OYSTER GROW-OUT CAGES FUNCTION AS ARTIFICIAL REEFS FOR TEMPERATE FISHES

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Abstract

We compared relative fish density, growth and disappearance rates (mortality plus emigration) on 3 oyster grow-out sites, 6 natural rocky reefs, and 1 artificial reef purposely built for fish habitat. All sites were located within Narragansett Bay, Rhode Island. Trap surveys were conducted in the summer and autumn of 2004 and 2005 using a range of trap types designed to sample juvenile and adult fishes. Cunner, *Tautogalabrus adsperus*, were more abundant on natural rocky reefs and the artificial reef than on oyster grow-out sites, whereas scup, *Stenotomus chrysops*, and tautog, *Tautoga onitis*, displayed the opposite pattern and were most abundant on aquaculture sites. The relative density of black sea bass, *Centropristis striata*, was similar in all habitats. A mark-recapture study on scup indicated that this species grew at higher rates on natural rocky reefs, but had a lower disappearance rate from aquaculture sites. Based on these criteria, the oyster grow-out cages provide good quality habitat for fishes typically associated with hard-bottom habitats. Habitat restoration programs for these fishes should thus consider grow-out cages alongside other types of artificial reef.

Introduction

Sea grass and macroalgae beds, marsh creeks, cobble and rocky reefs, and shellfish beds are often described as key inshore fish habitats, and the loss or degradation of these habitats is implicated in the decline of many coastal fisheries (Beck et al. 2001). Shellfish beds provide a good example of an inshore habitat much diminished in extent. Shellfish beds were once widespread in inshore habitats along the US east coast (MacKenzie 1997), including Narragansett Bay and several south shore salt ponds of Rhode Island (Oviatt et al. 2003). Like in most coastal Atlantic states (Ford 1997), oyster harvests in Rhode Island have declined by 90% over the past century (Rhode Island Aquaculture Initiative 2004), with a concomitant decline in the area of oyster bed habitat (MacKenzie 1997; Oviatt et al. 2003). Decline of oysters has been attributed to several factors including pollution, harvest pressure, disease, and severe storms (Seliger et al. 1985; Rothschild et al. 1994; Ford and Tripp 1996).

The complex three-dimensional structure of oyster beds provides habitat for a diversity of benthic organisms (Lenihan & Peterson 1998; Rodney and Paynter 2006). These benthic species, in turn, provide prey resources for fin fishes and other mobile consumers (Kaiser et al. 1998; Peterson et al. 2003). The restoration of oyster beds may thus have both fishery-related and ecological benefits (Mann and Harding 1997; Breitburg et al. 2000). Oyster aquaculture is a promising way to restore the economic benefits of oyster harvesting. Typically, part of the aquaculture process involves suspending juvenile oysters above the bottom in shallow water where they grow to market size (Rheault and Rice 1995; Powell 1996). In Rhode Island, oysters are often held in tiered racks that are placed on unvegetated soft sediment (Rheault and Rice

1995). The racks thus provide a complex three-dimensional structure that remains on the bottom continually, except when racks are briefly removed from the water every 3-6 months to harvest legal-sized oysters. In 2005, grow-out cages at 25 sites covered 35 hectares of subtidal habitat in Rhode Island.

The few surveys of macrofaunal communities on oyster grow-out cages (Luckenbach et al. 2000; Dealteris et al. 2004; O'Beirn et al. 2004), and anecdotal reports by SCUBA divers (D. Hudson, University of Rhode Island, and R. Rheault, Moonstone Oysters, personal communication), revealed that grow-out cages are colonized by some finfish. These finfish typically occupy natural rocky-reef habitats, raising the possibility that oyster grow-out cages provide habitat for these species and effectively act as artificial reefs. Artificial reefs deliberately designed to mimic natural rocky reefs are widely used. A common motivation for their deployment is to enhance the production of reef-associated species (Seaman and Sprague 1991; Pratt 1994). Enhanced production will occur if the availability of natural rocky reefs is limited, so that adding artificial habitat increases overall fish abundance (Bohnsack 1989). The extent of natural rocky reef habitat in Narragansett Bay is little known, but existing data suggest that virtually all of the 380 km^2 of subtidal habitat in the bay is soft sediment (McMaster 1960; Poppe 2003; Tiner et al. 2004).

Evaluating the performance of artificial reefs must include contemporaneous comparisons with the natural reefs they are designed to mimic (Carr and Hixon 1997). Although oyster grow-out cages are not designed to mimic natural rocky reefs, providing habitat for finfish would constitute an important, albeit unintentional, side-effect of their deployment. Consequently, we tested the hypothesis that oyster cages provide fish

habitat that is functionally equivalent to natural rocky reef habitats and artificial reefs specifically designed to mimic natural rocky reef. To assess functional equivalence, we compared the relative density, growth, and disappearance rates (mortality plus emigration) of finfish captured on oyster grow-out cages to equivalent measures of fish occupying nearby natural rocky reefs and one artificial reef. The study focused on four economically valuable or ecologically significant finfish species known to inhabit both natural rocky reefs and oyster grow-out cages: (1) black sea bass, *Centropristis striata*; (2) cunner, *Tautogalabrus adsperus*; (3) scup, *Stenotomus chrysops*; and (4) tautog, *Tautoga onitis*.

