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Ontogenetic Changes in Dispersal and Habitat Use in Hatchery-Reared Lingcod

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Preliminary experiments that optimize release methods pave the way to larger-scale releases and proper evaluation methods. One evaluation method is before-after-control-impact, which requires that more animals remain at release areas ("site fidelity" to impact areas) than disperse to control areas. This study tested whether there are release methods that maximize fidelity to the release area and minimize dispersal to nearby areas, which might enable a before-after-control-impact experiment. Lingcod that were 17-months old at release showed greater fidelity to release areas (23% remaining one year after release) than lingcod that were 9- and 11-months old at release. None of the 17- and 21-month-old release groups were detected on more distant structured habitats 44 weeks after release, but 8% and 13% of lingcod from the 9- and 11-month-old release groups were detected at distant structured habitat. Thus, releasing 17-month-old lingcod maximized fidelity to the release area and minimized dispersal to other areas. Differences in fidelity and dispersal rates among release-age groups may reflect ontogenetic changes in dispersal and habitat use patterns that have also been reported for wild lingcod. These behavioral similarities with wild lingcod also suggest that hatchery lingcod have potential to interact and integrate with wild lingcod in nature.

Keywords *Ophiodon elongatus*, stock enhancement, before-after-control-impact, release methods, movement

INTRODUCTION

The behavior of hatchery-reared fish is an important determinant of the success of stock-enhancement programs (Masuda, 2004). The behavior of wild conspecifics can provide expectations for how hatchery-reared fish will behave after release, but typical hatchery environments, where fish are confined in barren tanks with predictable and plentiful food, may impair their ability to display wild-like behaviors (Huntingford, 2004). Despite the importance of behavior after release, the impact of hatchery rearing on behavior has received relatively little attention in marine fish (Huntingford, 2004). Important advances have been made with studies on short-term behaviors, such as predator avoidance, feeding, and exploratory behavior (Fairchild and Howell, 2004; Olla et al., 1998; Braithwaite and Salvanes, 2005), but less attention has been paid to long-term behaviors, such as seasonal or ontogenetic changes in habitat use, movement patterns, and dispersal (Yokota et al., 2006; Lee et al., 2011; Kawabata et al., 2008).

For stock enhancement to be successful, released hatchery fish must capture prey, avoid predators, and navigate novel environments. When fish are released to help replenish wild populations, hatchery fish must also eventually find adult breeding habitat and interact with wild conspecifics. The long-term behavior of hatchery fish can also indicate the optimum age and habitat for release and can determine monitoring methods best suited to quantify the outcomes of stock-enhancement programs.

Lingcod (*Ophiodon elongatus*) populations along the west coast of North America have recovered from overfishing (Jagielo and Wallace, 2005), but the status of genetically distinct lingcod in Puget Sound, Washington (Marko et al., 2007; Jagielo et al., 1996), is less clear. In Puget Sound, commercial and recreational lingcod fisheries landed an average of 364,000 fish per year from 1965 to 1980 (Bargmann, 1982), but strong

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harvest restrictions have since ended the commercial fishery and reduced the recreational fishing season to six weeks per year. This study monitored pilot-scale releases to learn about the behavior of hatchery-reared lingcod and to prepare for future larger-scale releases. This study tested (a) whether the behavior of hatchery-reared lingcod would allow a future before-after-control-impact (BACI) evaluation study and (b) whether hatchery-reared lingcod can exhibit long-term (ontogenetic) spatiotemporal movement patterns similar to wild lingcod.

The effects of stock-enhancement releases can be assessed through control–impact studies (Underwood, 1992), in which areas where hatchery-reared individuals are released (“impact” areas) are compared to areas where no individuals are released (“control” areas). However, a key prerequisite for a control–impact study is that more released individuals must stay at impact areas than move to control areas. Dispersal from impact areas will weaken the strength of any impact (e.g., changes in prey populations), and dispersal into control areas can further decrease the resolution between control and impact areas (e.g., Eggleston et al., 2008). Consequently, most control–impact studies focus on relatively sedentary animals, like some invertebrates, or geographically separated habitats, such as lakes and streams (Alford et al., 2009, Purcell and Cheng, 2010). This study investigated how release age and release habitat would affect the long-term (one-year) fidelity of hatchery-reared lingcod to a potential future impact (stocked) area as well as dispersal to other areas, all within a single large estuary (Puget Sound, Washington, USA). Only small numbers of telemetry-tagged individuals were released so that future control and impact areas would not be compromised.

