

Structural complexity in relation to the habitat preferences, territoriality, and hatchery rearing of juvenile China rockfish (*Sebastes nebulosus*)

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Abstract Conservation efforts require an understanding of the basic behavior and ecology of target species. However, limited information exists for a wide range of taxa, including declining species of rockfish (genus *Sebastes*). First, we observed captive juvenile China rockfish (*S. nebulosus*) to determine how they interact with their environment and conspecifics. Juveniles exhibited site fidelity and territoriality. These aggressive interactions occurred within the context of size-biased dominance, centered on competition for structurally complex habitat. Given the apparent importance of structure and the absence of structure in typical hatchery environments, we then asked how the absence of structure affects future behavior. When barren-reared and structure-reared juveniles were combined into a structurally complex aquarium, barren-reared fish displayed less structure use and less site fidelity than structure-reared fish. However, after 1 to 2 weeks, barren-reared fish began to use structure and showed site fidelity that eventually equaled that of structure-reared juveniles, showing that those behavioral effects of the rearing environment were not permanent. Though these short-term effects may still impact survival after

hatchery release, we were unable to detect significant effects on vulnerability to a predator (lingcod, *Ophiodon elongatus*) in laboratory trials.

Keywords Stock enhancement · Conservation hatchery · Predation risk · Rearing effects

Introduction

Rockfishes of the genus *Sebastes* are economically important for commercial and recreational fisheries (Parker et al. 2000). However, long life spans and delayed sexual maturity in many species make them vulnerable to overfishing; many populations have declined in recent decades (Levin et al. 2006; Parker et al. 2000). Declining populations have prompted programs aimed at protecting and bolstering wild stock (Parker et al. 2000). Whether those efforts involve the preservation (Soh et al. 1998) or creation (West et al. 1994) of critical habitat, or intentional release of hatchery fish (e.g., Murakami et al. 2005), knowledge of basic behavior is crucial (Curio 1996; Kramer and Chapman 1999).

We used aquarium observations to learn how juvenile China rockfish might interact with their environment and conspecifics in the wild. Captive observations can provide insight into fishes that may be difficult to observe in nature and can generate predictions about wild behavior that can be tested in the field. Aquarium work also allows for controlled

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experiments and replication that would be difficult in the wild.

Knowledge about site fidelity is important for hatcheries that release juveniles into nature to bolster wild populations (stock enhancement), since monitoring methods will differ depending on whether juveniles are site-faithful or mobile. For the establishment of protected areas (Lea et al. 1999), knowledge about site fidelity is important since refuge size for mobile juveniles will differ from that for a site-faithful species (Kramer and Chapman 1999). We tested whether juvenile China rockfish would display site fidelity in aquaria.

Adult China rockfish defend territories from conspecifics (Love et al. 2002). We tested whether juveniles can also show territorial behavior; these data would enable the prediction of how they establish spatial relationships with each other in nature (Brown and Orians 1970). See Hoelzer (1987; 1988) for observations of early aggression and site fidelity in two other rockfish species. Understanding mechanisms of competition enables the prediction of which individuals will have an advantage in obtaining resources (e.g., Brown et al. 2005; Nakano 1995). We tested whether relative or absolute body size predicted access to resources.

Juveniles of many rockfish species are associated with structure, including rock, sponges, seagrass, and kelp (Dean et al. 2000; Freese and Wing 2003; Nelson 2001). Wild juvenile China rockfish are also associated with structured habitats (NMFS Game ADoFa, Council NPFM 1998), but it is unknown if this reflects random preference followed by differential survival, or habitat preferences (e.g., Tolimieri 1995; Tupper and Boutilier 1995). Habitat preference data can aid hatchery releases by identifying areas that are likely to attract and retain juveniles. We tested for juvenile habitat preferences in aquaria.

We investigated how rearing in relatively barren hatchery environments might affect the habitat use and site fidelity of fish reared for release into the wild. When we found differences, we used predation trials to test whether these effects would influence predation rates.

Methods

In April 2006, a female was stripped of her offspring. Young fish were put into a mesocosm bag and supplied with wild zooplankton, cultured rotifers,

and enriched *Artemia*. Fish were transferred to a land-based tank in August 2006.