Methods

Study sites

The study was conducted in Narragansett Bay, Rhode Island, in 2004 and 2005 (Figure 1). We studied three habitats: oyster aquaculture sites, natural rocky reefs, and an artificial reef. The three aquaculture lease sites were located in areas where the seabed was soft-sand or silt-clay. Leases had been active for several years prior to this study. Juvenile cultured eastern oysters (*Crassostrea virginica*) were held in mesh bags on tiered racks inside a mesh cage (1.8 m x 0.6 m x 0.6 m). Each cage was attached to one of several trawl lines that ran the length of the lease. Each aquaculture site was in water 4-8 m deep and contained approximately 100 cages spread over 0.8 to 1.6 ha. The six natural rocky reef sites were outcroppings of natural rock (mostly granite) covered with algae and located between 4 and 9 m deep. Some reefs were offshore and ranged in area between 0.4 and 0.8 ha, whereas other reefs, similar in size, adjoined land. The single artificial reef was built in 1997 and designed to mimic local

natural rocky reefs and provide lobster habitat (Castro et al. 2000). Six modules (each 10 m x 20 m) of granite cobbles were positioned approximately 33 m apart in water 5 m deep. Each module was divided into two 10-m x 10-m halves; one of which was constructed from cobbles (10 to 20-cm in diameter) and the other was constructed of larger rocks (21 to 40 cm in diameter). Overall, the six modules provided 0.16 ha of habitat (Castro et al. 2000, Robbins 2004).

We sampled the same three aquaculture sites and artificial reef in both 2004 and 2005, whereas the number of natural rocky reefs increased in the second year (Fig. 1). The 3 aquaculture and 5 natural rocky reef sites were interspersed spatially, and were all within 5 km of each other (Fig. 1), so we considered them comparable as statistical replicates. Trap sampling was conducted from mid-July through early-October in both years. In 2004, there were two sampling sessions, separated by three weeks. In 2005, there were three sampling sessions, with just over two weeks separating them. The sampling dates were as follows: Session 1, 2004: 26 June – 20 August; Session 2, 2004: 15 September – 10 October; Session 1, 2005: 11 July – 29 July; Session 2, 2005: 15 August – 29 August; Session 3, 2005: 19 September – 6 October.

Trapping methods

We used several types of traps to ensure that we captured fish of a range of sizes. Trapping in 2004 utilized six commercial black sea bass pots (International Marine Marketing, Wakefield, Rhode Island) and three O-pots built to Robbins (2004) specifications. The O-pots were cylindrical, with a diameter of 91 cm and a height of 61 cm. They had two opposing “wrap-in” V entrances, 61 cm high and 3.8 cm wide. For the 2005 field season, we used 30 O-pots similar in shape to the 2004 O-pots except

that each exterior dimension was reduced by 25%. O-pots and black sea bass pots were covered with 1.3 cm plastic mesh. In 2005, we also used 18 Gee minnow traps (Memphis Net and Twine, Memphis, Tennessee) to more effectively sample age-0 fish. Minnow traps (23 cm x 44 cm) were made of 0.64 cm galvanized steel wire with two entrances (each 2.5 cm in diameter).

All traps were baited with frozen whole clam bellies and were placed to sit undisturbed on the seafloor (soak) for 2 d, though some soaked for up to 5 d when inclement weather delayed retrieval. In 2004, because we had only 9 traps, we divided the six sites into two groups of three and sampled each group on alternate dates (allocating 3 traps per site per date). In 2005, we simply divided the traps among the nine sites and sampled continually at all sites (5 traps per site per date). Traps were deployed and retrieved between 0800 and 1600 hours.

Mark-recapture methods

Once traps were retrieved, individuals of the four study species were placed in water-filled bins on the boat and anesthetized in dilute ethyl 3-aminobenzoate. All fish were measured to the nearest millimeter. For comparability with previous work on these species, we measured standard lengths (SL) of black sea bass, tautog, and cunner, and fork lengths (FL) of scup. After measuring, we tagged all fish greater than 71 mm SL (or, if scup, FL) in 2004 and all fish greater than 109 mm FL in 2005. Fish were tagged with numbered anchor tags (Floy Tag® types FF-94 and FD-68B FF; Floy Tag®, Seattle, Washington). All fish were allowed to recover from the anesthetic before being released at their point of capture.

Relative fish density

We used the number of fish caught per trap as an index of relative density, which assumes that traps sample an equal volume of water with equal efficiency in all three habitats. We tested for effects of soak time on the number of fish captured per trap, by including soak time as a covariate in the models testing for effects of habitat on fish relative densities (described below in the results). Soak time always had a negligible effect ($P > 0.05$), so relative densities were not adjusted for variable soak times. Relative density was calculated for each species at each site for each sampling day. Data from 2004 and 2005 were analyzed separately. In 2004, data from the black sea bass pots and O-pots were pooled because we assumed they would sample with similar effectiveness. Fish relative densities were, however, calculated separately by trap type in 2005 to test this assumption explicitly.

We used analysis of variance (ANOVA) to test for effects of habitat (a fixed effect), individual sites (a fixed effect nested within habitat), sampling session (a random effect), and interactions between these factors. The primary goal was to compare oyster cage and natural rocky reef habitats. Because there was only one artificial reef site, this habitat was not included in the ANOVAs, but mean relative densities on the artificial reef are presented for comparative purposes. Scup were sufficiently abundant to allow separate analyses of three age-class, defined using established size-age relationships: age-0 (< 99 mm fork length (FL)), age-1 (100 mm –154 mm FL), and age–1+ (>154 mm FL) (Morse 1978; Gray 1991).

Growth and disappearance rates of scup

Of the four study species tagged, only scup were recaptured in great enough numbers to permit calculation of growth and disappearance rates. Individual growth rates were obtained by remeasurement of all tagged scup that were recaptured after being at liberty for more than 4 d. We selected this minimum interval between captures because after 4 d, growth was always greater than measurement error. Growth rates were calculated as percent increase in initial FL per day. We combined data from 2004 and 2005 and used analysis of covariance (ANCOVA) to test for differences in growth of scup between oyster cage and natural rocky reef habitats, using individual fish as replicates. ANCOVA models included effects of habitat type and sites (nested within habitat) as fixed categorical variables. Initial FL and relative density were tested as linear covariates. Prior to testing our hypotheses using ANOVA and ANCOVA, we checked that data conformed to model assumptions (Sokal and Rohlf 1995). Following Winer et al. (1991), we used post-hoc pooling procedures to sequentially remove non-significant interactions and nested terms from models.

