Contents lists available at ScienceDirect



Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe



Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*)

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ARTICLE INFO

Article history: Received 11 March 2008 Received in revised form 15 December 2008 Accepted 19 December 2008

Keywords: Atlantic cod Edge effects Eelgrass Habitat patches Predation Tethering

ABSTRACT

Postsettled age 0 Atlantic cod (Gadus morhua) seek refuge from predation in eelgrass (Zostera marina) habitat within shallow, coastal nurseries. Laboratory and field experiments have demonstrated that predation risk on small fish is reduced in habitats of greater structure compared to less complex or barren environs. To determine if predation risk is linked to the areal extent of eelgrass coverage, we tested the hypothesis that predation risk of age 0 cod decreases with increasing eelgrass patch size. Predation on tethered age 0 cod (G. morhua and G. ogac) was quantified in eelgrass patches (1–80 m²) at three sites in northeastern Newfoundland, Canada, during September and October 1999 and 2000. Based on evidence of edge effects in terrestrial landscapes, we also tested the hypothesis that predation is elevated at ecotones separating eelgrass from adjacent barren mud substrate. We examined predation at the edge (i.e., 0 m) and both 5 and 10 m from this edge into and away from eelgrass cover along an 18 m long barren mud-gravel and eelgrass boundary, at two sites. Logistic regression analysis showed that the risk of predation, as measured by the odds ratio, increased with area over a small range of patch sizes (1-35 m² in 1999). When the study was extended to a wider range of patch sizes (1-80 m²) in 2000, a parabolic relationship emerged, with patches on the order of 25 m² providing the least safety and the largest patches (80 m²) providing the most safety. Predation on tethered cod was highest at the edge of eelgrass patches, compared with barren and eelgrass locations; predation generally decreased with distance from the eelgrass boundary. Our results are consistent with the hypothesis that predators are drawn to large patches of eelgrass because of increased prey numbers, that predators increase their success by searching edges, and that this results in greatest predation risk to prey in isolated patches of intermediate size.

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1. Introduction

Landscapes (including the seafloor) are comprised of mosaics of habitat patches, defined as contiguous, homogeneous structure at the finest available spatial scale (Nikora et al., 1999) with an edge that separates the patch from surrounding habitats (Fagan et al., 1999). In recent years, the abundance, density (Wiley et al., 1984; Maceina, 1996; Irlandi, 1997; Bell et al., 2001; Johnson and Heck, 2006), individual growth (Irlandi, 1996), and mortality (Irlandi, 1997; Hovel and Lipcius, 2001; Hovel, 2003; Hovel and Fonseca, 2005; Johnson and Heck, 2006) of organisms have been linked to the patch size of a preferred habitat for a given species. In aquatic environments, this research has predominantly focused on low mobility species such as decapods and bivalves. Patch size investigations have not resulted in consistent outcomes; in some cases, survival increases with patch size, and hence an increase in refuge area (Irlandi et al., 1995; Irlandi, 1997; Eggleston et al., 1998). However, some studies have found the opposite to be true (Hovel and Lipcius, 2001; Hovel and Fonseca, 2005). Explanations for these contradictory results include differences in life stage, in faunal species (Micheli and Peterson, 1999; Bell et al., 2001), in spatial or temporal scale (e.g. patch size, seasonality) of assessment (Hovel and Fonseca, 2005), in nature of the habitat (e.g. structural complexity), or in the physical and biological make up of local communities (Eggleston et al., 1998; Tewksbury et al., 1998; Micheli and Peterson, 1999).

Behavioral responses to predators can differ within patches or microhabitats. For example, unique species interactions may occur at the boundary—or edge—between two habitats that differ in structural complexity (Forman and Godron, 1981; Donovan et al., 1997). Edges often function as a microhabitat between a less structurally complex area, which allows for greater vision and mobility necessary for prey searching, and a habitat of greater structural complexity, serving as

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^{0022-0981/\$ -} see front matter © 2008 Elsevier B.V. All rights reserved. doi:10.1016/j.jembe.2008.12.008

refuge from predation. Some studies have found higher densities of species and survival rates at edges (Bologna and Heck, 1999) or in fragmented habitats that have more edge per unit area (Hovel and Fonseca, 2005), while others found the patch interior to be safer (Johnson and Heck, 2006). Young fish may seek edge zones that place them in close proximity to cover while foraging. Consequently, edge zones may increase risk by attracting predators to areas of high prey numbers. Edges may also act as a 'line of travel' for predators in pursuit of prey (reviewed by Andren, 1995). If edge effects are important, then the spatial layout of habitats of different structural complexities will affect the overall risk of predation.

Juvenile marine fish, including postsettled Atlantic cod (Gadus morhua) in their first year of life, often inhabit nursery areas consisting of structurally complex environments. In coastal Newfoundland, age 0 Atlantic cod are more abundant in complex areas, particularly in shallow water eelgrass (Zostera marina) habitats (Gotceitas et al., 1997; Grant and Brown, 1998b; Laurel et al., 2004), which have been shown to reduce predator efficiency in laboratory experiments (Gotceitas et al., 1997). Young cod are able to assess the degree of predation risk between active and inactive predators (Gotceitas et al., 1995), and they select habitats that minimize predation risk (Keats et al., 1987; Lough et al., 1989; Gotceitas and Brown, 1993; Tupper and Boutilier, 1995; Fraser et al., 1996; Borg et al., 1997; Gotceitas et al., 1997; Gregory and Anderson, 1997; Linehan et al., 2001). Predator avoidance is critical due to the distribution overlap of these cod with predators such as older (1-3 year old) gadids, including conspecifics (Bogstad et al., 1994; Salvanes et al., 1994; Grant and Brown, 1998a; Linehan et al., 2001), cunner (Tautogolabrus adspersus) and sculpin (Myoxocephalus scorpius) (Tupper and Boutilier, 1995; Linehan et al., 2001). Despite higher predator densities in areas with more eelgrass (Laurel et al., 2003a), predation risk on age 0 cod is lower in eelgrass areas than in less complex or barren habitats (Gotceitas et al., 1997; Linehan et al., 2001). Eelgrass habitats fragment and merge naturally with the passage of time (Tveite, 1984; Preen et al., 1999; Hovel and Lipcius, 2001). For the isolated patches in this experiment, the amount of patch edge within a fixed distance of the patch edge (e.g. 5 m) will increase in proportion to patch perimeter and hence length plus width of a patch, while patch area will increase roughly as the product of length by width. Knowledge of the relationship between both these structural components of habitat and relative fish mortality rates provides valuable insight into the effects of habitat fragmentation on juvenile fish survival.