Experiment 1—site fidelity, territoriality, dominance, and habitat preference

Experiment 1 tested the following hypotheses: 1) juveniles display site fidelity, 2) juveniles are territorial, 3) territoriality occurs within the context of size-biased dominance, 4) juveniles prefer structured over barren environments. On 17 and 18 October 2006, juveniles were tagged on each side with an individually identifiable spot of color (Northwest Marine Technology, Tumwater, Washington, USA) and transferred to 20 110-L aquaria (76 cm×48 cm×32 cm) at a density of six juveniles per aquarium. The aquaria were arranged in two rows, one row on each side of a 9.0-m by 1.5-m flume that served as a water bath. Fish could not see fish in neighboring tanks because the back and two sides of each aquarium were opaque. The aquaria were allocated to structural and social treatments. The structural treatments were ‘structured’ and ‘barren’. Structured aquaria contained four rocks (8 cm diameter) with plastic plants tied to two of those rocks. One 1.9-cm diameter vertical PVC pipe extended 19 cm into the water, delivering water into the aquarium at a rate of 1.4 L m⁻¹, and at the other end of the aquarium, another vertical pipe (2.5-cm diameter) extended 19 cm into the water and served as a siphon to equalize water levels inside and outside of the tank (38 cm water height). Barren aquaria were identical to structured aquaria except the rocks and plastic plants were absent. Structural treatments were crossed with social treatments—size-segregated and size-integrated. All fish within a tank were equal in standard length (size-segregated) or different in standard length (size-integrated). Five aquaria were allotted to each treatment: a) barren, size-segregated, b) barren, size-integrated, c) structured, size-segregated, and d) structured, size-integrated (Table 1). Treatments were distributed randomly within the flume. Fish were fed dry commercial salmon diet once per day, 5 days per week, ad libitum.

We conducted 15 min observations on each aquarium 1, 2, and 4 weeks after stocking. Observations were made from behind a blind; the only light in the room emanated from the aquaria.

We recorded the location where each individual spent the majority of its time in each 5 min period

Table 1 Standard length (mm) of each fish in each aquarium

	Size-integrated	Size-segregated
Structured	44, 47, 48, 49, 50, 52	All six fish 44
	44, 46, 47, 48, 49, 51	All six fish 46
	45, 47, 48, 49, 51, 52	All six fish 48
	45, 47, 48, 49, 50, 52	All six fish 50
	44, 47, 48, 49, 50, 51	All six fish 52
Barren	44, 47, 48, 49, 50, 52	All six fish 45
	44, 46, 47, 48, 49, 51	All six fish 47
	43, 48, 49, 50, 51, 52	All six fish 49
	42, 46, 48, 49, 50, 51	All six fish 51
	44, 46, 47, 48, 49, 50	All six fish 52

Under each column (size-integrated or size-segregated), each row represents a single aquarium that contains six fish. Twenty aquaria were divided among the four treatments

(0–5, 5–10, and 10–15 min). In barren aquaria, individuals could be at any one of ten locations. Aquaria were visually divided into four equal-sized sections from left to right, and two equal-sized sections from front to back (totaling eight sections). When fish were within 1 cm of either PVC pipe, we recorded the fish as being at the ‘inflow’ or ‘outflow’ pipe (total: 10 sections). We used the same methods in structured aquaria, except we also recorded whether the fish was within 1 cm of rocks or plants. In the final 10 min of each observation, we noted the location of any aggressive interactions and the identity of the aggressor and victim. Fish were weighed with a digital scale to the nearest 0.1 g and measured for standard length to the nearest 1 mm upon stocking into the 110-L aquaria.

Experiment 2—hatchery effects on future behavior

Experiment 2 tested the hypothesis that the absence of structure early in life reduces future structure use. On 14 February 2007, all fish from Experiment 1 were removed from the 20 110-L aquaria. Rocks and plants were removed from structured aquaria. Four rocks and two plants were then added to each of 16 110-L aquaria, along with fish from the previous experiment, following three criteria. 1) Each aquarium received one fish from each rearing treatment. 2) We removed variance caused by size-biased dominance by equalizing body length within each aquarium. 3) To prevent prior residence effects, no fish was returned to its aquarium from the previous experiment. Locations of the rocks and plants also differed from their locations in the previous experiment.