We also used the mark-recapture information on scup to calculate their disappearance rate. These analyses were based on recapture histories, where each tagged scup was recorded as being either recaptured or not for each of the three sampling sessions. A few scup were recaptured at sites outside the study area (see results), indicating that at least some emigration occurred. Recorded instances of emigration were, however, too few to estimate emigration rates. Calculated disappearance rates thus include both emigration and mortality. We fit models commonly used for survival analysis to the data, using the date of tagging as a common

start day (Lee 1992). The recapture histories yielded a mix of interval-censored (disappearance between sample sessions) and right-censored (alive at end of study) observations. We fit the simplest exponential model, which assumes a constant instantaneous loss rate because it appeared to fit the data adequately, and only very slight improvements in fit were obtained with more complex Weibull and Cox models. All statistical analyses were done using SYSTAT, version 11.0 (SYSTAT Software, Inc., Richmond, California).

Results

Scup relative density, growth and disappearance

Age-1 and older scup were at higher relative densities at oyster cage sites than at natural rocky reefs in both 2004 (age-1 scup ANOVA: $F = 5.629$; df = 1,52; $P = 0.021$, age-1+ scup ANOVA: $F = 14.790$; df = 1,52; $P < 0.001$) and 2005 (age-1 scup ANOVA: $F = 12.582$; df = 1,141; $P < 0.001$, age-1+ scup ANOVA: $F = 22.286$; df = 1,141; $P < 0.001$) (Figure 2). Age-0 fish, however, showed no consistent pattern, with significantly higher relative densities at natural rocky reefs in 2005 (ANOVA: $F = 4.825$; df = 1,141; $P = 0.03$), and no detectable difference among habitats in 2004 (ANOVA: $F = 1.213$; df = 1,52; $P = 0.276$) (Figure 2). The relative density of scup at the artificial reef was neither consistently higher nor lower than at the other two habitats, and generally fell between the two (Figure 2).

Of the 735 scup tagged in 2004, 78 were recaptured (10.6%) and of the 632 scup tagged in 2005, 100 were recaptured (15.8%). The higher recapture rate in 2005 may be due to the increased trapping frequency, or because larger fish (>109 mm FL) were tagged in 2005 than in 2004 (>71 mm FL). The ANCOVA model testing effects of

habitat type, sites (nested within habitat), initial FL and relative density on scup growth revealed no significant interactions between factors (*P* always > 0.29), so interaction terms were removed from the model. Small scup did, however grow faster than large scup (ANCOVA: $F = 20.427$; df = 1,112; $P < 0.001$; Fig. 2). Growth rates differed among habitats (ANCOVA: $F = 9.745$; df = 1,112; $P = 0.002$), but did not differ among the sites within each habitat (ANCOVA: $F = 1.718$; df = 5,112; $P = 0.136$). Overall, the mean growth rate of scup at natural rocky reefs was roughly 1.5 times faster ($\bar{x}$ = 0.279%/d) than that at oyster cages ($\bar{x}$ = 0.169%/d) (Figure 3). Relative density had no detectable effect on growth (ANCOVA: $F = 1.718$; df = 5,112; $P = 0.136$), but the test for this effect was confounded with habitat because scup were more abundant at oyster cages than at natural rocky reefs.

While trapping at our study sites, no scup was recaptured at a site other than the site at which it was tagged. We thus found no evidence of emigration amongst our study sites. We did, however, verify three records of tagged scup caught elsewhere. In two instances, the fish were caught by anglers about a month after tagging within 10 km of the initial tagging sites. The third scup was caught six months after being tagged by a fishing vessel in Hudson Canyon, approximately 250 km southwest of Narragansett Bay.

Most scup recaptures at our study sites occurred less than16 d after the date of initial capture (91% on natural rocky reefs, 89% on oyster cages, and 83% on the artificial reef). Thirteen scup were recaptured more than 30 d after initial capture, and one was recaptured almost a year later (334 d). In both years, the disappearance rate of scup was lower at oyster cages than on natural rocky reefs. When 2004 and 2005

data were pooled, the instantaneous disappearance rate from oyster cage habitats (n = 881) was 0.234 and the disappearance rate from natural rocky reefs (n = 253) was 0.312. Based on the lack of overlap in the 95% confidence intervals (CI), this roughly 25% reduction in disappearance rate from oyster cage habitat was statistically significant (Figure 4). The rate at which scup disappeared from the artificial reefs (0.334, n = 84) was not distinguishable statistically from that at the other two habitats (95% CI = 0.273 - 0.430).

Relative densities of black sea bass, cunner and tautog

In both 2004 and 2005, the relative density of black sea bass increased from July to October (2004 ANOVA: $F = 16.391$; df = 2,52; $P < 0.001$, 2005 O-pot ANOVA: $F = 19.084$; df = 2,141; $P < 0.001$, 2005 Minnow trap ANOVA: $F = 17.373$; df = 2,135; $P<0.001$). Relative densities of black sea bass did not, however, show any consistent differences among habitat types (Figure 5). In 2004, all 68 black sea bass caught were age-1 or older (Able and Hales 1997) and relative density showed no obvious differences between natural rocky reefs and oyster cages (ANOVA: $F = 0.337$; df = 1,52; $P = 0.564$). In 2005, however, 542 of the 549 black sea bass caught were age-0. There was a detectable difference in density measured using O-pots in 2005, with more black sea bass at the natural rocky reef sites (ANOVA: $F = 4.477$; df = 1,141; $P = 0.036$). However, this trend was not apparent in catches from minnow traps in 2005 (ANOVA: $F = 0.427$; df = 1,135; $P = 0.515$). Relative density at the artificial reef also showed no consistent tendency to be higher or lower than at the other habitats (Figure 5).

