, and parturition date was assessed with stepwise general linear models (GLM), using the program Systat, version 11. This approach was used to deduce the maternal trait from among the intercorrelated traits of age, length, and weight that provided the strongest relationship with each larval trait. Because data for each species were obtained across 2 or 3 yr, the year in which the females were captured was included as a categorical variable in the model. When year was a significant factor, analysis of covariance (ANCOVA) was used to compare slopes between years. For fecundity analyses, we calculated weight-specific values (total number of larvae/female body weight) to adjust for differences in body weight across females. Data for black rockfish were previously published by Berkeley et al. (2004b) and are included in the present study to provide comparison with an additional species of *Sebastes*. Our

Table 1. *Sebastes* spp. Summary statistics (mean ± SD and range) for female rockfishes—black *S. melanops*, blue *S. mystinus*, gopher *S. carnatus*, kelp *S. atrovirens*, olive *S. serranoides*, and yellowtail *S. flavidus*—that produced larvae used in assessment of maternal effects. Black rockfish data were derived from Berkeley et al. (2004b). Date range format: mm/dd

Species	n	Total length (mm)	Weight (g)	Age (yr)	Parturition date
Black	21	430 ± 38 (372–532)	1537 ± 416 (858–2590)	8 ± 3 (5–17)	Feb 23 ± 13 d (01/27–03/21)
Blue	40	292 ± 24 (257–352)	378 ± 94 (242–674)	8 ± 4 (4–21)	Feb 9 ± 18 d (12/27–03/08)
Gopher	28	293 ± 20 (255–340)	500 ± 111 (354–792)	10 ± 3 (7–22)	Apr 22 ± 17 d (03/22–05/31)
Kelp	25	311 ± 19 (275–352)	484 ± 80 (318–634)	12 ± 5 (6–21)	May 21 ± 14 d (04/22–06/19)
Olive	9	361 ± 28 (330–415)	597 ± 170 (478–984)	6 ± 2 (4–9)	Feb 13 ± 16 d (01/16–03/09)
Yellowtail	33	439 ± 33 (373–512)	1176 ± 251 (778–1822)	15 ± 5 (8–25)	Feb 23 ± 15 d (01/16–03/20)

analyses differ from that used by Berkeley et al. (2004b) in that we include year of collection as a factor in the GLM.

RESULTS

Female traits

Experimental fish comprised a broad range of sizes, ages, and parturition dates (Table 1), except for olive rockfish, for which we had a limited sample size and no older individuals. Within each species, female length, body weight, and age were positively correlated (Table 2). Length and weight were more tightly correlated with each other ($r^2 = 0.90$ to 0.96) than either trait was with age ($r^2 = 0.46$ to 0.86). As anticipated with these intercorrelated values, no additional maternal traits were significant in the stepwise GLM models after entry of the maternal trait with the highest correlation coefficient.

Oil globule volume

Maternal effects on larval oil globule volume were evident in 4 of the 6 species (Fig. 1). For black rockfish, as noted previously by Berkeley et al. (2004b), oil globule volume was correlated with maternal age. In our re-analysis of the black rockfish data using GLM, there were no significant effects of female length, weight, or

Table 2. *Sebastes* spp. Correlations (r, coefficient of determination) among total length, gonad-free body weight, and age for adult female rockfish used in assessment of maternal effects on larval traits

Species	n	Length–weight	Length–age	Weight–age
Black	30	0.90	0.53	0.51
Blue	40	0.95	0.86	0.78
Gopher	28	0.92	0.50	0.60
Kelp	25	0.93	0.58	0.48
Olive	9	0.96	0.73	0.85
Yellowtail	33	0.94	0.56	0.46