A 5-min observation on each aquarium was conducted every 3 or 4 days between 16 February 2007 and 8 March 2007 (total of seven observation days). We recorded the location where each fish spent the majority of its time.

Experiment 3—predation trials

Experiment 3 tested the hypothesis that the rearing environment affects predation rates after release. On 2 November 2006 we stocked 6 208-L rearing aquaria (123 cm×52 cm×33 cm), each with 22 China rockfish. Aquarium walls were opaque. Water entered through one PVC pipe at one end of the aquarium and exited through another pipe at the other end. Three aquaria were barren; the other three each had five rocks and four 28-cm plastic plants anchored to two 58-cm by 6-cm plastic planks. Fish were fed three times per day with dry commercial salmon diet.

Predation trials occurred in two 4.6-m diameter tanks, filled to a 30-cm depth. Each tank contained two rock piles that each consisted of two plants, two large rocks (each approximately 25 cm by 18 cm), and approximately 15 smaller rocks (each approximately 5 cm by 5 cm). Each pile had crevices large enough for the juvenile rockfish, but not the predator, to enter. Rock piles were placed 0.75 m apart from one another, 0.5 m from the aquarium wall. One half of a PVC pipe (25 cm diameter, 30 cm long, split lengthwise) was placed near the center of the tank, creating an arch under which lingcod could hide.

On 17 April 2007 at 10:00, two barren-reared and two structure-reared juveniles were transferred from the 208-L rearing aquaria to a predation-trial tank. Standard lengths were recorded to enable identification by size. At 15:00, one hatchery-reared lingcod (*Ophiodon elongatus*) was added to the aquarium (nine lingcod were used, range: 23 to 29 cm standard length). The next day at 09:00, the lingcod was removed and the survivors were identified. In future trials, if no fish were eaten, we still removed the lingcod but then added a different lingcod at 15:00.

Data analysis

Experiment 1

Site fidelity To determine whether fish were site faithful, we calculated the number of times individu-

als were spotted in the same location between consecutive observation-days. For both structured and barren treatments, we averaged scores across individuals in each aquarium to create an ‘aquarium score’ and used *t*-tests to determine if scores in each treatment differed from the score expected if fish were randomly placing themselves. A greater-than-random score would indicate site fidelity.

Territoriality A binomial test determined whether aggressive interactions were initiated more frequently by the resident than by the intruder. We define the area in which a fish spends the majority of its time as its ‘station,’ while a ‘territory’ is a station that is defended against conspecifics (Brown and Orians 1970). If juveniles are territorial, then aggressive interactions at a station should be initiated by the resident more often than by the intruder.

Size-biased dominance If aggressive interactions are structured by size-biased dominance, then larger individuals in size-integrated aquaria should more frequently give than receive aggression, while smaller individuals should show the opposite pattern. Because a mixed model ANOVA found no effect of the aquarium (random effect) but found an effect of body size rank (fixed effect) on the number of times aggression was given versus received, we calculated a Spearman rank-order correlation coefficient to further explore the relationship between body size rank and aggression. A significant positive relationship would indicate that larger individuals give more aggression than they receive, while smaller individuals follow the opposite pattern.

When we detected an effect of body size rank in size-integrated aquaria, we conducted another analysis on size-segregated aquaria. If effects of body size rank on aggression are due to absolute size, then aquaria with only large individuals should display more aggression than aquaria with only small individuals. If effects are due only to relative size (e.g., an individual will be more aggressive if it is the biggest fish in the group), then this relationship should not exist. We used ANCOVA to test for a relationship between fish size (covariate) and the number of aggressive interactions among size-segregated aquaria, while also testing for the main effect of the structural treatment (barren or structured).

Size-biased aggression may decrease when the body size difference between competitors is over-

whelming (e.g., like-versus-like aggression; Moller 1987). To further test the hypothesis of size-biased dominance, we used the Spearman rank-order correlation coefficient to test the prediction that aggression between individuals would decrease as the size difference between them increased.

