

Selection of Estuarine Habitats by Juvenile Gags in Experimental Mesocosms

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Abstract.—The degradation and destruction of estuarine habitats threaten the organisms that depend on these habitats for food and shelter. Gags *Mycteroperca microlepis* reside on rocky reefs for most of their lives but initially settle and rear in estuarine habitats before moving to offshore reefs. Gag populations have declined to the point where some consider them vulnerable to extinction, and the recovery of the species requires an understanding of what habitats these fish use and why they use them. We examined the habitat selection of juvenile gags in North Carolina using experimental mesocosms. We manipulated the shelter characteristics of habitats and compared the foraging rates of gags to determine the specific attributes of habitats that influence habitat selection. Gags selected structured seagrass or oyster reefs over sand and shell hash habitats. While gags did not show a preference between eelgrass *Zostera marina* and oyster reefs, they did choose oyster reefs over shoal grass *Halodule wrightii* and selected seagrass habitats with high shoot densities over those with lower densities. The addition of a small shelter to the habitat that the gags did not choose dramatically increased their use of that habitat. Finally, when we provided pinfish *Lagodon rhomboides* as prey, gag foraging rate did not vary among seagrass habitats with different shoot densities. However, gags consumed penaeid shrimp at much lower rates in seagrass habitats of high shoot density. Our results agree with those of other studies suggesting that seagrass habitats are important to gags. However, our results also emphasize that gags select specific attributes within seagrass landscapes and suggest that oyster reefs may be important habitats for them.

Worldwide declines of exploited fish species (e.g., Music et al. 2000) are widely publicized examples of crises in resource management. Recognition of the drawbacks of traditional fishery management schemes, which focused on assessing stock size and controlling fishing mortality, was codified in the Magnuson–Stevens Fisheries Conservation and Management Act of 1996. This act requires fisheries agencies to protect, restore, and enhance all “essential fish habitats,” thereby making the conservation of fish habitats an integral part of fishery management. The vegetated habitats typical of many estuaries are complex habitats with a diversity of microhabitats that may contribute to the growth and survival of fish that depend on estuaries (Orth et al. 1984; Irlandi and Crawford 1997; Levin et al. 1997; Minello 1999). While seagrass meadows and the emergent vege-

tation of marshes and mangroves are considered critical habitats for most estuarine-dependent species, specific habitat types essential to maintaining the productivity of most such species have not been identified (Minello 1999). Because microhabitat quality can be an important determinant of recruitment success (Levin 1991; Carr 1994), there is a clear need to determine which microhabitats within estuaries are essential to fish productivity.

We examined habitat selection by juvenile gags *Mycteroperca microlepis*. Historically, gags were one of the most important components of recreational and commercial fisheries in the South Atlantic Bight (Harris and Collins 2000). Indeed, in the United States gags accounted for 27% of recent recreational catches by weight (Levin and Grimes 2002). Gags have been overfished to the point where some consider them vulnerable to extinction (Music et al. 2000). The dire status of gag stocks clearly makes understanding the factors affecting the production of new recruits of fundamental importance.

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Postlarval gags settle in estuarine waters in spring and early summer (Keener et al. 1988). Once settled, juvenile gags show strong site fidelity (Heinisch and Fable 1999) and suffer low rates of mortality (Koenig and Coleman 1998). Newly settled gags occur in structurally complex habitats and are frequently reported as members of seagrass communities (Summerson and Peterson 1984; Ross and Moser 1995; Koenig and Coleman 1998). After a 4–6 month period during which body length increases by about 700%, gags leave the estuary for offshore reef habitats, where they reside for the rest of their lives (Adams 1976; Keener et al. 1988).