In contrast to black sea bass, cunner did show a consistent habitat-specific pattern of relative density. Cunner were always denser at natural rocky reefs and at the artificial reef, than at oyster cages (Figure 6). The difference in density between natural rocky reefs and oyster cages was statistically significant in 2005 (O-pot ANOVA: F = 5.929; df = 1,135; P = 0.016; Minnow trap ANOVA: F = 7.265; df = 1,141; P = 0.008), but not in 2004 (ANOVA: F = 1.261; df = 1,52; P = 0.267).

Tautog were generally less abundant than the other three study species, and there were no obvious changes in tautog relative density among sample sessions (2004 ANOVA: F = 2.029; df = 1,52; P = 0.135, 2005 O-pot ANOVA: F = 0.59; df = 1,141; P = 0.556, 2005 Minnow trap ANOVA: F = 4.05; df = 1,135; P = 0.046). Like cunner, and scup, tautog differed consistently in relative density among habitat types. Tautog were always denser at oyster cages than at natural rocky reefs (Figure 7), but this difference was only statistically significant for minnow trap catches (2004 ANOVA: F = 3.021; df = 1,52; P = 0.088, 2005 O-pot ANOVA: F = 2.502; df = 1,141; P = 0.116, 2005 Minnow trap ANOVA: F = 4.05; df = 1,135; P = 0.046). Although the artificial reef was not compared to the other habitats statistically, it appears that tautog were denser at the artificial reef than at either oyster cages or natural rocky reefs (Figure 7).

Discussion

Do fish traps accurately measure relative density?

All methods of estimating fish density in the field have potential biases (Rozas and Minello 1997). We used fish traps because all of our study species are known to readily enter traps (e.g. Able and hales 1997; Able et al. 2005), and the three commercially valuable species are harvested using traps (Eklund and Targett 1991).

Our primary concern in this study is not bias in the absolute catch rate of traps, but that relative catch rates among habitats accurately reflect relative differences in fish density. One step we took to reduce possible trap bias was to use multiple trap types. The fact that three different trap types yielded the same patterns of captures across habitats eliminates the possibility of bias unique to any one trap type. Nonetheless, we cannot rule-out the possibility that all three trap types sampled more efficiently in one habitat than another. One way to assess any bias common to all three trap types would be to directly observe fish interacting with traps in each habitat (e.g. Able et al. 2005), but poor underwater visibility thwarted most of our attempts at this. We also considered comparing trap-based density estimates with estimates from an alternate method (e.g. Layman and Smith 2001; Edgar et al. 2004). Unfortunately, the most promising alternate methods for our study species, seining, trawling, and visual census using SCUBA, were not usable at our sites because the habitat interferes with nets and underwater visibility is low.

Are oyster grow-out cages equivalent to natural and artificial reefs?

In this study, we assessed a poorly studied, environmental effect of oyster grow-out cages - their value as habitat for reef-associated fishes. Assessing the value of artificial habitats requires explicit comparison of the artificial and natural habitat (Carr and Hixon 1997). Interestingly, the relative density of our four study species showed no consistent pattern of difference among the oyster cages and natural rocky reefs. Both tautog and scup (age-1 and older) were at least three times denser on the oyster cages than on natural rocky reefs, whereas cunner were roughly three times more dense on natural rocky reefs. Black sea bass, however, showed no discernible difference in

density among habitats. For scup, the only species abundant enough to analyze by age-class, their preference for different habitats was age-specific. Although age-1 and older scup were denser on oyster cages than natural rocky reefs, age-0 scup showed no consistent difference. Clearly, then, although oyster cages provide suitable habitat for reef-associated fishes, they will support a finfish community quantitatively different in composition from that on natural rocky reefs. The same is true, however, of most artificial reefs deliberately constructed to mimic natural habitat (Seaman and Sprague 1991; Pratt 1994). In our study, for example, Tautog showed a strong preference for the granite artificial reef over either the natural rocky reefs or the oyster cages.

Do oyster grow-out cages increase regional fish abundance?

The most controversial, and difficult to assess, putative benefit of artificial reefs is whether they can increase regional fish abundance (Bohnsack 1989; Pickering and Whitmarsh 1997; Osenberg et al. 2002). The regional benefit of artificial reefs depends on (1) the amounts of natural and artificial habitats, (2) the extent to which artificial reefs redistribute individuals that would otherwise recruit to natural habitats, and (3) the strength of density dependent growth and survival in each habitat afterwards (Osenberg et al. 2002). No studies have addressed this issue unambiguously (Osenberg et al. 2002), and ours is no exception.

The species we studied occupy natural reefs of rock/cobble and biogenic materials (e.g. oysters, mussels, coral, and tube worms). They also occupy a variety of hard, three dimensional man-made structures (e.g. jetties, submerged pipelines and cables, shipwrecks and debris). It is difficult to precisely estimate the coverage of these natural and artificial reef habitats in Narragansett Bay (McMaster 1960; Poppe 2003;

Tiner et al. 2004) and in the Mid-Atlantic Bight generally (Steimle and Zetlin 2000; Stevenson et al. 2004). It is clear, however, that natural reefs are relatively rare in the region compared to soft sediments, and that natural oyster reefs in particular have declined dramatically over the past 100 years. Man-made structures, whether purposely or inadvertently deployed as reefs, are also rare but have increased in abundance over the past 100 years. The culture of oysters in grow-out cages is increasing in many parts of the US. The area covered by oyster grow-out cages in Rhode Island, for example, has been growing by 30% per year over the past 10 years and in 2005, grow-out cages at 25 leased sites covered 35 hectares of previously soft-sediment habitat.