Habitat preferences To test the hypothesis that juveniles prefer structural complexity, we used a mixed model ANOVA to test for an effect of body size rank on the structural complexity of the fish’s station within structured, size-integrated aquaria. The aquarium was included as a random effect. Structural complexity was quantified with rugosity indices. The profile of each structure was traced with string, then the length of the string was divided by the width of the profile (see Luckhurst and Luckhurst 1978). We used the average value of six pieces of each type of structure. The rugosity indices (\pm s.e.) were 1.83 ± 0.09 (rock); 9.43 ± 0.002 (pipe); 31.43 ± 3.37 (plant). If the station did not encompass structure, the rugosity index was zero. There was an effect of body size rank but no aquarium effect, so we further explored the relationship between body size rank and structural complexity with a Spearman rank-order correlation coefficient. We predicted that larger fish would be associated with more structurally complex areas of aquaria.

When we found a relationship between body size and structural complexity, we tested whether the relationship was due to absolute or relative body size. We used the Spearman rank-order correlation coefficient to determine whether the relationship in size-integrated aquaria also existed among size-segregated aquaria. If the effect in size-integrated aquaria is due to absolute size (e.g., large fish prefer structure while small fish do not), then we should detect an effect of body size among size-segregated aquaria. However if the effect is due to only relative size (e.g., larger fish exclude smaller fish from universally preferred habitat), then aquaria with all-large fish should not show greater structure use than aquaria with all-small fish.

Experiment 2

Hatchery effects on future behavior We used repeated measures ANOVA with independent contrasts to determine whether rearing treatment affected future structure use and site fidelity.

Experiment 3

Predation trials If rearing in barren environments increases future predation risk, barren-reared fish should be eaten more frequently than structure-reared fish. For each trial, we subtracted the number of eaten structure-reared fish from the number of eaten barren-reared fish and tested whether the median differed from zero with the Wilcoxon signed-ranks test. We used the Wilcoxon test to test whether the structure-reared fish differed in size from the barren-reared fish used in this experiment. Separately for structure-reared and barren-reared fish, Wilcoxon tests were used to test whether size predicted whether a fish would be predated.

Results

Experiment 1

Site fidelity In both structured and barren aquaria, juveniles were found in the same location through time more frequently than expected by chance. The expected number of matches given ten possible locations was 0.2. The average number (\pm s.e.) of matches in barren aquaria was 1.05 ± 0.09 , $n=10$, $t=9.13$, $p<0.0001$; for structured aquaria, 1.13 ± 0.08 , $n=10$, $t=11.43$, $p<0.0001$).

Territoriality We observed a total of 287 aggressive interactions, involving 92 individuals. In three of the 20 aquaria, residents initiated aggression against intruders as many times as the reverse. Of the remaining 17, 15 aquaria had residents initiating aggression against intruders more often than the reverse. Thus, residents were more likely to initiate aggression than receive it, at a rate greater than that expected by chance (binomial test, 15 of 17: $p<0.01$). Fifty of the 92 individuals that we observed in aggressive interactions had more instances of being a resident showing aggression to an intruder than an intruder showing aggression to a resident; 25 were intruders showing aggression to residents more often than receiving from residents; and 17 gave aggression as many times as it was received.

In size-integrated aquaria, larger individuals were more likely to give aggression than receive it, while smaller individuals showed the opposite pattern (Fig. 1; aquarium effect, $F=0.004$, $p>0.99$; size rank

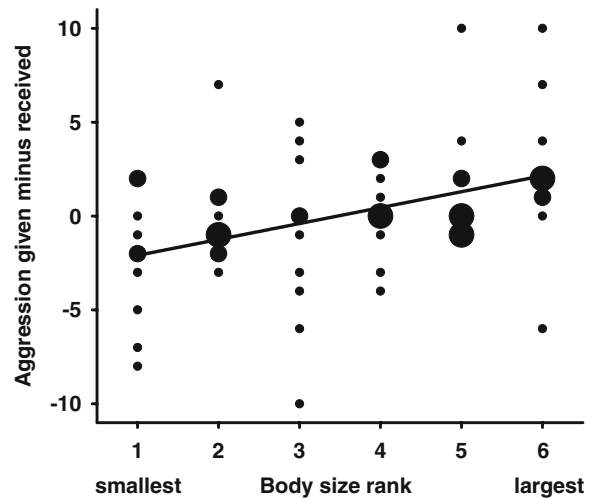


Fig. 1 Size-integrated aquaria. The larger the fish, the more likely it was to give more aggression than was received. Small, medium, and large circles represent one, two, and three data points, respectively

effect, $F=8.61$, $p<0.01$; size rank and aggression, $r_s=0.42$, $p<0.001$). In contrast, among size-segregated aquaria, where all juveniles within each aquarium were equal in size, there was no positive correlation between the size of fish in the aquarium and the number of aggressive acts observed in the aquarium. That is, aquaria with all-large fish did not have more aggressive acts than aquaria with all-small fish. Instead, there was a trend towards a negative correlation ($F=5.02$, $p=0.06$). More aggression occurred in barren than structured environments ($F=12.01$, $p=0.01$).