Although seagrass meadows are typically considered gag nursery habitat (Ross and Moser 1995; Koenig and Coleman 1998), seagrass beds are complex habitats with a diversity of microhabitats that may or may not contribute to the growth and survival of gags. For instance, in Texas, nearly four times more red drum *Sciaenops ocellatus* were captured in seagrass beds dominated by shoal grass *Halodule wrightii* as in those dominated by turtle grass *Thalassia testudinum* (Rooker and Holt 1998). While it is important to determine which microhabitats are essential for successful recruitment of juvenile gags, low densities of fish make this difficult. To overcome this obstacle, we examined the habitat selection of gags using outdoor experimental mesocosms. Specifically, we asked whether juvenile gags choose among typical estuarine habitats (seagrass, oyster reefs, shell hash, and sand) that vary structurally. We then manipulated the shelter characteristics of these habitats and compared the foraging rates of gags to determine the specific attributes of habitats that influence habitat selection.

Methods

Experimental organisms.—We collected juvenile gags from Back Sound near Beaufort, North Carolina (34°42'N, 76°35'W), using standard minnow or Morton (Schwartz 1986) traps. Upon capture, fish were placed in 379-L insulated containers and subsequently transferred to 5,000-L running seawater tanks at the University of North Carolina Institute of Marine Sciences. Fish were housed in these holding tanks and exposed to ambient light and temperatures for 24–72 h before being placed in the experimental mesocosms described below. Each gag was used only once and in one experimental replicate. After use, gags were released.

Selection of estuarine habitats.—Experiments evaluating habitat selection were conducted in ten

1.44-m² enclosures (1.2 m × 1.2 m) placed within a large (6.2-m × 9.2-m) concrete pond supplied with running seawater from adjacent Bogue Sound. The enclosures were 90 cm deep and arranged in two rows of five about 1 m from the edge of the pond, with about 40 cm between enclosures. Each enclosure was divided into four quadrants arranged such that they formed a square, and a wooden tray (60 × 60 × 5 cm) filled with sand was placed in each quadrant. Experimental habitats were then constructed in each sand-filled tray. In the first experiment, one of the following habitat structure treatments was randomly assigned to each quadrant: (1) eelgrass *Zostera marina* at a density of 800 shoots/m² (approximately the mean density at nearby sites; see also Irlandi et al. 1999); (2) oyster shells (9.5 L) forming a reeflike structure; (3) a 2.5-cm-thick layer of shell hash (i.e., broken shells); and (4) bare sand. We collected seagrass from a nearby site, rinsed all sediment from the roots and washed the plants in freshwater to remove macrofauna before planting them haphazardly in the sand-filled frame. Oyster shells and shell hash were also collected from nearby sites, allowed to sun-dry for 7 d, and washed with freshwater prior to being placed in the enclosures.

A juvenile gag (mean standard length [SL] = 95.5 mm, SD = 7.5) was placed in the center of each enclosure between 0700 and 0800 hours. The behavior of fish in the enclosure was qualitatively similar to that of gags we had observed in the field on other occasions. At 0900 hours and every hour thereafter until 1700 hours, we noted the position of each fish within the enclosure. We observed fish from the side of the enclosure, and fish were never seen moving in response to observers. A priori, we were interested in addressing two questions: first, whether gags associated disproportionately with structured habitats (i.e., eelgrass and oyster reefs), and second (because we expected them to associate with such habitats), whether there were differences between their associations with eelgrass and oyster habitats. These analyses were conducted using a planned comparison of means within an analysis-of-variance (ANOVA) framework (Day and Quinn 1989).

The seagrass beds in our study area are at the biogeographic boundary between eelgrass and shoal grass, with the southern species (shoal grass) becoming dominant as the summer progresses (Ferguson et al. 1993). Consequently, we repeated the experiment described above with shoal grass instead of eelgrass in our seagrass treatment. Al-

though we used the same density (800 shoots/m²) of shoal grass and eelgrass in these experiments, the biomass of a given density of shoal grass is less than that of eelgrass. Consequently, we provided less structure in the shoal grass than in the eelgrass treatments. During these assays, we also increased the number of replicates to 20. Data were analyzed as described above.

Effects of added structure on habitat selection.—In these experiments, we asked whether the presence of added structure affected habitat selection by juvenile gags. First, within the replicate 1.44-m² enclosures, we created two habitats: (1) seagrass (shoal grass at a density of 800 shoots/m²) and (2) oyster reef. Following the protocol described above, we noted the frequency with which gags used each habitat and used a paired *t*-test to determine whether gags selected one habitat over the other. We then added a shelter site (a polyvinyl chloride [PVC] pipe 23 cm long and 5 cm in diameter) to the habitat that the gags did not select and repeated the experiment.