Given the paucity of natural reef habitat in Narragansett Bay, it seems unlikely that all of the fishes recruiting to oyster cages would simply have colonized nearby natural rocky reefs had the oyster cages been absent. If that supposition is correct, the growth and disappearance rates of scup on the oyster cages can provide a rough indication of the potential enhancement of production attributable to oyster cages (Peterson et al. 2003). Interestingly, scup on oyster cages disappeared at a lower rate than scup on natural rocky reefs (by roughly 25%), indicating that some combination of mortality and/or emigration is reduced on oyster cages. This indication of better habitat quality on oyster cages was, however, offset by reduced growth rates at the aquaculture sites (by roughly 40%). The net consequence of these countervailing patterns of loss and growth is not certain, but they are relatively subtle in magnitude compared to the more than three-fold increase in scup density on oyster cages. Consequently, scup

production measured on a per-unit-area basis is almost certainly higher on oyster cages than on natural rocky reefs.

An important aspect of the aquaculture process that may affect the ultimate habitat value of grow-out cages is the protocol for cage maintenance and harvesting of oysters. Juvenile finfish might be trapped in the cages, or simply displaced by the removal of their habitat, when cages are pulled from the water for cleaning or harvest (O'Beirn et al. 2004). Aquaculture methods typically used in Rhode Island should however, minimize these sources of finfish mortality. Harvesting and maintenance usually occurs only two to four times a year, and cages are dragged through the water before being hauled above the surface to reduce by-catch. Because only a few cages are hauled up at one time, and returned to the water quickly, displaced finfish and invertebrates are likely to be able to seek refuge in other nearby cages. Evidence suggesting that most finfish do indeed escape is the fact that Kilpatrick (2002) recovered hundreds of juvenile fish when he enclosed grow-out cages in fine-meshed nets prior to removal from the water. In contrast, hauls of un-netted cages typically bring up only a handful of fish (R. Rheault, Moonstone Oysters, personal communication). Encouraging practices that minimize the impacts of harvesting and maintenance will be important in order to fully realize the benefits of grow-out cages as quality finfish habitat. With that caveat in mind, our results suggest that oyster grow-out cages do provide valuable habitat for finfishes and should be considered alongside other artificial reef designs as part of habitat restoration programs.

Do oyster-grow out cages provide habitat similar to natural oyster reefs?

The loss of natural oyster reefs has spurred much recent interest in restoring this habitat and the ecological services it provides (Ulanowicz and Tuttle 1992; Coen et al. 1999; Luckenbach et al. 1999). We did not compare grow-out cages to natural oyster reefs, simply because suitable oyster reefs are not present in Narragansett Bay. All of our study species have, however, been reported on natural oyster reefs in the Mid-Atlantic Bight (Steimle and Zetlin 2000; Peterson et al. 2003). It is thus possible that grow-out cages can provide habitat for reef-associated fishes that is similar to that provided by natural oyster reefs. Future research testing this hypothesis explicitly would be extremely informative.

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Figure captions

Figure 1. Map of the study sites indicating which sites were studied in 2004 only, 2005 only, or in both years.

Figure 2. Mean (±SE) relative density of scup in three habitat types. Only one artificial reef was sampled, so this datum has no SE and is displayed as a point rather than a bar. Separate plots are drawn for three age classes: age-0, age-1, and age-1+.

Figure 3. Mean (±SE) growth rates of age-1 and age-2 scup on natural rocky reefs and aquaculture sites.

Figure 4. An exponential model for disappearance rates (mortality and emigration) of scup on natural rocky reefs and aquaculture sites. Dotted lines represent 95% confidence intervals.

Figure 5. Mean (±SE) relative density of black sea bass in three habitat types. Only one artificial reef was sampled, so this datum has no SE and is displayed as a point rather than a bar.

Figure 6. Mean (±SE) relative density of cunner in three habitat types. Only one artificial reef was sampled, so this datum has no SE and is displayed as a point rather than a bar.

Figure 7. Mean (±SE) relative density of tautog in three habitat types. Only one artificial reef was sampled, so this datum has no SE and is displayed as a point rather than a bar.