In size-integrated treatments, most aggressive interactions occurred between individuals that were close in rank (Fig. 2; $p<0.02$, $r_s=1.00$). Thus, one might predict that size-segregating would increase aggression, but this relationship was not found (mean aggressive interactions initiated by an individual, averaged across aquaria within a treatment, \pm s.e.: barren, size-segregated, 2.6 ± 0.3 ; structured, size-segregated, 1.6 ± 0.2 ; barren, size-integrated, 2.8 ± 0.5 ; structured, size-integrated, 2.5 ± 0.5).

Habitat preferences In structured, size-integrated aquaria, size rank was positively associated with use of structurally complex habitat (Fig. 3; aquarium effect: $F=0.39$, $p=0.81$; size rank effect: $F=8.09$, $p<0.01$; size rank and structural complexity: $r_s=0.52$, $p<0.004$). In contrast, across structured, size-segregated aquaria, fish size was not related to structure use ($r_s=0.50$,

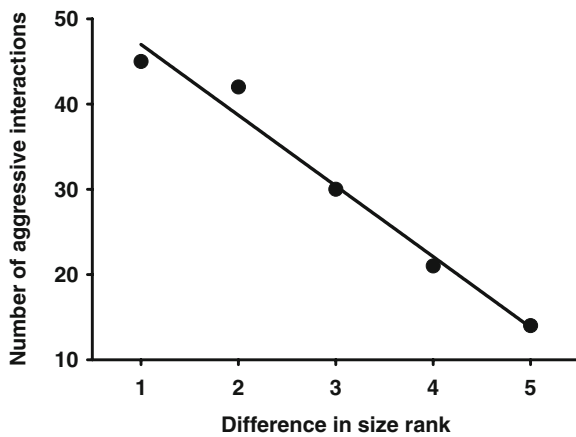


Fig. 2 Size-integrated aquaria. Most aggressive interactions occurred between fish that were similar in body size rank

$p > 0.24$). Instead, juveniles occurred in structured areas of all aquaria, regardless of whether the aquarium contained all-large or all-small individuals (average rugosity indices for each aquarium ranged from 16 to 24).

Experiment 2

Hatchery effects on future behavior The structural rearing treatment affected structure use (Fig. 4, $F = 9.56$, $p < 0.003$) and site fidelity (Fig. 5, $F = 15.16$, $p < 0.0001$), though the effects were limited to the periods shortly after the fish were introduced to the test aquaria. The effect on structure use was significant at the first observation (Fig. 4, $p < 0.002$) but not

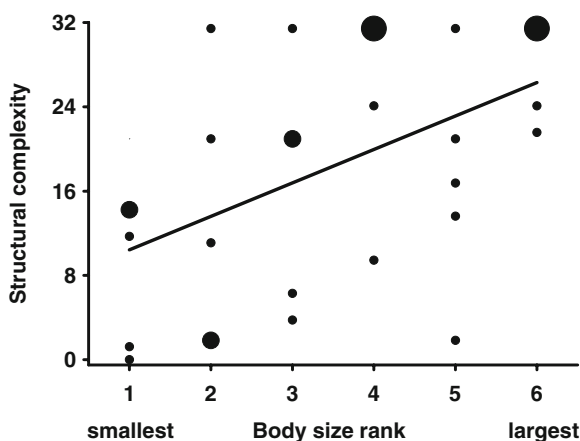


Fig. 3 Size-integrated aquaria. Fish with higher body length ranks inhabited more structurally complex areas. Small, medium, and large circles represent one, two, and three data points, respectively