Increased behavioral similarity between wild and hatchery-reared individuals should help released hatchery fish integrate with and replenish the wild population. Strong behavioral similarity may also reduce negative ecological consequences stemming from unnatural social behavior, predator–prey interactions, or habitat use. Lingcod spawn during winter months. Most reports on the early life history of lingcod are anecdotal. After a pelagic stage, lingcod are thought to settle to bottom habitat in or near eelgrass or kelp beds in middle to late spring and disperse to a wider geographic range of sandy bottoms in late summer or early fall (Cass et al., 1990). Around age 2, lingcod have been reported to appear on rocky, structured habitats that are similar to adult habitat (Cass et al., 1990; Miller and Geibel, 1973). This study was designed to test the hypothesis that hatchery lingcod exhibit spatio-temporal movement patterns and habitat associations similar to wild lingcod and to determine the potential for hatchery-reared lingcod to integrate with wild lingcod. The behavior of hatchery lingcod released at ages 9, 11, 17, and 21 months (hereafter, 9mo, 11mo, 17mo, and 21mo) was compared to previously published reports on wild lingcod behavior. Ontogenetic behavioral changes were examined by monitoring movements of released lingcod for up to one year after release.

METHODS

Egg Collections and Rearing

Male lingcod defend egg masses on rocky structured habitat in the winter (LaRiviere et al., 1981). Between January and April in 2008 and 2009, divers collected eggs from a total of 42 lingcod nests from locations ranging from west of Seattle to the southern-most parts of Puget Sound. All collections were made less than 70 km from the eventual release locations. For most nests, only a small portion (15 to 25%) of each nest was taken. Eggs were incubated in PVC pipes that released hatched larvae into mesocosm bags for rearing, generally following methods described by Rust et al. (2005). Lingcod were transferred to net pens in late spring of each year and to land-based tanks in the summer.

Tagging

Coded acoustic telemetry tags emit individually identifiable acoustic signals that can be remotely detected by hydrophones and provide position data on free-living, undisturbed animals (Voegeli et al., 2001). Tags were surgically implanted in the body cavity following the methods in Moore et al. (2010). Lingcod were implanted with Vemco V7 (9mo, $n = 24$; 11mo, $n = 45$) or V9P (17mo, $n = 30$; 21mo, $n = 26$) acoustic tags (Table 1). Fish were tagged at least 2.5 weeks before release, except for eight fish in the 11mo group, which were tagged 2 days before release. None of the statistical significance levels change if these eight fish are excluded from analyses. Each tag emitted an acoustic signal at random intervals within a range of 110–250 seconds (180 average). All tags alternated between two-week “on” periods and two-week “off” periods to preserve battery life. The on and off periods were synchronized among tags. V7

Table 1 Four release ages from two brood years were released into a range of habitats

Age in months and season	Brood year	Depth and habitat	Fish length and weight (*SD*)	Acoustic tag
9, Fall	2008	3 m, B ($n = 12$); 3 m, V ($n = 12$)	195 ± 18 mm, 57 ± 16 g	V7-2L, 20 × 7 mm
11, Winter	2009	3 m, V ($n = 15$); 15 m, B ($n = 15$); 15 m, S ($n = 15$)	236 ± 18 mm, 113 ± 28 g	V7-2L, 20 × 7 mm
17, Summer	2008	15 m, B ($n = 15$); 15 m, S ($n = 15$)	312 ± 12 mm, 258 ± 35 g	V9P-1L, 40 × 9 mm
21, Fall	2008	15 m, B ($n = 13$); 15 m, S ($n = 13$)	341 ± 15 mm, 374 ± 56 g	V9P-1L, 40 × 9 mm

B = barren, V = vegetated, and S = structured. The two younger groups were implanted with Vemco V7-2L tags (1.6 g in air), and the two older groups were implanted with Vemco V9P-1L tags (5.3 g in air).

and V9P tags emitted signals for 13 months and 21 months, respectively.

Releases

In a previous study, age-4 lingcod were released at two structured habitats in South Puget Sound: Itsami Reef and Zees Reef (Lee et al., 2011). Additional releases at Zees Reef were not conducted because of ongoing Washington Department of Fish & Wildlife monitoring at that site, so this study conducted releases only near Itsami Reef. Depending on age, lingcod were released at depths of approximately 3 m and/or 15 m and in barren, vegetated, and/or structured habitats (Table 1). The vegetated habitat was primarily composed of non-floating kelp but also contained ulva and red algae. The structured habitat was Itsami Reef, which is an artificial reef created in 1982 and composed of remnants of concrete sidewalk, curb, and slabs piled into a complex arrangement with crevices and overhangs (Hueckel and Buckley, 1987; M. LaRiviere, Tacoma Power, personal communication). Of the eight late-tagged 11mo, two were released in shallow vegetated habitat, three were released in deeper barren habitat, and three were released in deeper structured habitat. Fish were gently released over the side of the boat at 3-m-deep locations. At 15-m-deep locations, fish were lowered over the side of the boat in buckets that released fish soon after nearing the Puget Sound bottom.

