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Using life history characteristics to determine optimum placement of marine reserves

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The purpose of this study is to use rockfish life history and reproductive dynamics to determine marine reserve locations to protect the species that demonstrate age-related differences in parturition timing or quality of larvae produced. These long-lived species are extremely vulnerable to overfishing because of their slow population growth rates and late ages at reproduction. Several species of California rockfish are currently in overfished status. Previous research by the principal investigator has demonstrated that in a number of nearshore rockfish species, older females spawn earlier in the season and produce larvae with characteristics that are more likely to survive (Berkeley et al. 2004). Evidence of similar age-related patterns in spawning seasonality and progeny quality has been observed in a diverse range of teleost species. Because even moderate rates of fishing rapidly eliminate older fish from the population, the burden of reproduction is shifted to younger and younger fish. Elimination of older age classes would effectively shorten the parturition season and eliminate reproductive output from the early part of the spawning season. As a consequence, the likelihood of larval production matching peak plankton production will be reduced (the match-mismatch hypothesis; Cushing 1969, 1990). Fish species that display these "maternal age effects" are most likely to benefit from the protection offered by marine reserves, where no fishing is allowed and the population ages naturally, creating a higher percentage of older individuals.

The objective of current west coast groundfish management is to maintain a target level of spawning biomass (usually 40% of the level that would exist without fishing), without regard to the age structure of fish comprising that spawning biomass. If our results are broadly applicable to other species, then changes in the age composition of the spawning stock, despite the maintenance of harvesting within these target fishing mortality levels, have the potential to reduce recruitment or make it much more variable.

In this study, our objective is to determine if some of the more commercially important deeper water species exhibit similar maternal effects to those found in shallow water species. Specifically, we are measuring the timing of parturition and the amount larval oil globule reserves (an energy supply that effects the probability of survival by buffering starvation) in several rockfish species caught from central California to northern Oregon, and inhabiting nearshore, continental shelf and continental slope habitats. Using these results we will make recommendations on the relative importance of protecting population age structure for each of these species. Results will be analyzed by general life history type, which should allow us to infer the likelihood of observing similar maternal age effects in other species of rockfish.

Species Collected

During a two-year period, we collected mature females of several species off California and Oregon (Table 1). The fish were collected both through focused research charters and by sampling the commercial trawl fishery. Age-specific patterns in parturition timing are difficult to observe because rockfishes tend to have protracted spawning seasons, with individuals reaching parturition over a period of two or three months, requiring large sample sizes throughout the season. We sampled adult female fish for larvae and fertilized eggs, otoliths to determine age, length, weight, liver weight (an index of energy reserves) and developmental stage of the ovary. We then took calibrated photographs of larvae through a dissecting scope to measure oil globule volume and to create an index of the yolk utilization rate during gestation. Maternal age was determined from the otoliths.

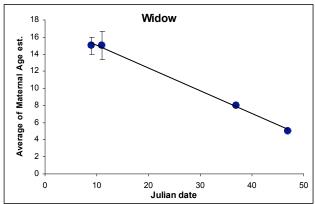
Species	Number of adult females
Aurora rockfish (Sebastes aurora)	26
Chilipepper rockfish (S. goodei)	369
Darkblotched rockfish (S. crameri)	155
Greenstriped rockfish (S. elongatus)	38
Olive rockfish (S. serranoides)	12
Pacific ocean perch (S. alutus)	400
Widow rockfish (S. entomelas)	94
Yellowtail rockfish (S. flavidus)	191
Total	1,285

Table 1. Numbers of female rockfish collected in 2005-2007.

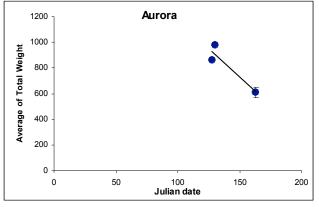
Temporal Patterns in Parturition

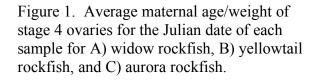
Previous research on black rockfish (a live bearer as are all *Sebastes* spp) established that older fish extrude larvae earlier in the season than younger fish (Bobko and Berkeley 2004), and that these larvae may contribute disproportionately to the subsequent year class (Bobko, 2001). In 1996, larval extrusion along the central Oregon coast occurred from the third week of January through the second week in March, and the youngest fish extruded larvae mostly at the end of the season. However, most survivors in the young of the year black rockfish were born earlier in the season when most of the spawning output was from the older fish.