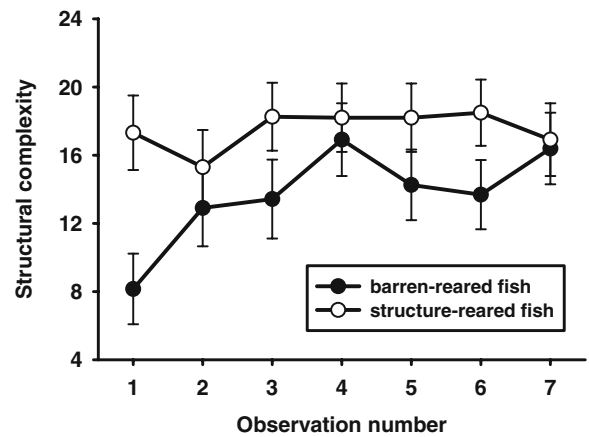


Fig. 4 When fish reared with and without structure were exposed to structure, structure-reared fish showed greater structure use than did barren-reared fish. This effect became reduced through time

for any of the subsequent six observations (Fig. 4, all $p > 0.10$). Similarly the effect on site fidelity was significant for the pair of observations that began with starting observation number one (Fig. 5, $p < 0.0001$) and starting observation number two (Fig. 5, $p < 0.03$). The effect for starting observation number three was not significant (Fig. 5, $0.05 < p < 0.10$); neither were any of the subsequent data (Fig. 5, all $p > 0.57$).

Experiment 3

Predation trials In each of the 21 predation trials, an average (\pm s.e.) of $0.76 (\pm 0.15)$ structure-reared and

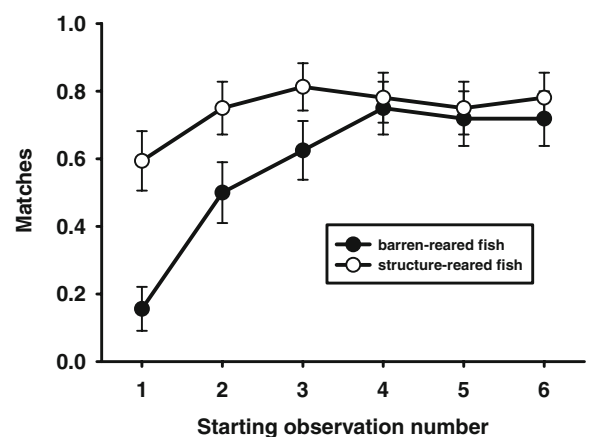


Fig. 5 When barren-reared and structure-reared fish were placed in aquaria with structure, structure-reared fish showed greater site fidelity (higher number of matches) than barren-reared fish. This effect disappeared by the end of the experiment

1.10 (± 0.17) barren-reared fish were predated per trial. Of the 21 trials, six were discarded from statistical analyses because the number of predated structure-reared and predated barren-reared fish were equal. Rearing treatment did not have an effect on predation ($N=15$, $T^+=85$, $p=0.17$). Structure-reared and barren-reared fish that were used in these trials did not differ in body length ($Z=1.26$, $p>0.20$). Body length did not predict whether a fish would be predated (structure-reared: $Z=0.68$, $p>0.49$; barren-reared: $Z=-0.18$, $p>0.85$).

Discussion

Experiment 1

Site fidelity, territoriality, dominance, and habitat preferences Juvenile China rockfish exhibited site fidelity and territoriality within the context of size-biased competition. Size treatments were crossed with structural treatments to enable further explorations of aggression and habitat preference.

In size-integrated aquaria, larger juveniles initiated aggression more, and received it less, than smaller individuals. This may be caused by A) differences in inherent levels of aggressiveness (e.g., juveniles may become inherently more aggressive and territorial as they grow larger, Brown 1985), B) dominance interactions (dominants show aggression toward subordinates, Huntingford et al. 1990), or both factors. Hypothesis A predicts that aquaria with all-large juveniles should exhibit more aggression than aquaria with all-small juveniles. Hypothesis B, which implicates relative rather than absolute size, predicts no positive relationship between size and aggression. No positive relationship was found. In fact, there existed a marginally non-significant trend for a negative relationship ($p<0.06$). Thus, hypothesis B was supported.