Monitoring

The Vemco VR28 is a mobile acoustic tracking system consisting of four hydrophones that together give the directional location of detected tags. To identify individuals that remained near the release area, the Vemco VR28 was towed behind a boat within Zone A (Figure 1) for all release groups 4, 36, and 52 weeks after each release. The towed zone was expanded to include Zone B for the last three release groups (11mo, 17mo, and 21mo). Range testing indicated a detection range of up to 400 m, but detection ranges can vary with ambient noise levels (Heupel et al., 2006). A detection range of 100 m was conservatively assumed, and the hydrophone was towed along routes that came within 100 m of every point within each zone to provide complete zone coverage. Boat speed was maintained between 4.5 and 6.0 km/hr. Other areas to the southwest, south, and northeast of Zones A and B were also surveyed but not consistently since few fish were found there. Only results from consistently surveyed areas (Zones A and B) are reported here. Seventy percent of detected fish were detected more than once on the day of detection, which allowed their position to be determined through triangulation. When a fish was detected only once, its position was assumed to be 50 m away in the direction indicated by the VR28. Undetected individuals were assumed to have moved to unsurveyed areas or to have been consumed within the study area and carried to unsurveyed areas.

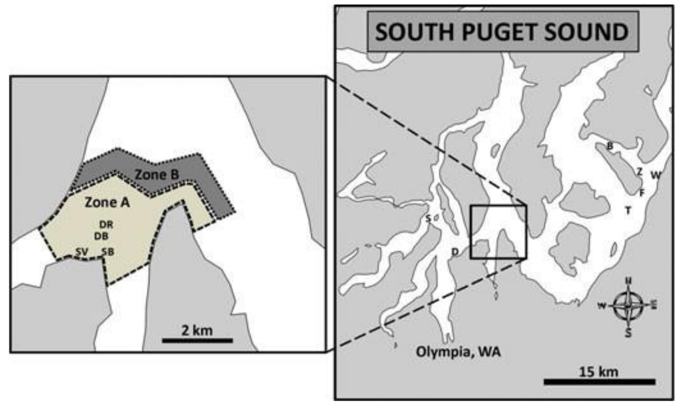

Figure 1 The large map shows South Puget Sound and the seven sites surveyed 44 weeks after release (B = Fox Island Bridge, Z = Zees Reef, W = Day Island Wall, F = Fox Island East Wall, T = Toliva Shoal, D = Dover Point, S = Steamboat Island). The zoomed map shows the four release locations (DR = deeper reef, DB = deeper barren, SB = shallower barren, SV = shallower vegetated). The two shaded areas represent Zones A and B, which were surveyed 4, 36, and 52 weeks after the release of most groups. (Color figure available online).

Forty-four weeks after each release, the Vemco VR28 searched known adult structured habitat for fish that had dispersed from the release area. These habitats were chosen based on personal knowledge of adult breeding habitat and recommendations from other local biologists, anglers, and divers. These areas were Steamboat Island, Toliva Shoal, Day Island Wall, Fox Island East Wall, Zees Reef, and Fox Island Bridge (Figure 1). Dover Point, which has a small amount of structure but not nearly as much as other sites, was also surveyed (Figure 1). With the exception of Fox Island Bridge and Dover Point, these sites are structured habitats where breeding adults have been previously observed.

Data Analysis

Chi-square tests compared the proportion of fish detected in Zone A among the four release ages at each survey timepoint (4, 36, and 52 weeks after release). Significant results were followed by paired chi-square tests. For this and analyses described below, Bonferroni corrections were applied to the resulting *p*-values to account for multiple comparisons. Only data from Zone A were statistically analyzed, since Zone B was not tracked for all release groups.

For each release age and each time after release (4, 36, and 52 weeks after release), Fisher's exact test was used to determine whether release habitat affected the likelihood that a fish would remain near its release point (within 200 m). The 200-m radius was chosen as a somewhat arbitrary threshold before surveys began.

If fish are distributed randomly with respect to habitat type, the proportion of fish in structured habitat should not significantly differ from the proportion of surveyed habitat that is composed of structured habitat. An exact binomial test compared the proportion of fish in structured habitat to the proportion of structured habitat available in the surveyed area for each release age and each time-point (4, 36, and 52 weeks after release). A side-scan sonar and depth sounder were used to document habitat as structured or unstructured in Zones A and B. Data from Zone A were analyzed for all release ages. Zone B was only surveyed for the other three release groups but was included in analyses for these three groups because the method of data analysis standardized for different survey areas (these data are presented later in Figure 4 as proportional habitat use [PHU] indices):

$$PHU = \frac{n_r \bullet n_t^{-1}}{a_r \bullet a_t^{-1}},$$

where n_r is the number of fish detected in a particular habitat type, n_t is total number fish detected in all habitats, a_r is the area of the particular surveyed habitat type, and a_t is the total area of all surveyed habitats.