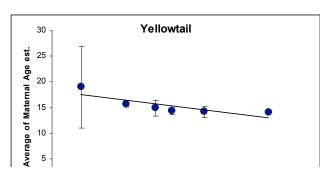
Preliminary results of temporal patterns in parturition in our eight study species suggest widow, yellowtail and possibly aurora rockfishes exhibit a reproductive development pattern where older (or larger) rockfish give birth earlier in the spawning season than younger fish (Figure 1). This is indexed using the mean age of stage 4 fish on any given sampling day. Stage 4 is the last stage prior to release of larvae. The mean age of mothers was highest early in the spawning season and decreased as the season progressed and younger fish reached that stage. Widow rockfish show the strongest trend (Figure 1a). A similar, but more variable pattern is seen in yellowtail rockfish (Figure 1b) and in aurora rockfish (although based on few fish, Figure 1c). In years when food becomes available early, larvae from these older fish would be present to take advantage of it, whereas younger fish would not produce larvae until later in the year when food supplies have diminished and predators are more abundant.

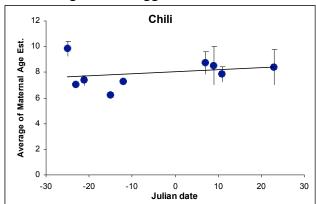


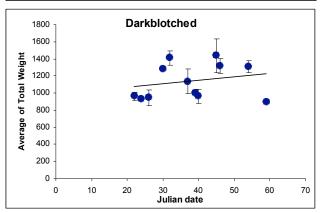
species would benefit less from a natural age structure than the other species we are studying. These results are equivocal, though, because the population of chilipepper rockfish is currently dominated by a single year class (currently age 7) and finding older or younger fish has proven difficult. We were unable to collect significant sample sizes spanning the reproductive season for greenstriped, and olive rockfish, and no strong trend was evident in the samples we obtained. In addition, these data do











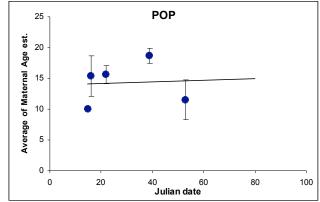


Figure 2. Average maternal age/weight of stage 4 ovaries for the Julian date of each sample for A) chilipepper rockfish, B) darkblotched rockfish and C) Pacific ocean perch.

not exclude other maternal age effects, only parturition timing. These findings of age-modulated timing in parturition

In contrast, chilipepper rockfish, Pacific ocean perch, and darkblotched rockfish do not demonstrate this pattern (Figure 2). The lack of a maternal age effect suggests these

suggest that widow, yellowtail, and aurora rockfish are strong candidates for marine reserves designed and sited to protect their adult habitats so that older age classes rebuild as productivity buffers for variable timing of larval food production.

Larval Quality

In an earlier series of laboratory experiments testing the performance of larvae from different females, larvae from the oldest females grew more than three times as fast as those from the youngest females and survived starvation more than twice as long (Berkeley et al. 2004). These relationships suggest that larvae of older females are much more likely to survive in a broader range of environmental conditions than those of younger fish, providing a logical explanation for the observations in the field of higher juvenile recruitment for older females. In addition to the higher larval quality and temporal spawning benefits of older females, they also found no tradeoff between larval quality and fecundity or larval size; older females had higher absolute and relative fecundity than younger fish.

The species we are working with in the present study are found only in deep water, and almost all die from decompression injuries when brought to the surface. It is currently not possible to collect them alive once pregnant, transport them to the laboratory and allow them to spawn in captivity. Samples must be collected from pregnant females immediately upon capture. Because the size of the oil globule changes during the period of larval development, we are developing a method to predict oil globule size at birth from the ratio of oil globule to yolk area in developing larvae (Figure 3). All estimates are thereby standardized to status at birth, when yolk is finally depleted. We can then compare oil globule size among larvae from females of different ages that were sampled at different times.



Figure 3. Photomicrographs of early and late stage chilipepper larvae illustrating the relative change in yolk and oil droplet volume during development.

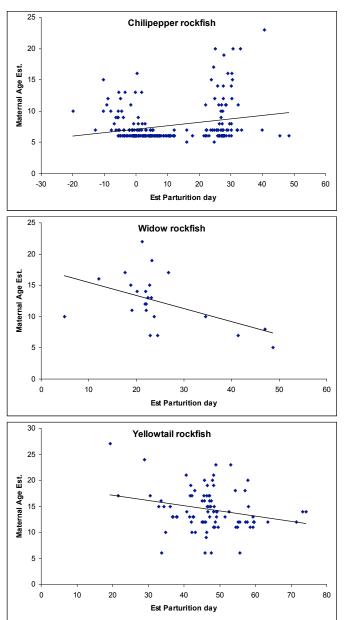


Figure 4. Estimated parturition dates for female rockfishes based on 100% depletion of yolk at parturition date. A) chilipepper rockfish, B) widow rockfish C) yellowtail rockfish

We determined the rate of yolk depletion by comparing chilipepper rockfish larvae at a known developmental stage to the same stage described in Eldridge et al. (2002), and calculated the utilization rate to achieve 100% depletion by parturition. We determined the depletion rate for chilipepper, yellowtail and widow rockfish. Using this method, we

were able to show that expected parturition dates for older females were earlier than for younger fish based on larval yolk depletion status, confirming what we observed from a macroscopic evaluation of ovary development (Figure 4).