Secondly, within the replicate enclosures, we created two shoal grass habitats, one with 1,200 and one with 400 shoots/m². As above, we first performed an experiment to determine which of the two habitats gags selected and then added a PVC pipe to the habitat not selected.

Effects of simulated seagrass structure on foraging rate.—To evaluate the effects of seagrass structure on the foraging rate of gags, we created five circular mesocosms 1.82 m² in area and 30.5 cm deep that had running seawater at ambient temperature. Within each mesocosm, we added sand to a depth of about 7.5 cm and used green ribbon to simulate seagrass habitats with 0, 300, 600, 1,800 and 4,900 shoots/m². The artificial seagrass habitats consisted of a 0.79-m² plastic mesh base onto which buoyant green ribbon (40 cm high and 0.5 mm wide) was woven. The base of the artificial seagrass patch was buried in the sand. Each habitat was randomly assigned to one of our five mesocosms.

We next added 10 juvenile pinfish *Lagodon rhomboides* (mean SL = 42.1 mm, SD = 3.0) to each mesocosm as prey. This density of pinfish (5.4/m²) was similar to what we observed in natural seagrass habitats in this area (Petrik and Levin 2000). Juvenile pinfish appear to be important prey of young-of-the-year gags in some locations (Mullaney and Gale 1996) and were the most common small fish present in the sites from which the gags were captured (Petrik and Levin 2000). We allowed the pinfish to acclimate for 24 h and then

added a single gag to each treatment. After 36 h, we drained the mesocosms, removed the gag, and counted the remaining pinfish. We performed the experiment 17 times. For each trial we rerandomized the assignment of treatments. An ANOVA with seagrass density as the main effect and date as a blocking factor was used to test the hypothesis that the number of pinfish consumed varied among mesocosms with different densities of seagrass.

We repeated the experiment using penaeid shrimp (mean length = 49.7 mm, SD = 8.9) as prey. Shrimp are an important component of the diet of juvenile gags (Mullaney and Gale 1996) and were very common in our field sites. We followed the same protocol as described above (10 shrimp/arena) and performed the experiment 18 times.

Results

Selection of Estuarine Habitats

When we provided juvenile gags with eelgrass, oyster, shell hash, and sand habitat, fish clearly did not use habitats at random. Gags occurred in eelgrass habitat in 32% of the observations, compared with 47% in oyster habitat, 11% in shell hash, and 10% in sand. Thus, although gags did use unstructured habitats, they were significantly associated with structured habitats ($F = 6.65$; $df = 1, 36$; $P = 0.01$). However, when we tested for differences in habitat use between eelgrass and oyster habitat, we were unable to detect a difference ($F = 0.84$; $df = 1, 36$; $P = 0.37$).

The replacement of eelgrass with shoal grass in experimental mesocosms did not alter the general result that gags do not use habitats at random. Gags occurred in shoal grass habitat in 24% of observations, compared with 54% in oyster habitat, 11% in shell hash, and 10% in sand. Again, in 79% of our observations, gags were located in either shoal grass or oyster habitat and thus selected structured over unstructured habitat ($F = 22.53$; $df = 1, 76$; $P < 0.001$). However, in contrast to the results with eelgrass, gags did demonstrate a preference for oyster habitat over shoal grass ($F = 9.42$; $df = 1, 76$; $P = 0.003$).