Structured habitat accounts for a very small proportion of the total habitat in South Puget Sound. An exact binomial test was used to determine whether the number of fish encountered on surveyed structured habitat during the week-44 distant survey was greater than would be expected if fish were distributed according to habitat availability. The most conservative assumption was made: that all undetected fish were on unstructured habitat in South Puget Sound. In addition to these habitats, Dover Point was also surveyed at each week-44 distant survey (Figure 1). Dover Point only contains small amounts of rocky structure and is not known adult habitat. It therefore was not considered as "structured habitat" for statistical analyses.

RESULTS

Fidelity to Release Area

Fidelity to the release area at each time-point varied as a function of release age (Figure 2; 4 weeks after release: chi-square = 9.89, $p < 0.05$; 36 weeks after release: chi-square = 14.84, $p < 0.01$; 52 weeks after release: chi-square = 12.26, $p < 0.01$). Pairwise chi-square tests indicated that the 17mo group showed greater fidelity than the 9mo group at 36 weeks after release ($p < 0.01$, chi-square = 10.51) and at 52 weeks after release ($p < 0.05$, chi-square = 9.06). The 17mo group also showed greater fidelity than the 11mo group at 4 weeks after release ($p < 0.01$, chi-square = 12.30) and 36 weeks after release ($p < 0.05$, chi-square = 7.74).

Fidelity by Release Habitat

Within each release age, fidelity within a 200-m radius from the release point did not significantly vary as a function of release habitat, though there was a non-significant tendency in the 17mo and 21mo groups released on structured habitat to show greater fidelity than fish released on barren habitat (Figure 3; all $p > 0.05$).

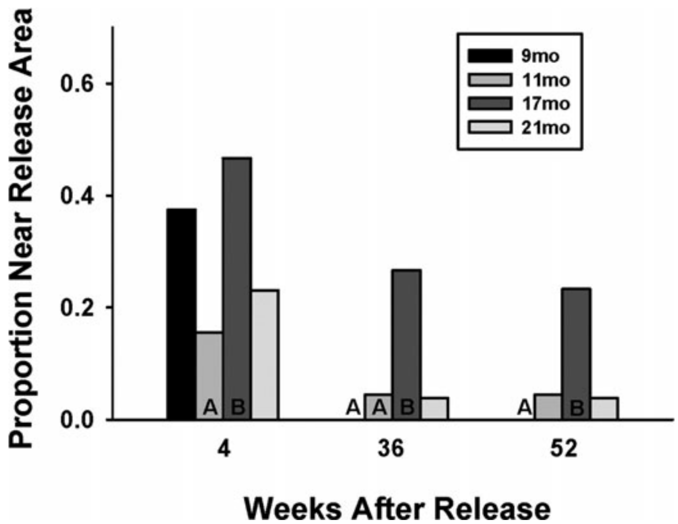

Figure 2 Lingcod released in 17mo group showed greater fidelity to Zone A than 9mo and 11mo lingcod. Different letters represent statistical significance after the Bonferroni corrections for multiple comparisons.

PHU

Fish in the 9mo group did not show any significant differences in use of unstructured versus structured habitat four weeks after release ($p > 0.05$). Analyses at subsequent time-points were not possible, because all fish had dispersed from Zone A by 36 and 52 weeks after release. The 11mo group showed greater-than-expected use of structured habitat 52 weeks after release ($p < 0.005$) but not at earlier time-points ($p > 0.05$). There was greater-than-expected use of structured habitat at all time-points for the 17mo group (4 weeks: $p < 0.05$; 36 weeks: $p < 0.0001$; 52 weeks: $p < 0.000001$; Figure 4). The 21mo group showed greater-than-expected use of structured habitat four weeks after release ($p < 0.001$) but not at any later time-point.

Dispersal to Distant Habitat

Individuals from 9mo and 11mo, but not 17mo or 21mo, release groups were detected at distant sites 44 weeks after release (Figure 5). Two out of 24 individuals from the 9mo group were detected at Toliva Shoal. Two more were detected at Dover Point. The hydrophone detected 2 of the 45 11mo fish at Steamboat Island, 3 at Toliva Shoal, 1 at Day Island Wall, and 1 at Dover Point. Detection rates at the surveyed adult habitats were greater than expected by chance (9mo: $p = 0.02$; 11mo: $p < 0.00001$).