Figure 1

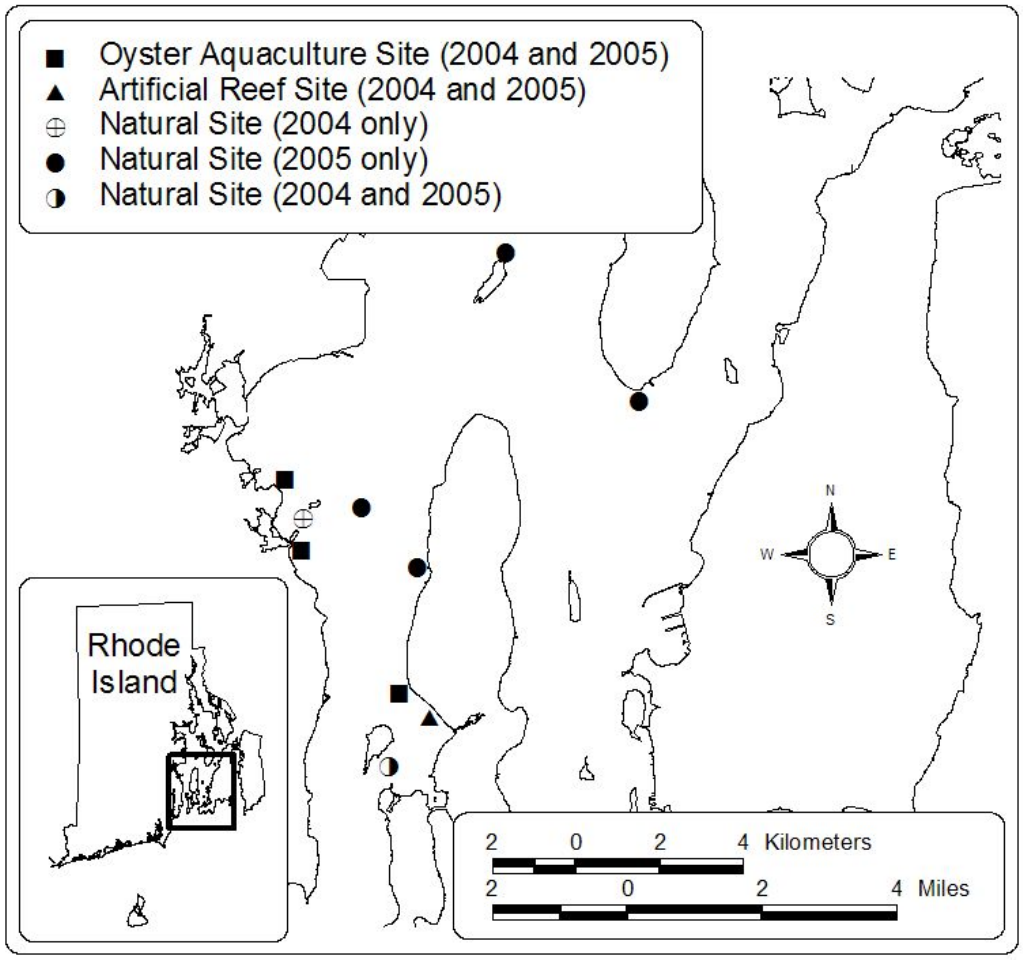

Oyster Aquaculture Site (2004 and 2005)
Artificial Reef Site (2004 and 2005)
Natural Site (2004 only)
Natural Site (2005 only)
Natural Site (2004 and 2005)
Rhode Island
N
W
E
S
2 0 2 4 Kilometers
2 0 2 4 Miles

Figure 2

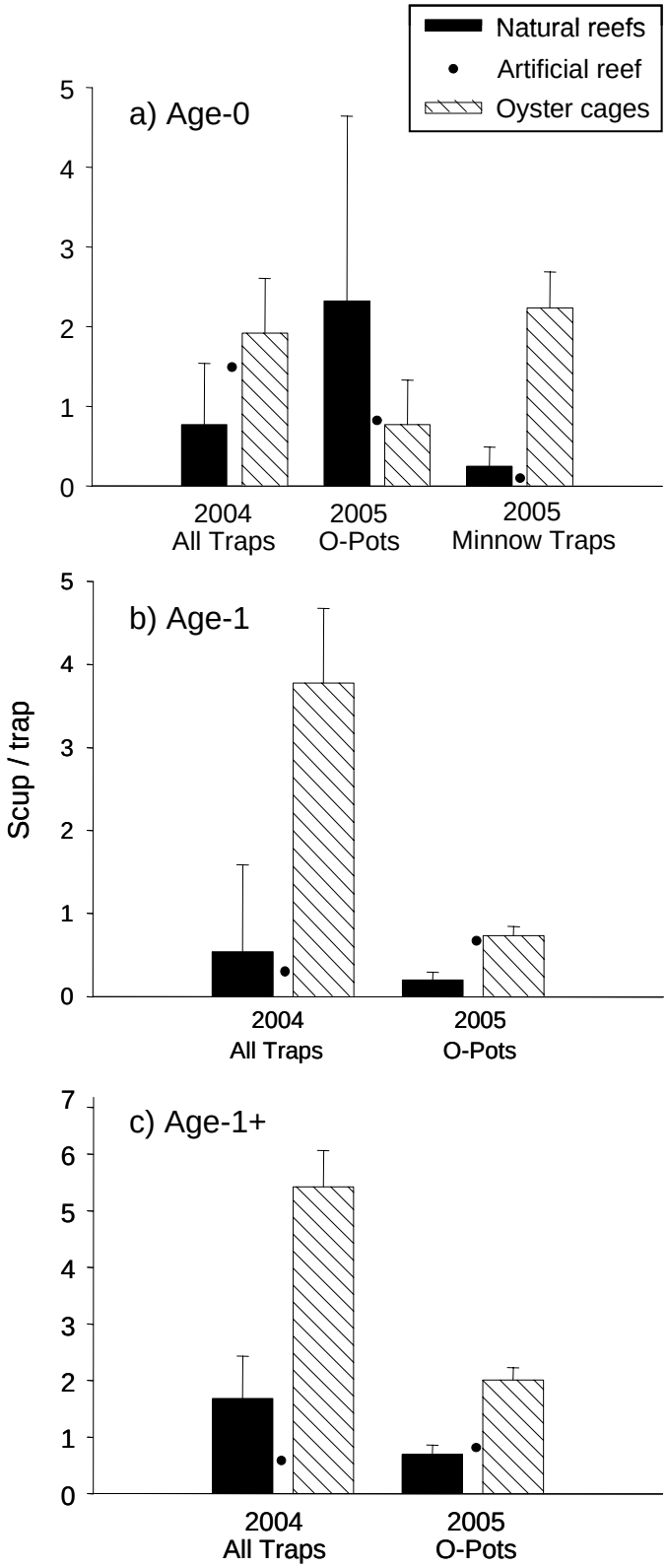

Natural reefs
Artificial reef
Oyster cages
a) Age-0
5
4
3
2
1
0
2004
All Traps
2005
O-Pots
2005
Minnow Traps
b) Age-1
Scup / trap
5
4
3
2
1
0
2004
All Traps
2005
O-Pots
c) Age-1+
7
6
5
4
3
2
1
0
2004
All Traps
2005
O-Pots