year of capture after maternal age ($F_{1,19} = 85.34$, p < 0.001) was entered in the stepwise model. For blue rockfish, female length ($F_{1,30} = 35.24$, p < 0.001) and year of capture ($F_{1,30} = 9.86$, p = 0.004) were significant effects in the GLM model. Larger females provisioned their larvae with larger oil reserves compared to smaller females. The positive relationship was significant in both years, but the slope was higher for fish captured in 2003 than in 2004 (ANCOVA, $F_{1,29} = 4.45$, p = 0.043). For gopher rockfish, maternal age was significant in the GLM model ($F_{1,20} = 7.06$, p = 0.015), with no differences across years of capture. Oil globule volume increased with female age. This relationship was, however, influenced by the oldest female, which was 22 yr old. We did not have female gopher rockfish between the ages of 14 and 22 in our samples, limiting our comparison across this age range. For yellowtail
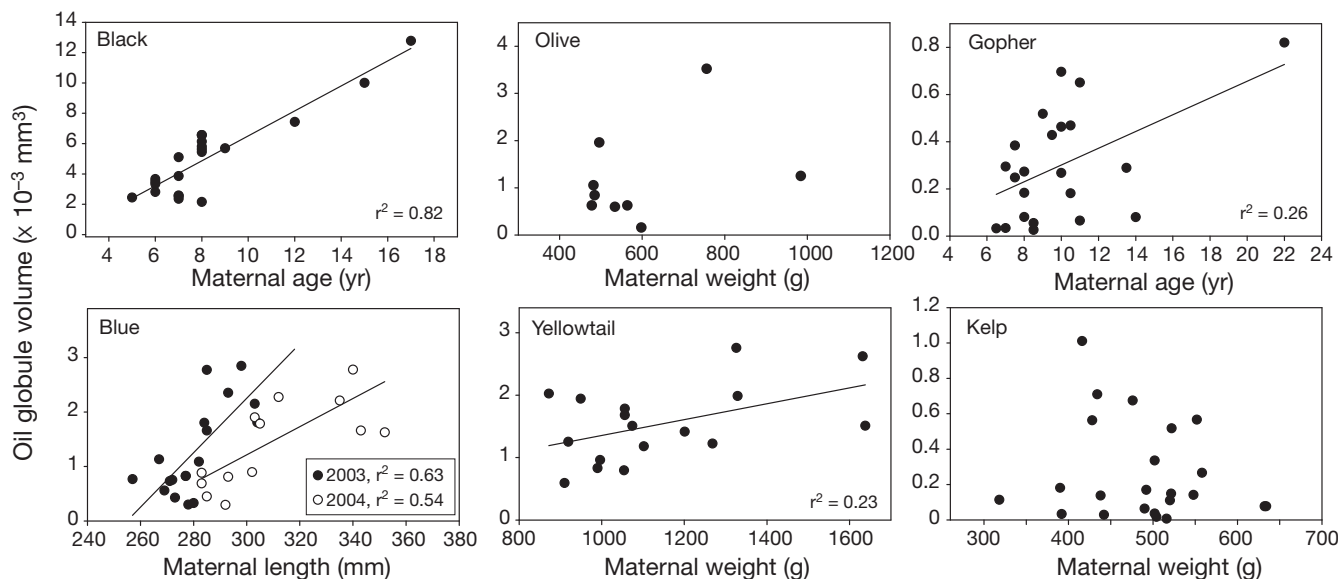

Fig. 1. *Sebastes* spp. Maternal effects on oil globule volume in 6 species of rockfishes. Plots display the maternal factor with the highest coefficient of determination based on stepwise general linear models including female age, total length, body weight, and year as available factors. Data for different years are displayed with different symbols when year was a significant factor in the general linear model (GLM) model. Regression lines and r^2 values are shown only for significant relationships

rockfish, oil globule volume was most closely related to maternal body weight ($F_{1,15}$ = 4.56, p = 0.049), with larger oil globules present in larvae from larger females. There were no differences between years for yellowtails. For kelp and olive rockfish, no maternal or year effects on oil globule volume were detected (GLM, all factors non-significant).

Notochord length

Maternal effects on notochord length were not evident for any of the 6 species (Fig. 2). Differences in length across year of capture were observed for black ($F_{2,18}$ = 6.28, p = 0.008), olive ($F_{1,7}$ = 12.01, p = 0.010), and kelp rockfish ($F_{2,20}$ = 4.84, p = 0.019). A trend of increasing larval length with increasing maternal length was suggested for olive rockfish but was not significant in the GLM due to small sample sizes and interannual differences in maternal length. Black rockfish also exhibited a trend of increasing larval length with increasing maternal age, but the effect was likewise confounded across years.