We conducted two field experiments to investigate predation risk of postsettled age 0 cod with respect to the spatial configuration of individual eelgrass patches:

- 1) a "patch size" experiment, in which we examined relative predation in eelgrass patches varying in size from 1 to 80 m², and
- an "edge effects" experiment, in which we measured predation away from, at the edge, and within an eelgrass meadow along a transect across a boundary between eelgrass and barren mud-gravel.

In the patch size experiments, we expected that risk would be greater in smaller patches than in larger patches, which provide more cover. In the edge effects experiment, we expected that risk would be high in the barren, mud locations and low in the eelgrass refugia. We expected that cod tethered at the eelgrass edge would be subjected to greater predation than those tethered in the interior meadow and that risk would decrease with increasing distance to the edge.

2. Methods

2.1. Study area

Newman Sound is a fjord in the southwestern waters of Bonavista Bay, Newfoundland, Canada (48° 35'N, 53° 55'W). Newman Sound (41 km by 1.5–3.0 km) is comprised of inner and outer portions, separated by a sill 7 km from the head of the fjord. The maximum depth of the inner sound is 55 m, whereas the outer sound reaches depths up to 300 m toward the open ocean. The tidal maximum amplitude is 1.5 m. The variable slope along the shoreline results in both steep banks and shallow deltas.

In shallow subtidal areas along the coast of Newfoundland, eelgrass, a subtidal flowering plant, provides vertical relief amongst the barren mud, sand, and gravel substrates. In Newman Sound, we have observed maximum blade length of the plant to be approximately 0.75 m. As with most seagrasses, eelgrass beds fragment, contract, and expand due to seasonal growth and die off cycles, storm events (Preen et al., 1999), and anthropogenic impacts (Tveite, 1984). Throughout most of our study area, a mosaic of discrete eelgrass patches and extensive beds can be found in a band tens of meters wide and at water depths from mean low tide to ~8 m. The band itself is not continuous; it is broken in many places along the shore by areas of boulder and bedrock substrate. Although patch sizes can range from ~1 to 30,000 m² elsewhere (e.g., Chesapeake Bay, Hovel and Lipcius, 2001), most discrete patches we observed in Newman Sound were less than 20 m².

We chose five sites within Newman Sound to conduct our two studies. Individual sites were more than 4 km apart during each study. For the patch size study, we identified three of these sites (Big Brook: P1, Heffern's Cove: P2, and Mistaken Cove: P3), each with an abundance of spatially discrete eelgrass patches that were variable in size (Fig. 1). For the edge effects study, we chose two sites (Dockside: E1 and Buckley's Cove: E2, Fig. 1) that had a distinct lateral mudeelgrass interface greater than 18 m long, running perpendicular to shore (Fig. 2). These edges were created as part of a concurrent eelgrass removal experiment (see Laurel et al., 2003b), where scuba divers had previously uprooted a 400 m² area of eelgrass in depths of 1.5-3 m, 10-60 m offshore. Except for the plant removal itself, there was no apparent difference between the mud-barren substrate at this site and natural mud-barren substrates elsewhere throughout the study area. Eelgrass growth occurred along the edge boundary in the year between the removal and this experiment, thus naturalizing the distinct boundary that had been created.

2.2. Predation assessment

Predation risk was quantified using a tethering technique, which allows relative predation risk to be quantified amongst habitats (McIvor and Odum, 1988; Rozas and Odum, 1988; Ruiz et al., 1993; Gregory and Levings, 1998; Post et al., 1998; Halpin 2000). Discussions of the artefacts associated with tethering are numerous-e.g., reduced escape response of tethered prey, chemical queues, attraction to "wounded" prey, etc. (Curran and Able, 1998; Kneib and Scheele, 2000; Linehan et al., 2001). While tethering cannot be used to quantify absolute mortality due to predation, it can be used to compare rates of predation under the assumption that artefacts of the technique do not covary among the habitat conditions being tested (see Linehan et al., 2001). Tethering has been successfully used to investigate relative predation on both invertebrate and fish taxa in several aquatic habitats (see Linehan et al., 2001). The resulting measure depends on the relative encounter rate of predators with prey, and thus reflects the aggregate effect of predator abundance and foraging intensity (e.g., Post et al., 1998).

We attached a live age 0 cod (45–105 mm standard length, SL) to a 0.5 m monofilament tether line (0.9 kg test) through the caudal peduncle with a #16 fishing hook (~5 mm long) in our experiments. The tether line was attached 0.25 m from the seabed on a placement line (11.4 kg test monofilament), which was anchored with a 0.9 kg lead weight and held vertical in the water column with a series of small cork floats. The top float acted as a site marker. This tether line allowed juvenile cod prey a 1.0 m diameter sphere of mobility and access to the substrate. A full description of the technique can be found in Linehan et al. (2001).

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