The distant surveys for the 17mo and 21mo groups narrow the possible dates on which fish from the 11mo group arrived at distant sites to between 32 weeks and 44 weeks after release. The 44-week distant surveys for the 17mo and 21mo groups were

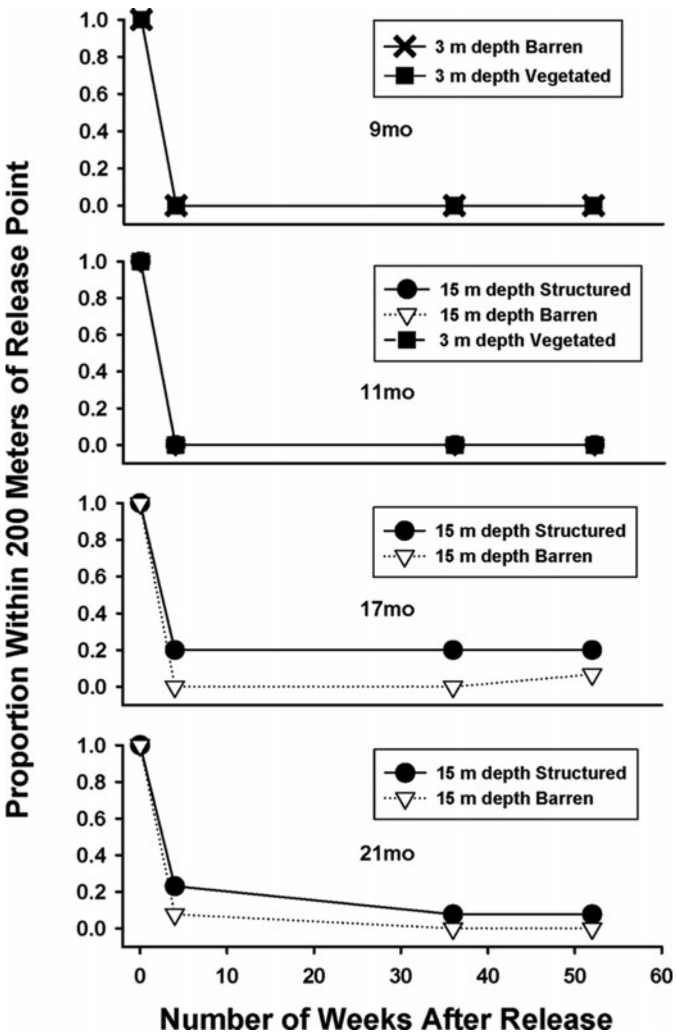

Figure 3 Though the trend was not statistically significant, 17mo and 21mo lingcod released in structured habitat tended to show greater fidelity to the release habitat than 17mo and 21mo fish released in barren habitat.

conducted in May 2010 and September 2010, which corresponds to 16 weeks and 32 weeks after the release of the 11mo group. No fish from the 11mo group were detected in May 2010, but one was detected on Toliva Shoal in September 2010. However this fish was not one of the three fish detected at Toliva Shoal 44 weeks after the release of the 11mo group.

DISCUSSION

Developing Release Methods

Preliminary experiments that identify the best life-history stage for releases are an important step in the development of a well-designed stock-enhancement program (Lorenzen et al., 2010). This study sought to find release methods that would minimize dispersal in advance of implementing a BACI experiment. The 17mo group showed the best combination of high fidelity to release area, low dispersal to other structured habitats in South Puget Sound, and high total number of detections, and it may therefore be an optimal age for future BACI experiments.

A number of factors might contribute to the finding that the 17mo group showed higher detection rates near the release area than the 9mo and 11mo groups. Studies comparing release ages typically find that younger release groups have lower survival rates (Lorenzen, 2000; Leber, 1995; Willis et al., 1995), but survival differences do not appear to have caused the differential redetection rates in this study. The two youngest release groups (9mo and 11mo) showed the lowest detection rates near the release area, but these groups also showed the highest detection rates at distant sites. If the last survey results from the release area (52 weeks after release) and distant sites (44 weeks after release) are pooled, the total detection rates of the two youngest release groups (16% and 19%) are only slightly below that of the 17mo group (23%) and higher than that of the 21mo group (4%). Thus, high dispersal by the two youngest release groups, not mortality, likely explains their lower detection rates near the release area.

Possible interactions among the four release groups are unlikely to explain redetection rate differences among groups. The youngest release group (9mo) showed the lowest redetection rate near the release area, but all individuals had left the area before later groups were released. The last three release groups were released closer in time to each other, but Itsami Reef should provide enough habitat for all released fish, considering the small release numbers and the large amount of uninhabited structure at Itsami Reef (E. Berntson and M. Cook, NOAA, personal communication).