Effects of Added Structure on Habitat Selection

When given only a choice between shoal grass and oyster habitat, gags again tended to select oyster habitat (Figure 1); gags occurred in oyster habitat in about 62% of observations and in shoal grass habitat in 38% of observations ($t = 1.92$; $df = 28$; $P = 0.06$). The addition of shelter to the shoal grass habitat eliminated this apparent dif-

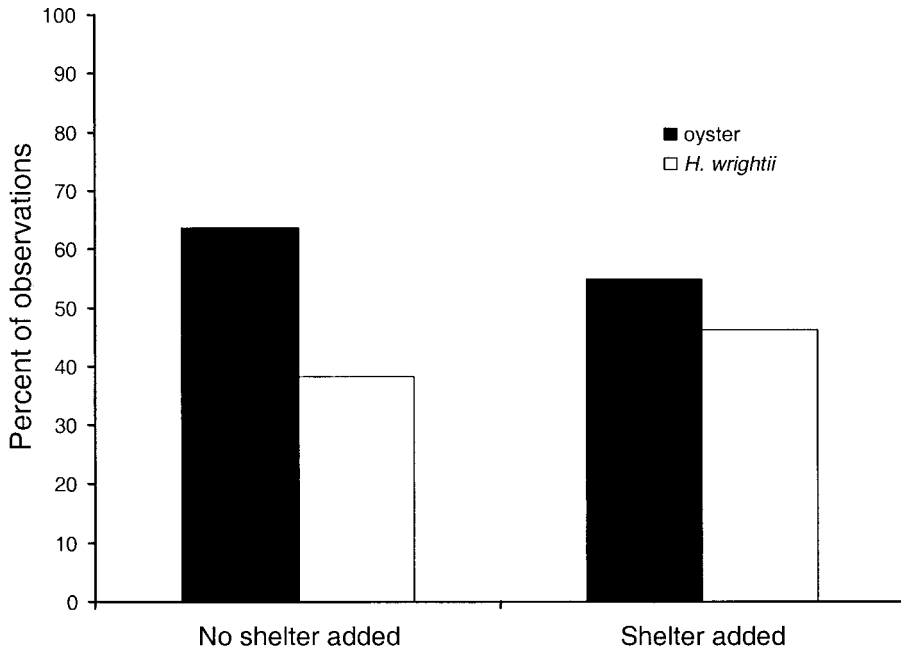


FIGURE 1.—Percent of juvenile gags in experimental mesocosms that were observed in oyster and shoal grass (*H. wrightii*) habitats, with and without added shelter (i.e., a polyvinyl chloride pipe).

ference (Figure 1). With it, gag use of shoal grass increased to 46% while use of oyster habitat declined to 54% ($t = 0.42$; $df = 13$; $P = 0.67$).

When we created high-density (1,200 shoots/m²) and low-density (400 shoots/m²) shoal grass habitats, gags again selected the habitat with more structure (Figure 2). Gags occurred in high-density habitats in 85% of observations but in low-density habitats only 15% of the time ($t = 6.31$; $df = 11$; $P < 0.001$). The addition of shelter to the low-density treatment removed this difference (Figure 2); the use of low-density habitat increased to 45% while that of high-density habitat declined to 56% ($t = 0.25$; $df = 8$; $P = 0.80$).

Effects of Seagrass Habitat on Foraging Rate

The rate at which gags consumed shrimp differed significantly among seagrass habitats (Figure 3). In habitats with 0, 300, or 600 seagrass shoots/m², gags consumed about twice as many shrimp per observation period as in habitats with 1,800 or 4,900 seagrass shoots/m² ($F = 4.49$; $df = 4, 68$; $P = 0.003$). No difference among sampling dates was evident ($F = 1.67$; $df = 17, 68$; $P = 0.07$). The rate at which pinfish were consumed, however, did not vary among seagrass habitats (Figure 3); about 4–5 pinfish were consumed in all habitats ($F = 1.31$; $df = 4, 64$; $P = 0.28$).

Discussion

Effective habitat conservation requires knowledge about what specific habitats fish use and why they use them. Previous field studies demonstrated that gags are associated with seagrass meadows (Ross and Moser 1995; Koenig and Coleman 1998). In addition, our experiments suggest that gags not only select seagrass over unstructured habitat but also select specific attributes of seagrass habitats. Gags clearly preferred high-density to low-density seagrass patches. Our results also suggest that they distinguish among seagrass species, although we did not explicitly test this. When gags were given a choice between eelgrass and oyster habitat, we were unable to detect a difference in habitat use. However, gags did select oyster over shoal grass habitat. Thus, at similar blade densities, gags may prefer eelgrass to shoal grass. Importantly, the morphologies of eelgrass and shoal grass are different. Eelgrass tends to have wider blades (1.5–3 mm) than shoal grass (0.3–1 mm) (Thayer et al. 1984). Furthermore, the shallower distribution of shoal grass results in shorter blades than in eelgrass (Thayer et al. 1984). Thus, the difference that we observed between species may reflect selection for greater structure rather than selection for a specific seagrass species (but see Levin and Hay 2002).