Parturition date

Maternal effects on parturition date were evident in 4 of the 6 species (Fig. 3). For black rockfish, a significant trend of earlier parturition by larger females was observed ($F_{1,19}$ = 27.36, p < 0.001), with no interannual differences. Blue rockfish likewise exhibited a trend of larger females releasing larvae earlier in the spawning season than smaller females ($F_{1,35}$ = 47.95, p < 0.001). There was a marginally non-significant effect of year in the GLM ($F_{1,35}$ = 3.88, p = 0.057). The slope of the relationship was similar between the 2 yr, but parturition was about 8 d earlier in 2004 than in 2003. Parturition dates for yellowtail rockfish were also closely related to female size, with larger females releasing larvae earlier than smaller females ($F_{1,33}$ = 34.85, p < 0.001). Parturition date was significantly different across years, with parturition about 10 d earlier in 2006 than in 2005 ($F_{1,33}$ = 7.90, p = 0.008), but the slope of the relationship did not differ between the 2 yr. For kelp rockfish there was a significant relationship of parturition date with maternal weight, again with larger females releasing larvae earlier than smaller females ($F_{1,22}$ = 6.74, p = 0.016). No interannual differences were evident for kelp rockfish. For olive and gopher rockfish, no significant maternal or year effects on parturition date were observed.

Weight-specific fecundity

Maternal effects on fecundity were evident in 2 of the 5 species examined (Fig. 4). Fecundity analysis was not conducted for black rockfish used in laboratory experiments. For blue and yellowtail rockfish, weight-
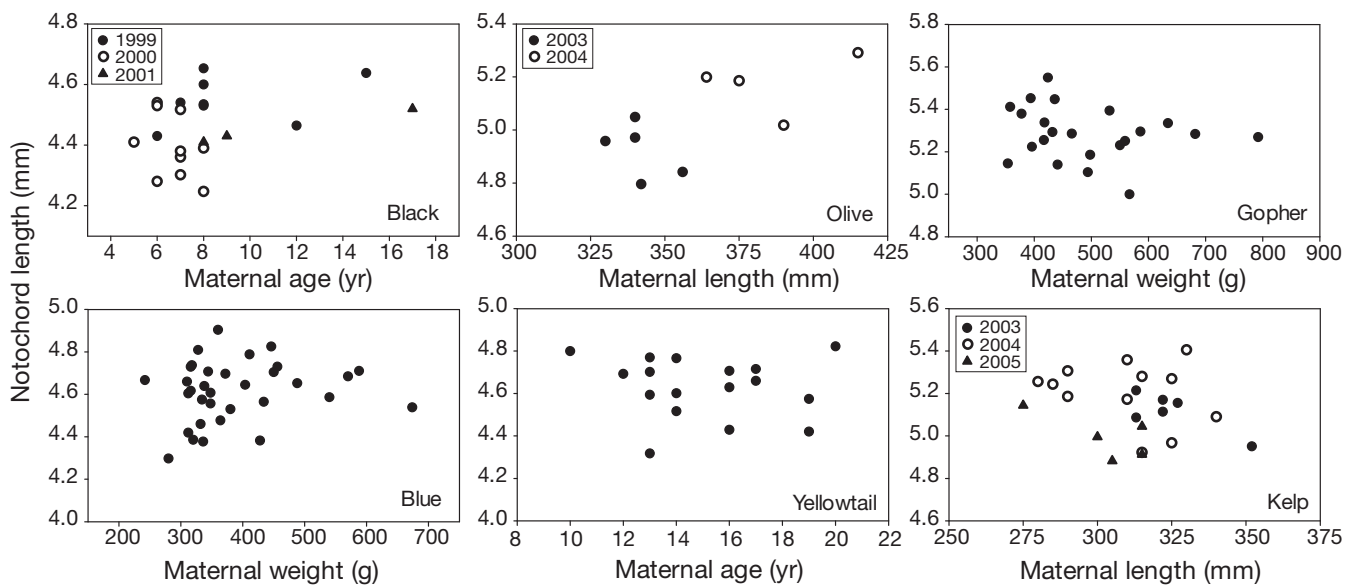