Seasonal effects could contribute to the higher redetection rate near the release area for the 17mo group. Since lingcod only breed in the winter, release age and release season are necessarily confounded. Lingcod reach 17 months of age in the summer, 11 months of age in the winter, and 9 and 21 months of age in the fall. Some adult lingcod seasonally migrate to reefs in the fall and winter (Cass et al., 1990). In those seasons, the higher adult density should create a higher risk of cannibalism (Martell et al., 2000; Beaudreau and Essington, 2007). Lingcod released in the summer (17mo) may have time to establish home ranges with refuges before cannibalism risk becomes high in the fall and winter, while lingcod released in the fall and winter (9mo, 11mo, and 21mo) may disperse from the reef to avoid the threat of cannibalism from older, larger fish.

In addition to releasing 17mo lingcod, releasing onto structured habitat may further limit dispersal. Both 17mo and 21mo groups released on the structured habitat tended to stay within 200 m of the release point in greater proportions than those released on barren habitat at every time-point (4, 36, and 52 weeks), though the effect of release habitat was not statistically significant. In contrast, at no time-point did 11mo fish released on structured habitat stay at a greater rate than same-aged fish released in other habitats. These results are consistent with the observation that the preference for structured habitat develops near the second year of life, as higher fidelity in structured

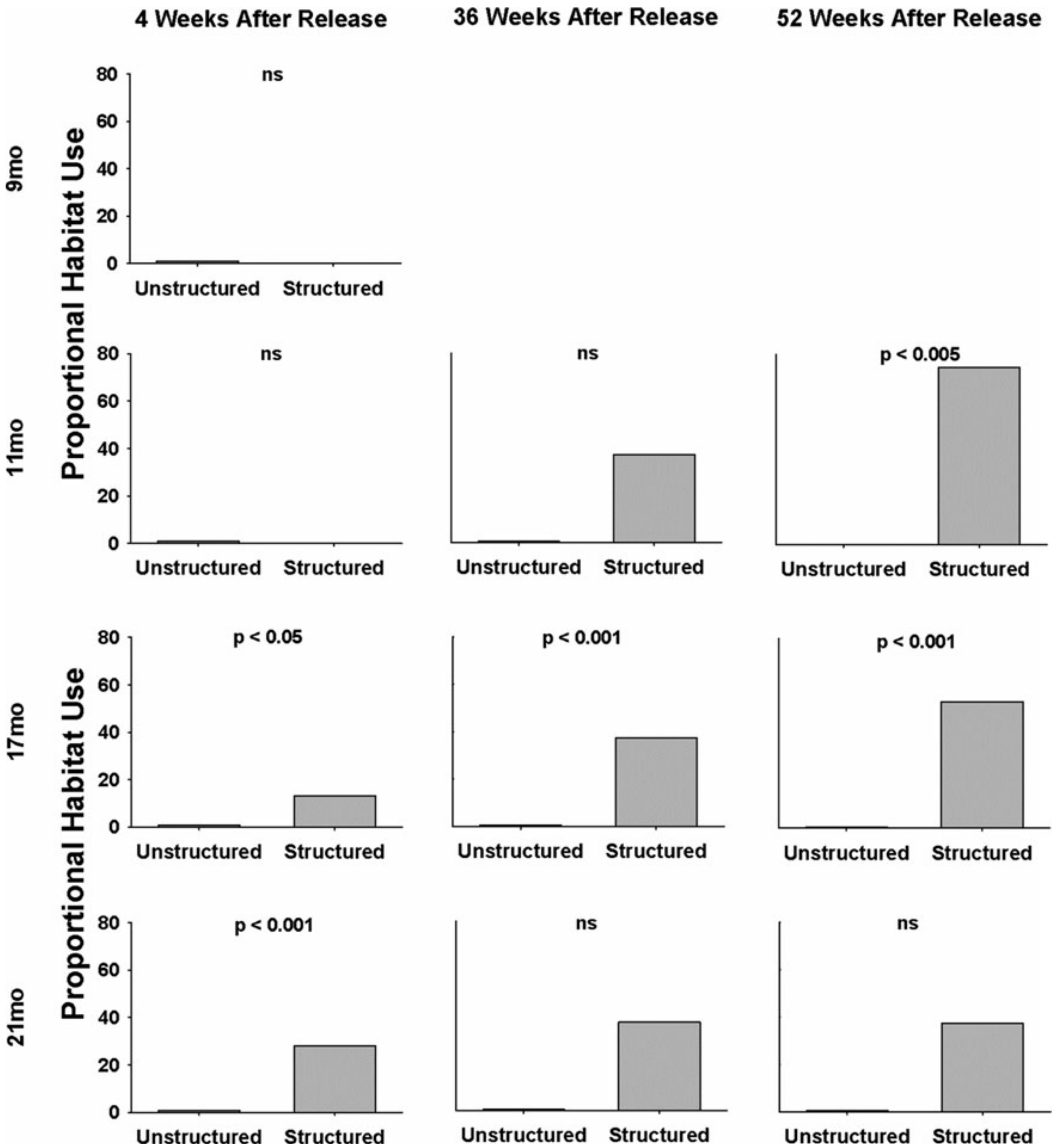

Figure 4 At various time-points after release, the three oldest release groups showed disproportionately greater use of structured habitat over unstructured habitat in Zones A and B. No data are shown in the last two time-points for the 9mo released group because no fish were detected in the surveyed zone at those time-points.

habitats seemed to occur with 17mo and 21mo lingcod but not with 9mo or 11mo lingcod. In addition, dispersal rates may also vary with release density, particularly if carrying capacity is exceeded. Future work should estimate carrying capacity so that proper numbers of fish are released.