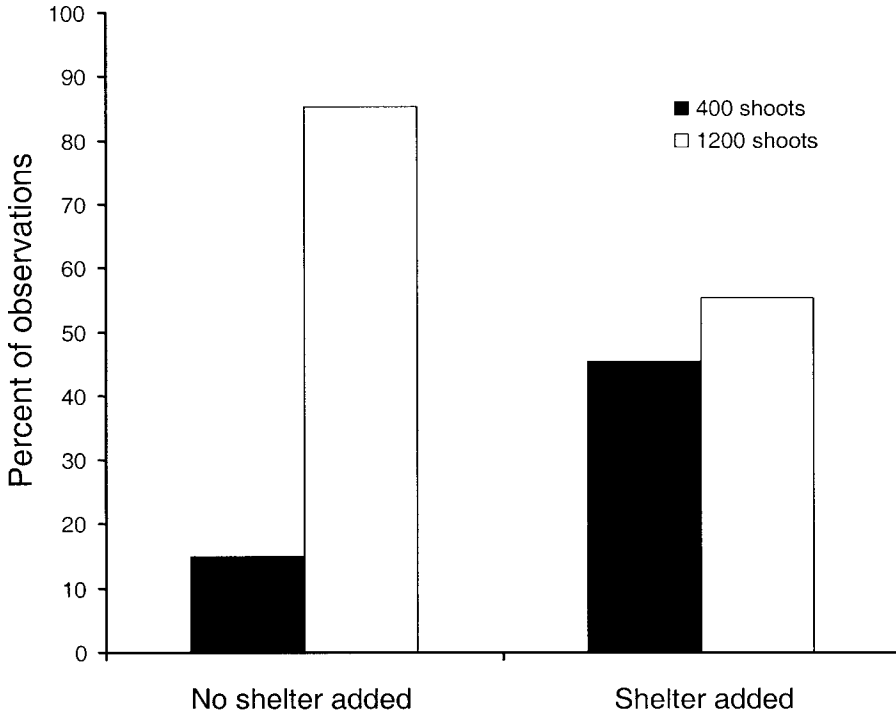


FIGURE 2.—Percent of juvenile gags in experimental mesocosms that were observed in shoal grass at densities of 400 and 1,200 shoots/m², with and without added shelter.

Our experiments in which shelter was added to seagrass patches indicate that gags use whatever structure is available within seagrass beds. Since groupers in general and gags in particular tend to use habitats that are structurally complex, this re-

sult is not surprising. Indeed, observations of juvenile gags in the field suggest that they use whatever topographic complexity is available in seagrass meadows (Levin and Grimes 2002). Our results, however, emphasize that the additional