Fig. 2. *Sebastes* spp. Maternal effects on larval length in 6 species of rockfishes. Plots display the maternal factor with the highest coefficient of determination based on stepwise general linear models including female age, total length, body weight, and year as available factors. Data for different years are displayed with different symbols when year was a significant factor in the GLM model. None of the maternal factors of age, total length or body weight was significantly correlated with larval length in the models
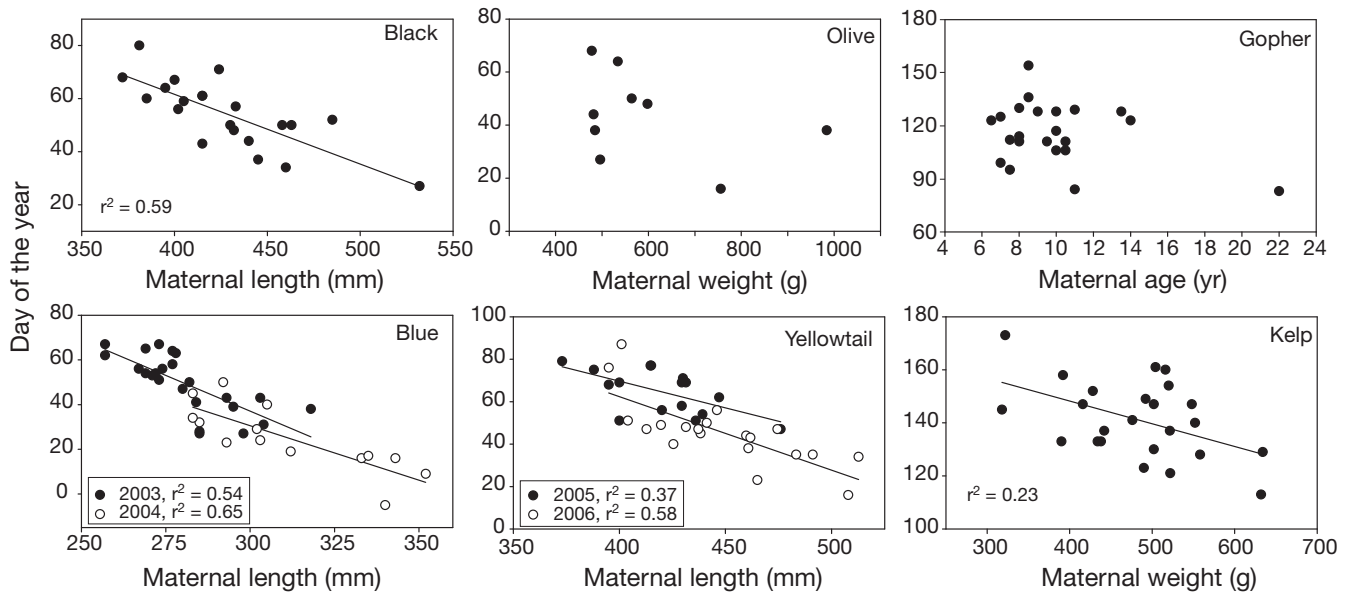
Fig. 3. *Sebastes* spp. Maternal effects on parturition date (day of the year) in 6 species of rockfishes. Plots display the maternal factor with the highest coefficient of determination based on stepwise general linear models including female age, total length, body weight, and year as available factors. Data for different years are displayed with different symbols when year was a significant factor in the GLM model. Regression lines and r^2 values are shown only for significant relationships

specific fecundity increased with maternal length (blue: $F_{1,15} = 11.18$, p = 0.004; yellowtail: $F_{1,16} = 8.81$, p = 0.009) and did not differ across years. Fecundity in olive rockfish differed across years ($F_{1,5} = 26.91$, p = 0.003), but was not related to female age or size. However, size was confounded by year in this species and