This study sought to identify the optimal release age(s) for a future BACI experiment with local control areas, but the optimal release age depends on the goals of the study. For example, high dispersal rates make 9mo and 11mo lingcod unsuitable for control–impact monitoring in Puget Sound on the scales evaluated in this study, but high overall detection rates that result when the last nearby and distant survey detections are pooled (16 and 19% for 9mo and 11mo versus 23 and 4% for 17mo and 21mo) suggest that these 9mo and 11mo ages should be considered for other studies that are compatible with high dispersal rates, such as full-scale stock-enhancement releases that assess through methods other than control–impact or where control–impact areas are more distant. If economic effectiveness of releases later becomes important, 9mo and 11mo releases may be preferable since reduced time in the hatchery should reduce operating costs with potentially small differences in mortality rates. Reduced time in the hatchery may also lead to fewer behavioral deficits in released fish, which can in turn increase survival after release (Masuda, 2004). In striped mullet, 85–110 mm is the most cost-effective release-size range within a 45–130 mm range, when "optimal" is defined by post-release

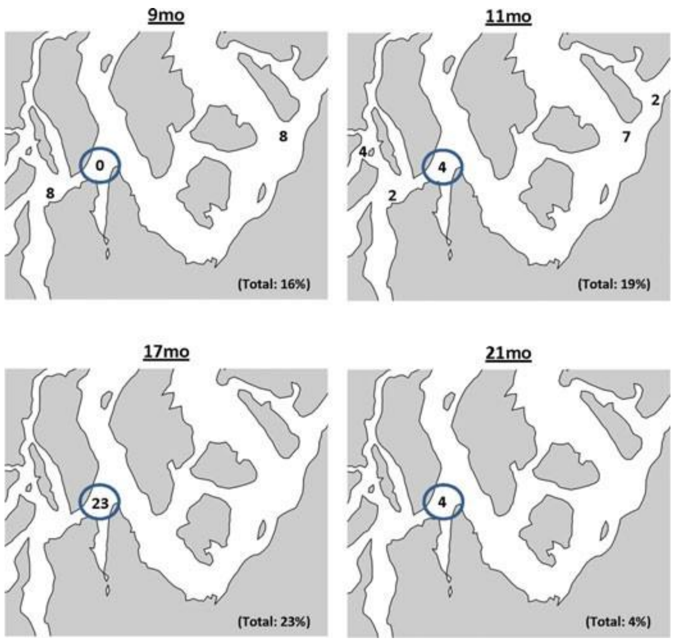

Figure 5 Lingcod released at 9mo (*n* = 24 fish released), 11mo (*n* = 45), 17mo (*n* = 30), and 21mo (*n* = 26). The number in the circle represents the percentage of the released fish detected in Zone A one year after release. The numbers outside of the circle represent the percentage of the released fish detected at distant surveyed sites 44 weeks after release. (Color figure available online).

survival and rearing costs (Leber et al., 2005). If ecological costs are included in the equation that solves for optimal release size, then behavioral deficits or unintentional training can also potentially impact optimal release size by affecting interactions with wild conspecifics (Berejikian et al., 2000).

Comparisons to Wild Lingcod

The behavior and habitat associations of hatchery fish are important because they influence the likelihood that hatchery fish will interact and integrate with the wild population. Ontogenetic changes in habitat use in the hatchery-reared lingcod were similar to those reported for wild lingcod. After hatching in late winter, wild subyearling lingcod settle to sandy areas near eelgrass or kelp beds in the summer (Phillips and Barraclough, 1977). By September, they disperse to a wider geographic range of flat-bottomed areas (Cass et al., 1990). None of the hatchery-reared fish were released before September of their first year of life. In agreement with these wild lingcod reports, none of the release groups lingered near kelp beds. Even the youngest release ages (9mo and 11mo, released in November and January), which included release groups in kelp habitat, quickly dispersed to deeper water that lacked vegetation.