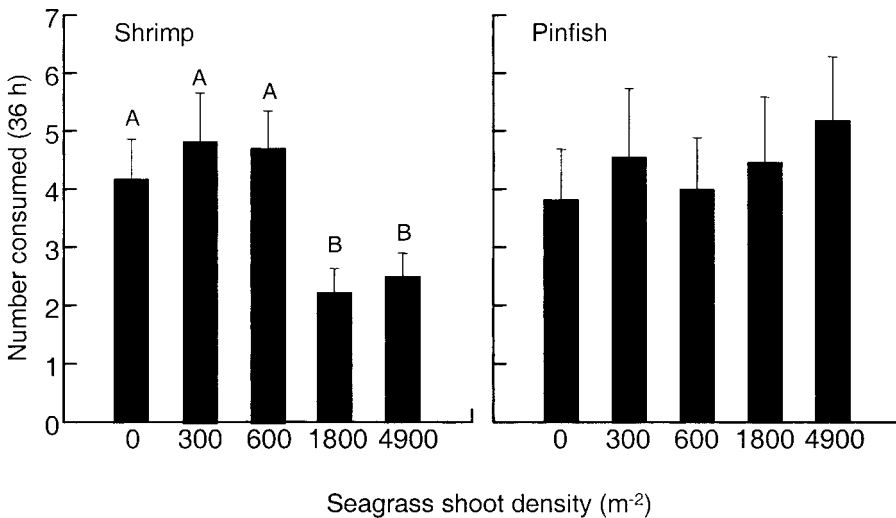


FIGURE 3.—Mean (+SE) number of shrimp and pinfish consumed by individual gags during 36-h periods in mesocosms of varying artificial seagrass densities.

structure associated with channels, mollusk shells, and hummocks may be important components of seagrass landscapes.

Although gags were strongly associated with structure, they also used unstructured sand or shell hash habitats more than 20% of the time. While this may be an experimental artifact, other juvenile groupers use unstructured habitat when it is associated with more structured habitat (Levin and Grimes 2002). For example, examination of the habitats used by juvenile coral trout *Plectropomus leopardus* on the Great Barrier Reef suggests that they selected coral rubble adjacent to sand (Light and Jones 1997). Similarly, the red drum *Sciaenops ocellatus*, a sciaenid, appears to use seagrass as a refuge and to forage in adjacent sand patches (Holt et al. 1983). Thus, it is possible that the use of unstructured habitats adjacent to seagrass or oysters by gags in our experimental enclosures is biologically meaningful and warrants further examination.

Although seagrass beds serve as gag nursery habitat (Ross and Moser 1995; Koenig and Coleman 1998), it is possible that seagrass is regarded as the primary habitat of gags simply because this habitat is better investigated than other habitats. Oyster reefs are abundant in many estuaries, but the difficulty of effectively sampling such reefs has resulted in there being few studies assessing their importance for juvenile fish (Coen et al. 1999; Minello 1999). Juvenile gags occur on oyster reefs in North Carolina (Lenihan et al. 2001) even though there are extensive seagrass meadows in this region. Additionally, juvenile gags occur in high densities on oyster reefs in bays where seagrasses are absent, and in such bays they prefer oyster reefs to other hard substrata (Keener et al. 1988). Our results further emphasize that oyster reefs may be critical habitat for juvenile gags. When we gave them a choice between seagrass and oyster habitat, they either selected oyster habitat over seagrass or used the two habitats at similar levels. Thus, the use of oyster reefs (and seagrass) by the gags seen in field studies ostensibly results from active habitat choice by the fish.

Mesocosms are useful for examining habitat utilization by fishes, as well as for identifying fruitful avenues of field research (e.g., Petrik et al. 1999; Gilliam and Fraser 2001; Stunz et al. 2001). However, caution is clearly warranted when extrapolating from mesocosms to field conditions. There may be artifacts associated with enclosure studies that influence the results (Peterson and Black 1994). Furthermore, such attributes as water depth,

turbidity, predator abundance, and food availability may interact with habitat structure and influence the distribution of fish (Ruiz et al. 1993; Benfield and Minello 1996; Levin et al. 1997; Stunz et al. 2001). For this reason, we feel that field studies testing our observations would provide additional insight into the full value of these habitats in natural estuaries.

The degradation and destruction of estuarine habitats threaten the organisms that depend on these habitats for food and shelter. The concept of essential fish habitat has brought habitat conservation to the forefront of fisheries management, but the difficulties of identifying essential habitat make this approach subject to the same problems that have plagued traditional fisheries management (Dayton et al. 1998). The low densities of fish, in concert with the difficulty of sampling habitats such as oyster reefs, make unequivocal demonstration of critical habitats difficult. For gags, seagrass beds are widely considered to be important, but the significance of other habitats is equivocal. Our results suggest that proper management of gag habitat may require the assumption that all structured habitats are critical unless it can be demonstrated that they are not (Underwood 1996; Dayton et al. 1998; Schmitt 1999). Such a risk-averse strategy increases the likelihood that active management of habitats will play an important role in the recovery of gag stocks.

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