the sample size was small, preventing a robust analysis of the fecundity relationship. In gopher and kelp rockfish, no significant maternal or year effects were observed. In gopher rockfish, a positive relationship of fecundity with maternal size was suggested, but the largest female in our samples was a clear outlier
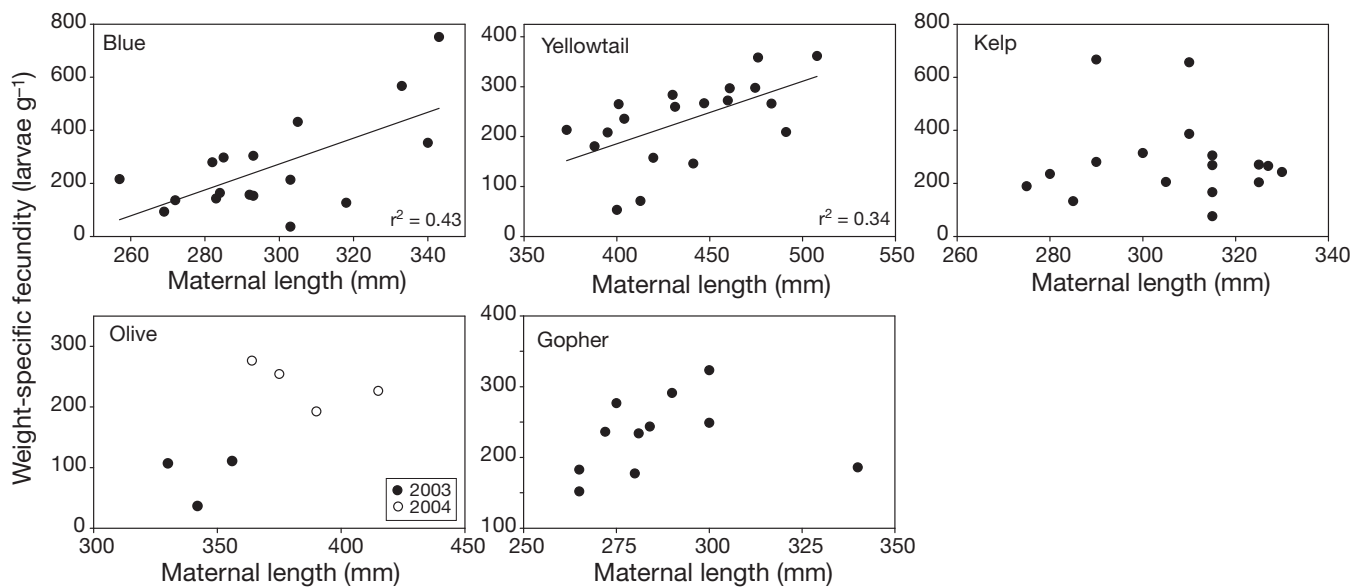

Fig. 4. *Sebastes* spp. Maternal effects on weight-specific fecundity (larvae per g of maternal weight) in 5 species of rockfishes. Plots display the maternal factor with the highest coefficient of determination based on stepwise general linear models including female age, total length and year as available factors. Data for different years are displayed with different symbols when year was a significant factor in the GLM model. Regression lines and r^2 values are shown only for significant relationships. Fecundity data were not available for black rockfish

with low fecundity. In kelp rockfish, 2 medium-size females had extremely high fecundities compared to all others.

Relative strength of maternal effects

To compare the degree of influence of maternal age or size on larval traits among species, we examined the r for regressions with each larval trait, using the maternal trait with the highest r^2 value from the GLM models after incorporation of a year effect if it was significant. For interactions with no significant maternal effects in the GLM analysis, we used r from simple linear regressions with the maternal factor producing the lowest p value (as depicted in Figs. 1–4). There was a clear trend for maternal effects to be stronger for species releasing larvae in the winter compared to those releasing larvae in the spring (Fig. 5).

DISCUSSION

Maternal effects were evident for larval traits of oil globule volume, parturition date, and weight-specific fecundity. For each significant relationship, the trend was the same in direction, with older or larger females producing larvae with larger oil globules, releasing larvae earlier in the spawning season, and producing more larvae per gram body weight than smaller or younger females. Although fecundity was not measured for the black rockfish females used in experi-
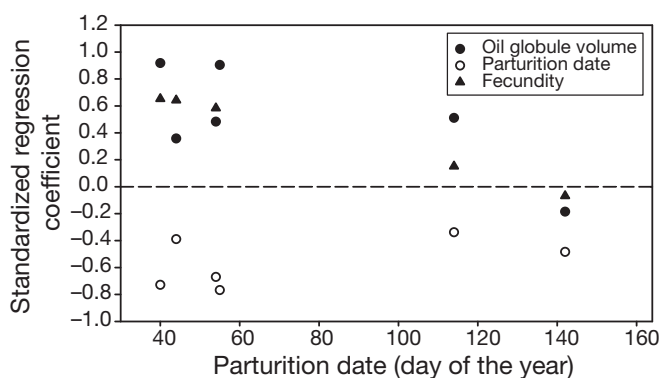