In their second year of life, wild lingcod begin to appear near adult-typical structured habitat (Martell et al., 2000). Similarly, hatchery-reared 9mo and 11mo did not show preferential use of structured habitat soon after release but were able to find adult-typical breeding habitat by 36 weeks or 44 weeks after release, as the lingcod approached or entered their second year of life. In contrast to the hatchery-reared 9mo and 11mo and in agreement with wild lingcod observations, hatchery-reared 17mo and 21mo groups showed immediate preferential use of structured habitat near the release area. The 17mo group showed preferential use at every time-point. The 21mo group showed preferential use at the first survey after release. Subsequent time-points for the 21mo group showed similar PHU but were not statistically significant, likely because of low statistical power due to the presence of only two fish at those time-points.

Cass et al. (1990) suggested that wild subyearling lingcod disperse over a wide geographic range before settling on reefs in the second year of life. This observation is mirrored in the hatchery-reared lingcod and explains why the final structured habitat locations differed between subyearling groups (9mo and 11mo groups on distant structured habitat) and yearling groups (17mo and 21mo groups on local structured habitat). Hatchery-reared 9mo and 11mo groups dispersed from the release area before developing preferences for structured habitat in the second year of life. In contrast, hatchery-reared 17mo and 21mo groups were beyond the dispersal stage and at the structured habitat preference stage, and so instead showed immediate preferences for the structured habitat near their release area and were not later detected on more distant structured habitat. Further, individual location data indicate that most of the individuals from the 17mo and 21mo groups that were present at Itsami Reef one year after release had consistently stayed at the reef since release. In contrast, of the two fish from the 11mo group that were at Itsami Reef one year after release, both had left the area soon after release but returned to the reef by 36 and 52 weeks after release. Thus, since 9mo and 11mo fish will disperse from the release area before developing a preference for structured habitat, their final distribution will likely be more dispersed than older release groups.

This study suggests that hatchery-reared lingcod exhibit complex, age-specific natural movements and habitat associations and the ability to find distant adult breeding habitat. This is important if hatchery-reared fish are to integrate with and replenish wild populations. Further, data on hatchery-reared lingcod improve our understanding of wild lingcod. The largely anecdotal knowledge about the early life history of wild lingcod is supported by the movement data on hatchery lingcod.

As with all tagging studies, the fate of undetected individuals is unknown. Particularly interesting are the low detection rates for the 21mo group. The sum of detections from week-44 distant surveys and week-52 Zone A surveys (Figure 5) is the lowest for the 21mo group. The only fish detected in Zone B one year after release was from the 21mo group, bringing the total detection rate 52 weeks after release to 8%. However, even with this extra fish, the group's summed week-44 and week-52 detection rates are still lower than any other group. Undetected lingcod could have been eaten by predators or moved to areas that were not surveyed. However, the most structured areas in South Puget Sound were surveyed in this study. Thus, if undetected fish moved to unsurveyed structure, that structure likely would have been far away from the release area (and far away from future control areas). Perhaps some yearling lingcod remain on release reefs, while others disperse to very distant reefs or even out of Puget Sound (also see Lee et al., 2011). Lingcod have displayed considerable variability in movement patterns, both among individuals and among populations (LaRiviere et al., 1981; Lee et al., 2011; Miller and Geibel, 1973). For example, some adults remain in small areas for extended periods, while others migrate seasonally between deeper habitat and shallower structured breeding areas (Miller and Geibel, 1973). This behavioral variation may point to fairly complex features of lingcod movement behavior and life history and deserves more attention.

This study demonstrates how very small-scale releases and acoustic telemetry can improve knowledge of the behavior of hatchery-reared and wild fish. From a stock-enhancement perspective, data on ontogenetic changes in behavior can inform decisions on optimal release age, especially for species with complex migratory life cycles (e.g., Hines et al., 2008). This study suggests that under certain release conditions, fidelity to the release area may be high enough to enable a control–impact study with a fish species in a single large estuary. Agreements between wild reports and data from hatchery lingcod suggest that hatchery-reared lingcod have potential to integrate with the wild population. From a natural history standpoint, such work with hatchery-reared fish can also improve our understanding of the life history of wild fish, particularly when wild fish are difficult to find and study and when wild fish knowledge is mostly anecdotal, as is the case for lingcod early life history.

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