The negative relationship between the magnitude of body size asymmetries and the frequency of aggressive interactions is consistent with the sequential assessment model (Enquist and Leimar 1983), in which fighters gather information about opponents' resource holding potential through aggressive signals. If body size indicates the ability to dominate, then individuals with similar body sizes will need to fight more than individuals that are very different in body

size in order to gain the resolution necessary to determine which individual has greater resource holding potential. This model has received strong empirical support through systems with size-biased dominance (Castro and Caballero 1998; Morris et al. 1995).

Larger juveniles were more likely than smaller juveniles to be associated with highly structured areas in size-integrated, structured aquaria. One interpretation is that there is a shift towards greater structure preference with increased size (e.g., juvenile lingcod, Petrie and Ryer 2006). However, in the size-segregated treatment, all juveniles exhibited a preference for structure. This suggests that the relationship between body size and habitat association in size-integrated aquaria was due to competition, not to an ontogenetic shift in habitat preference.

Little is known about differential habitat associations between small and large juvenile China rockfish in the field, but field work on other rockfish species has shown that juveniles and adults generally use different habitats (Love et al. 1991). In one study on an artificial reef, adult copper (*Sebastes caurinus*), quillback (*S. maliger*), and brown (*S. auriculatus*) rockfish occupied higher-relief habitat, while juveniles occupied environments with lower relief (West et al. 1994). Our data on juvenile China rockfish suggest that habitat limitation can lead to a parallel distribution on a smaller scale, in which larger juveniles occupy more complex environments than smaller juveniles. Moreover, our experimental approach identified competition as the mechanism through which these habitat associations arose.

The hatchery rockfish displayed site fidelity and a preference for structure, suggesting that hatchery juveniles released at low densities into structured areas in nature may be sedentary and amenable to monitoring. This is consistent with field observations of wild juvenile China rockfish, which show associations with structured habitats (e.g., NMFS Game ADoFa, Council NPFM 1998).

Our aquarium observations, along with previously published field observations (NMFS Game ADoFa, Council NPFM 1998) support the idea that the preservation or restoration of structured habitats will aid the recovery of China rockfish. Structured habitat may be particularly important since our study suggests that juveniles exclude conspecifics from preferred habitat. If structured habitat is reduced in nature, smaller juveniles may be excluded from

complex habitat that likely provides refuge from predators (P. Malecha, unpublished data on juvenile quillback rockfish).

Longer-term observations will be needed to learn about ontogenetic shifts in habitat use. Studies on other rockfish species show a large amount of interspecific variation in the timing and extent of movements to different depths and habitat types (Love et al. 1991). This aquarium study provides testable predictions for future targeted field experiments.

Experiments 2 and 3

Hatchery effects on behavior and predation risk Individuals transferred from barren aquaria to structured aquaria temporarily (a week or two) exhibited less structure use and site fidelity than those transferred from structured aquaria. Despite the temporary nature of these effects, there may still be negative effects when hatchery-reared fish are released into the wild. If hatchery fish are released into structured nursery grounds, barren-reared fish might wander away into inferior unstructured habitat before they begin to increase their structure use and site fidelity. Further, the highest mortality for fish released from hatcheries likely occurs shortly after release (Howell 1994). We did not detect a significant effect of rearing environment on predation risk, although more barren-reared rockfish were eaten by lingcod. Consequences of reduced structure use and reduced site fidelity may be more severe in the wild. In our predation trials, a fish could not wander too far from structure since our tanks limited the distance that a fish could move. However in the wild, a fish that wanders far from structure may become easy prey. Further, wild predators are likely more skilled at capturing prey than were the hatchery-reared lingcod used in our predation trials (Steingrund and Ferno 1997). Field experiments should allow a more powerful test of whether the behavioral effects we observed in our experiments have consequences for post-release movement and survival in the wild.

Conclusions

Our data suggest that structure plays an important role for juvenile China rockfish. The juveniles showed site fidelity and strong preferences for structure, compet-

ing over it and excluding smaller juveniles from it. This information, along with field tests of the results may be useful for habitat-based attempts to recover and conserve China rockfish populations. Conservation hatcheries that seek to enhance stocks through release of cultured fish may also benefit from taking the importance of structure into consideration in rearing and/or release practices. Field work that tests some of the predictions that arose from these experiments should be particularly informative.

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