Fig. 5. *Sebastes* spp. Standardized coefficients for 4 winter-spawning (black, blue, olive, and yellowtail) and 2 spring-spawning (gopher and kelp) species for regressions of larval traits on maternal size or age versus average date of parturition in laboratory experiments. Plots used the maternal factor (length, weight, or age) resulting in the highest correlation, regardless of statistical significance. Fecundity data were not available for black rockfish used in experiments. Larval length data were not included because all maternal relationships were non-significant

ments by Berkeley et al. (2004b), a comprehensive study of this species confirmed that weight-specific fecundity increases with female age (Bobko & Berkeley 2004). Widow rockfish *Sebastes entomelas* also exhibit increased relative fecundity with female age (Boehlert et al. 1982). Our results suggest a generality to these patterns of maternal effects across different species of *Sebastes*, although the expression of age- or size-dependent effects appeared to be more consistent for winter-spawning species of the subgenus *Sebastosomus* (black, blue, yellowtail, and olive rockfish) than the spring-spawning species of the subgenus *Pteropodus* (gopher and kelp rockfish). Future comparisons in other genera of *Sebastes* are needed to resolve this apparent confounding of spawning season and phylogeny in the degree of importance of maternal age or size on larval traits.

The experiments were limited in some cases by our ability to capture pregnant females in a range of sizes and ages. We had only a small sample of olive rockfish, all relatively young. Trends suggestive of maternal effects in this species may be confirmed by examination of older females. Likewise, some trends in gopher rockfish were influenced by a single female that was much older (22 yr) than the others and need to be confirmed with a more even age distribution. We do not know how laboratory conditions or time in captivity might have influenced the larval traits we measured. Females in our experiments were held in aquaria for 1 to 94 d prior to parturition. Based on a gestation period of 30 to 50 d, about half would have already fertilized their eggs prior to capture. Because most fish were captured prior to the spawning season, there is necessarily a correlation between time in captivity and parturition date. However, in the study of black rockfish conducted by Bobko & Berkeley (2004), females were sampled from the recreational fishery throughout the reproductive season. A total of 1643 females were examined and a clear trend of earlier parturition date with female age was observed. This pattern documents age-dependent parturition timing in an undisturbed rockfish population.

We did not observe clear maternal effects on larval size (although trends suggested a positive relationship of larval length with female age/size in black and olive rockfish). Larval length at parturition appears to be a more conservative trait than the size of the oil globule. Although there were significant differences in larval length among the species of *Sebastes* we have examined (Fisher et al. 2007), within-species CV for larval length ranged from 2.8 % (kelp rockfish) to 3.3 % (olive rockfish) for the mean values we calculated for each female in this study. In contrast, CV for oil globule volume ranged from 40 % (yellowtail rockfish) to 106 % (kelp rockfish). These differences suggest a greater

potential for maternal effects to be expressed in larval condition rather than larval size. Similar results were obtained for the damselfish *Pomacentrus amboinensis*; egg condition, as indexed by lipid reserves, varied across different maternal feeding regimes, but egg size remained constant (Gagliano & McCormick 2007).

A maternal effect on parturition timing occurred in 4 of the 6 species, with larvae released earlier in the season as females increased in size. Larger darkblotched rockfish *Sebastes crameri* also spawn earlier in the season compared to smaller females (Nichol & Pikitch 1994). This pattern suggests that individual females shift their timing of spawning as they get older and larger. Is this shift a consequence of physiology, with older, larger females better prepared to initiate egg development early in the season compared to younger females? Or is it an adaptive strategy in which long-lived females alter the timing of parturition across their life span? If the latter, such a strategy could be an example of diversified bet hedging (Philippi & Seger 1989). For broadcast spawners, temporal variability in environmental conditions can be countered by releasing larvae in many batches across an extended time period. Rockfish, however, are constrained to a single parturition date each year (or 2 in some southern populations, Love et al. 2002), thus prohibiting a contemporaneous bet-hedging strategy of spreading larval production across a spawning season. With overlapping generations, a sequential shift in parturition date with age will provide a spread in intra-annual timing across a maternal family lineage. As long as some female descendants survive, an age- or size-dependent timing of parturition will ensure that the maternal lineage as a whole releases larvae over a broad span of the reproductive season, increasing the probability of success for some females in the family.