Figure 3

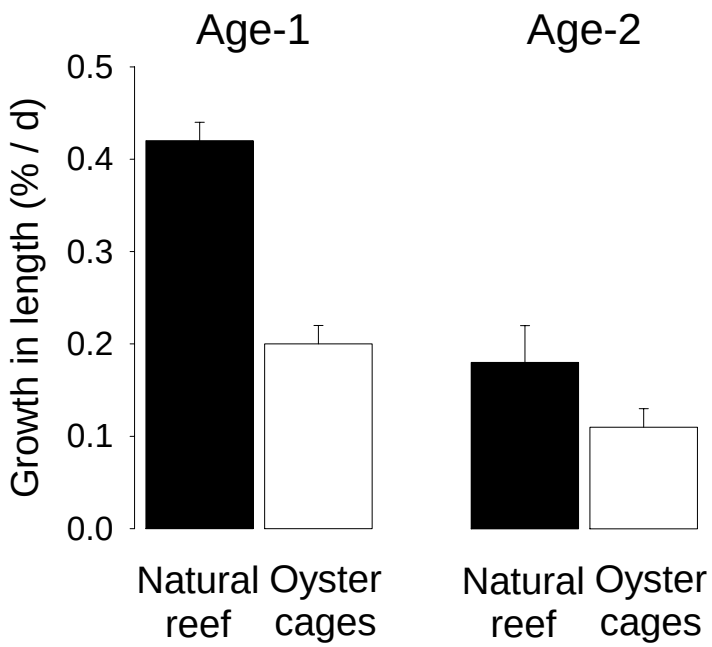

Age-1
Age-2
Growth in length (% / d)
0.5
0.4
0.3
0.2
0.1
0.0
Natural reef
Oyster cages
Natural reef
Oyster cages

Figure 4

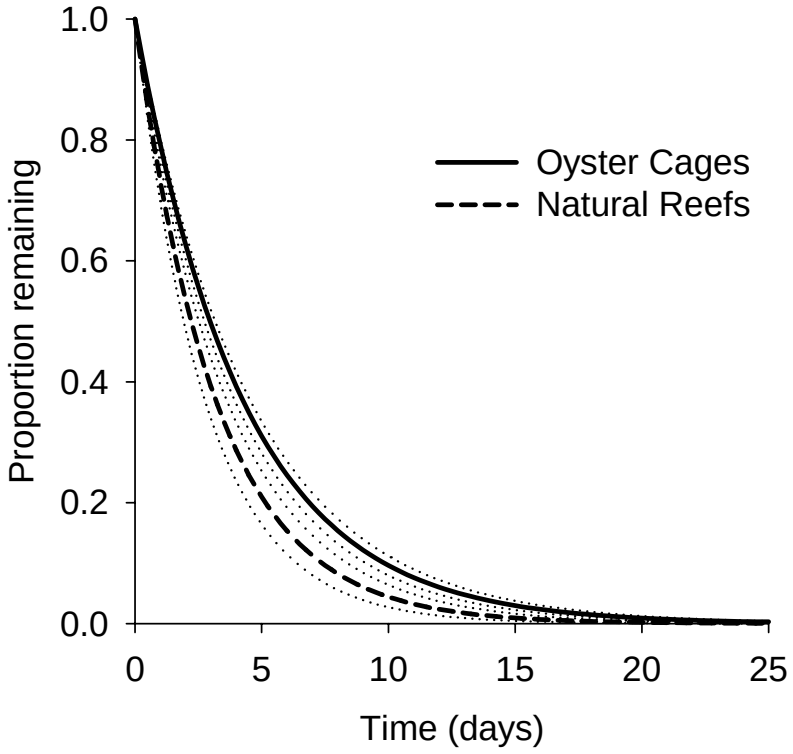

1.0
0.8
0.6
0.4
0.2
0.0
Proportion remaining
0
5
10
15
20
25
Time (days)
Oyster Cages
Natural Reefs

Figure 5

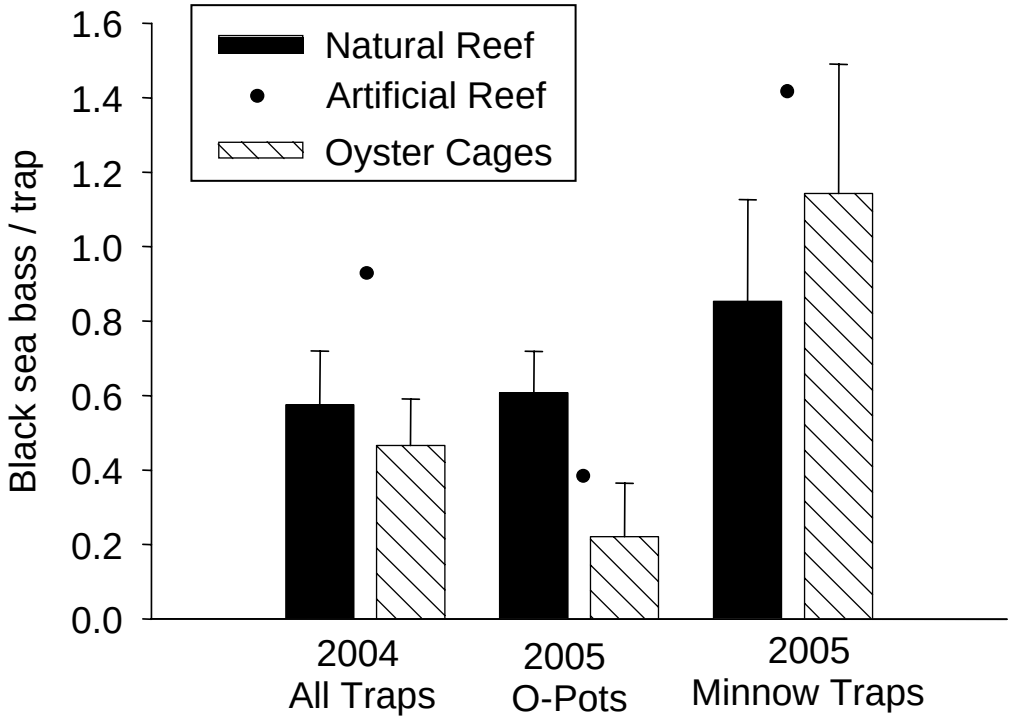

Natural Reef
Artificial Reef
Oyster Cages
Black sea bass / trap
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
2004
All Traps
2005
O-Pots
2005
Minnow Traps

