Habitat dependant growth of three species of bottom settling fish in a coastal fjord

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ABSTRACT

Settlement of juvenile fish is often associated with structurally complex habitat such as eelgrass (*Zostera marina* L.). We tested whether juvenile Greenland cod (*Gadus ogac* Richardson), Atlantic cod (*G. morhua* L.), and white hake (*Urophycis tenuis* Mitchill) have higher feeding and growth rates in structurally complex eelgrass habitat compared to barren seafloor or the water column. We conducted five single species field experiments from September 2002–October 2003, to test whether juvenile Greenland cod, Atlantic cod, and white hake had higher feeding and growth rates in structurally complex eelgrass habitat compared to barren seafloor or the water column. In two experiments with *G. ogac*, growth rates did not differ among habitats in autumn 2002, but in autumn 2003 fish grew fastest in the water column ($0.449 \pm 0.055\% \cdot d^{-1}$) compared to barren ($0.372 \pm 0.028\% \cdot d^{-1}$) or eelgrass habitats ($0.254 \pm 0.013\% \cdot d^{-1}$). In two experiments with *G. morhua*, growth rates over the winter (2002–2003) did not differ among habitats, but in spring of 2003 growth was significantly greater in eelgrass ($0.366 \pm 0.026\% \cdot d^{-1}$) compared to barren ($0.327 \pm 0.035\% \cdot d^{-1}$) or water column habitats ($0.065 \pm 0.013\% \cdot d^{-1}$). In one experiment with *U. tenuis*, growth was faster in eelgrass ($0.713 \pm 0.062\% \cdot d^{-1}$) than barren ($0.483 \pm 0.055\% \cdot d^{-1}$) or water column habitats ($0.271 \pm 0.040\% \cdot d^{-1}$). Zooplankton abundance was consistently highest among seafloor habitats (i.e., eelgrass and barren substrate) and lowest in the water column. More food (by weight) was consumed by *U. tenuis* and *G. ogac* in eelgrass than other habitats, while *G. morhua* consumed the most food over barren substrate. Results are generally consistent with predictions of higher growth rates and food rations among seafloor habitats for white hake and Atlantic cod. Greenland cod did not grow as predicted indicating that potential trade-offs in habitat selection may vary with season and the response to habitat is not uniform among species.

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1. Introduction

Rapid growth is a selective advantage that improves the survival of juvenile fish (Hare and Cowen, 1997; Sogard, 1997; Werner and Gilliam, 1984) by reducing size-dependant mortality to predation and starvation, both of which decrease with increasing body size (Kristiansen et al., 2000; Post and Evans, 1988; Werner et al., 1983a, b). Rapid growth is dependent on a variety of endogenous and exogenous factors each with associated metabolic costs (Horn, 1998; Houde and Zastrow, 1993; Mommsen, 1997; Peck et al., 2003a,b). It requires surplus energy that can be converted to mass after basal metabolic demands are satisfied (Hawkins et al., 1985; Mommsen, 1997; Sogard and Spencer, 2004). Given that the energetic value of prey is variable (Bowen et al., 1995; Steimle and Terranova, 1985)

foraging in habitats that support abundant, energy-rich prey may improve survival through growth maximization (Werner and Gilliam, 1984). Compromises (i.e., trade-offs) in habitat selection are suspected when juvenile fish do not reside in habitats that maximize growth.

Active habitat selection (Laurel et al., 2003; Sogard, 1992) influences the survival of juvenile fish (Lindholm et al., 1999). Atlantic cod (*Gadus morhua* L.), for example, are highly associated with eelgrass (Schneider et al., 2008) and experience lower predation rates in shallow water among biogenic structure than in unstructured habitats (Linehan et al., 2001). Eelgrass is also known to enhance juvenile fish survival (Adams, 1979; Dean et al., 2000) by concentrating the invertebrates (e.g., zooplankton, polychaetes, etc.; Gerking, 1957; Hasegawa et al., 2007; Short and Short, 1993) upon which they forage (Buzzelli et al., 1989; Keats and Steele, 1992; Keats et al., 1987). Higher abundances of prey items increase foraging opportunities and ultimately enhance growth. Under this ideal scenario, in which biogenic structure functions to simultaneously improve the predator refuge and maximize growth potential (Rozas and Odum, 1988), trade-offs or compromises in habitat selection are not implicated.