The rate of yolk depletion was then applied to the oil droplet volume to scale it to the volume remaining at birth (Figure 4). For chilipepper rockfish, where many of the fish were age 6, we generated an expected distribution for oil droplet volume at birth for a single age group, which indicated that almost all of the oil globule is utilized by parturition, confirming the results of Eldridge et al (2002).

There was no relationship detected between oil globule volume at birth and maternal liver weight or total weight for the chilipepper rockfish but both widow rockfish and yellowtail rockfish showed a positive relationship, suggesting that higher

maternal energy reserves may translate into larger oil droplets for larvae (Figure 5).

Although widow and yellowtail rockfish showed earlier development and parturition dates for older females, there was no clear relationship between maternal age and the amount of estimated oil droplet remaining in larvae at birth (Figure 6). However, there

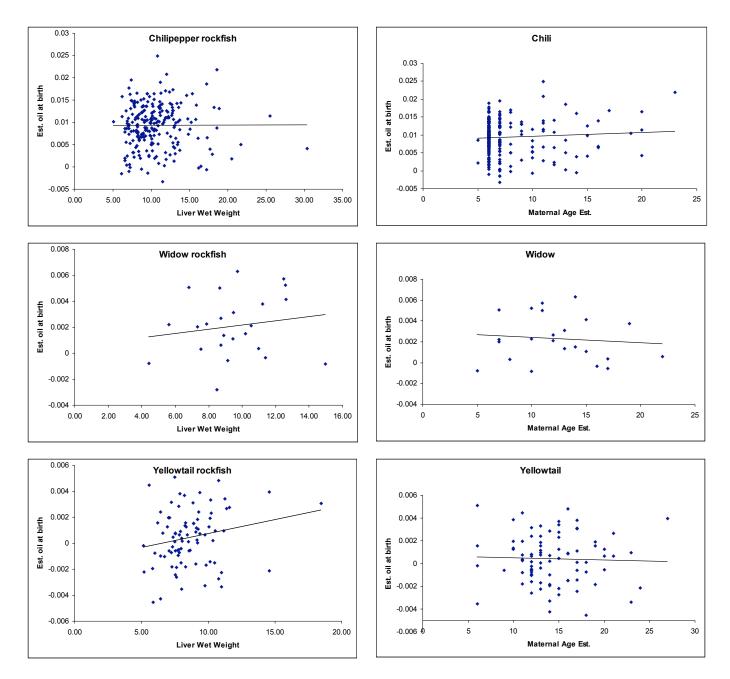


Figure 5. Relationship between liver weight and estimated oil droplet volume at birth for A) chilipepper rockfish, B) widow rockfish, and C) yellowtail rockfish.

Figure 6. Relationship between maternal age and estimated oil droplet volume at birth for A) chilipepper rockfish, B) widow rockfish, and C) yellowtail rockfish.

are still other potential mechanisms for maternal age or condition to effect larval quality not tested in this project. For example, larvae with larger energy stores may not need to utilize all of their yolk supply by parturition. This would be a mechanism that explains the longer times to starvation in higher quality larvae.

In summary, our data show that the pattern of older rockfish releasing larvae earlier in the spawning season occurs in other species of rockfish on both the continental shelf and slope, but that oil droplet volumes at birth may not be the functional link to enhanced

survival for all species. In addition, age-modulated parturition does not appear to be generalizable to all *Sebastes* species. The species showing this temporal pattern are not closely related phylogenetically, so the evolutionary pressure to develop this mechanism is likely the particular environmental conditions that encourage early parturition. To maintain the natural timing of spawning in these species, the natural age structure must be maintained. For Sebastes species, this means significantly less mortality on older fish, which is best accomplished through a network of appropriately sited and scaled marine reserves. To protect species showing maternal age effects in this study, new habitat types on the continental shelf and slope would need long-term protection. To date, this habitat has been only partially protected through rockfish conservation areas banning bottom trawl ,and to some degree, fixed gear. However, it does not restrict midwater trawl, or other methods that encounter these species of rockfish. This will be a challenge for some more broadly distributed and semi-pelagic species like widow rockfish, or species like aurora rockfish, which co-occur with other species of targeted rockfish and flatfishes. Failure to account for the differential recruitment success of older mothers could result in more variable recruitment and the inability to adequately model stock dynamics.

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