Figure 6

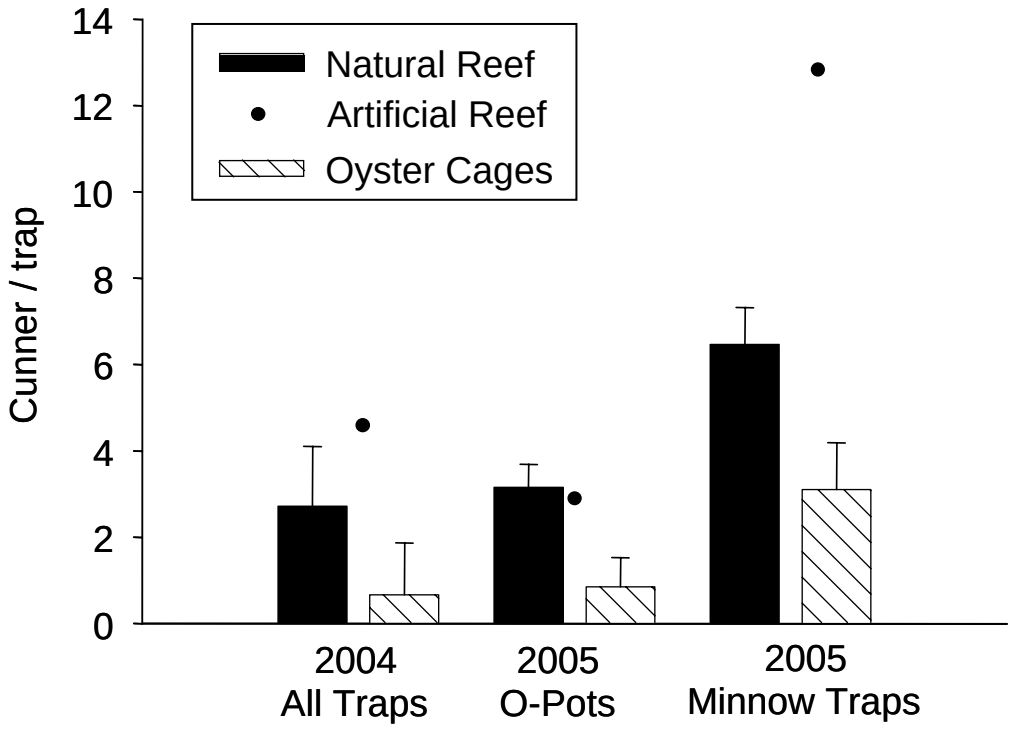
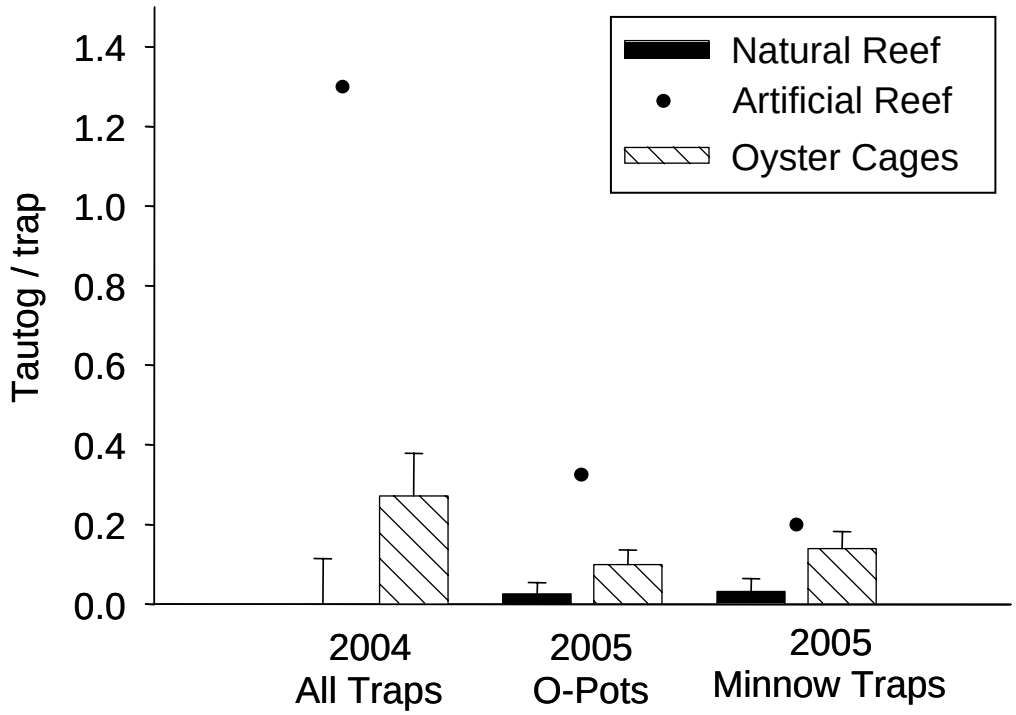

Natural Reef
Artificial Reef
Oyster Cages
Cunner / trap
0
2
4
6
8
10
12
14
2004
All Traps
2005
O-Pots
2005
Minnow Traps

Figure 7


Natural Reef
Artificial Reef
Oyster Cages
Tautog / trap
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
2004
All Traps
2005
O-Pots
2005
Minnow Traps