Alternatively, all females in a population may respond to environmental cues and simultaneously initiate the physiological sequences associated with reproduction, but larger and more experienced females are able to complete the process earlier, resulting in earlier fertilization and parturition. If physiological preparedness delays parturition by younger, smaller females, we might expect to see more variable timing by older females, who could presumably be more selective of when they release larvae. In this case we should see a wedge-shaped distribution of spawning dates, with young fish spawning late and old fish spawning throughout the season. Instead, those species with a maternal effect on parturition timing exhibited linear declines in spawning date with female size (Fig. 3). Further experimental studies can potentially distinguish between the 2 alternative hypotheses for age-dependent trends in reproductive timing. Cargnelli & Neff (2006) propose that both energetic constraints and adaptive behavior operate in the timing of reproduction for bluegill sunfish.

A maternal influence of age or size was also evident in the larval oil globule volume of 4 of the 6 *Sebastes* species. Why would females differ in lipid provisioning of their larvae? The size of the oil globule has a clear correspondence with resistance to starvation (Berkeley et al. 2004b, Fisher et al. 2007). Across all of the rockfish species we have tested in laboratory experiments, our survival index (time to 75% mortality in the absence of food) ranged from 2 to 14 d and survival was closely correlated with oil globule volume (power function for all species combined, $r^2 = 0.77$). Larger oil globules also were also associated with 3 to 4 times faster growth rates in black rockfish larvae (Berkeley et al. 2004b), although growth effects were less evident in other species (Fisher et al. 2007). Because of the negative correlation of female age or size with parturition date, larvae produced late in the spawning season generally had lower lipid reserves. For *Sebastes* species residing in the California Current, we have hypothesized that winter spawners produce larvae with large oil globules to improve starvation resistance under the food-poor, low production conditions experienced at that time of year (Roesler & Chelton 1987), whereas spring spawners sacrifice lipid reserves to produce larvae with larger body size and improved growth and swimming performance, a strategy more appropriate for post-upwelling, high productivity oceanographic conditions (Fisher et al. 2007). It is possible that changing environmental conditions across the spawning season influences the allocation strategy within a species. However, we did not observe a trade-off between larval size and oil globule size within species, suggesting that younger or smaller females were not producing larger larvae instead of better-provisioned larvae.

Alternatively, a trade-off between oil globule size and fecundity could drive the observed trends. Older and larger females clearly have far greater resources available for reproduction compared to young females, with not only higher absolute fecundity but often higher weight-specific fecundity as well. In dynamic ecosystems such as the California Current, the probability of larval survival can be strongly influenced by transport processes (Shanks & Eckert 2005). This physical limitation to successful recruitment operates regardless of larval quality and may set a lower bound for fecundity, thereby increasing the probability that at least some larvae will be transported to the appropriate juvenile nursery habitat (Hill 1991). For young, resource-limited females, a constraint of a minimum fecundity to offset advective losses and a trade-off of fecundity with larval condition may be more evident than in larger females. Thus, the overall balance of fecundity, larval size, larval condition, and timing of parturition may shift as females age.

CONCLUSIONS

Although maternal effects were expressed somewhat differently across the different species and varied in their degree of expression, it seems clear that some kind of maternal effect on larval quantity, quality or extrusion time is prevalent across a range of rockfish species. As females grow older and larger, they are presumably able to invest proportionately more energy into reproduction and produce greater relative numbers of larvae, which are often also of higher quality. Furthermore, by releasing larvae on an age-dependent temporal schedule, females spread the reproductive effort of their maternal lineage across the spawning season. The importance of maternal size and/or age to a suite of critical reproductive traits in these fishes suggests that the removal of older and/or larger females from a local population may have disproportionately detrimental consequences for total larval survival and subsequent recruitment.

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