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However, some optimal foraging habitats (i.e., those with high growth potential) might also jeopardize survival due to the increased predation risk (Walters and Juanes, 1993; Werner et al., 1983a, 1983b). Some species occupy barren seafloor in the absence of predators (Gotceitas et al., 1995), presumably to forage more efficiently on available prey in the open and maximize consumption and growth (Post and Evans, 1988). In the presence of actively foraging predators, these fish return to structured habitats for shelter (Gotceitas et al., 1995). This scenario illustrates an apparent trade-off in habitat selection; the best foraging habitat is vacated for enhanced shelter from predators when the risk is elevated.

In Newman Sound, Newfoundland, juvenile cod (_G. morhua_ L., _G. ogac_ Richardson, _U. tenuis_ Mitchill) are not strongly associated with habitat at small scales (10 m or less) but are positively associated with habitat at larger scales (Schneider et al., 2008). These species are associated with various eelgrass structural complexities at scales of 10s to 100 s of km compared to barren or cobble complexes (Thistle et al., 2010). The proximate mechanism is active habitat selection, as shown by rapid response to eelgrass removal and placement experiments (Laurel et al., 2003). One contributing factor is reduced predation risk in eelgrass compared to open habitats (Gorman et al., 2009; Linehan et al., 2001). In this study we tested whether growth, prey availability and prey consumption of newly settled cod differed among the water column, vegetated and unvegetated seafloor habitats. We used experimental enclosures, stomach content analysis, and zooplankton sampling to accomplish this. We expected more rapid growth among seafloor habitats compared to the water column, within each experiment, and that unvegetated habitats would support higher growth than vegetated habitats due to improved visibility of prey. We expected that prey consumption would follow a similar pattern as growth, but that zooplankton abundance would be greater in eelgrass than either barren seafloor or the water column due to the 'concentrating' effect eelgrass has on zooplankton. Results were evaluated to infer if observed settlement patterns and the subsequent association of juvenile cod with eelgrass is the result of a habitat-mediated trade-off in access to food and shelter from predators, or partially a response to enhanced growth performance.

2. Methods

2.1. Study area and site selection

Newman Sound is located within Bonavista Bay off the northeast coast Newfoundland (Fig. 1). Near-shore bottom habitat structure ranges in type and complexity from areas vegetated with eelgrass (_Zostera marina_ L.), Irish moss (_Chondrus crispus_ Stackhouse), rockweed (_Fucus sp._), and knotted wrack (_Ascophyllum nodosum_ L.) to unvegetated, fine-grained sediments, large boulder, and cobble complexes. Site selection criteria included 1) the presence of a large eelgrass patch (i.e., approximately 20 m²), 2) an adjacent barren area>20 m from the edge of any vegetation, and 3) a comparatively deep area (i.e., 8 m) near the eelgrass and barren habitats. Two sites were selected in 2002 and five sites were used in 2003, all located within 10 km of each other. Thermographs deployed in seafloor and water column habitats at each site verified that water temperatures were not different among habitats and sites during the experiments. Mean ($\pm$ sd) water temperature was warmest (14.1 ± 1.3 °C) during the summer (range 10.5–16.0 °C), followed by autumn when temperatures fell to 10.4 ± 0.4 °C (range 9.5–16.0 °C). Mean ($\pm$ sd) water temperature during the spring was coldest, 9.0 ± 2.6 °C (range 2.5–13.0 °C). Episodic intrusions of cold water, typical along this coastline during upwelling events (Ings et al., 2008), were evident in the temperature record.

2.2. Experimental enclosure construction and method validation

To determine if growth of juvenile cod differed among habitat type, we constructed 30, 1.0 m³ experimental enclosures in which to confine fish. Frames were constructed with PVC pipe and three-way elbow connectors at the corners and were wrapped with 6.35 mm flexible black polyethylene mesh on all six sides. This was of sufficient size to allow adequate water flow through the enclosure. The frames deployed on the seafloor were filled with sand to add weight and eliminate the need for an anchoring system. An opening was cut into the top of each enclosure and fitted with a meshed access panel. Four meter lengths of polypropylene rope were attached to the four
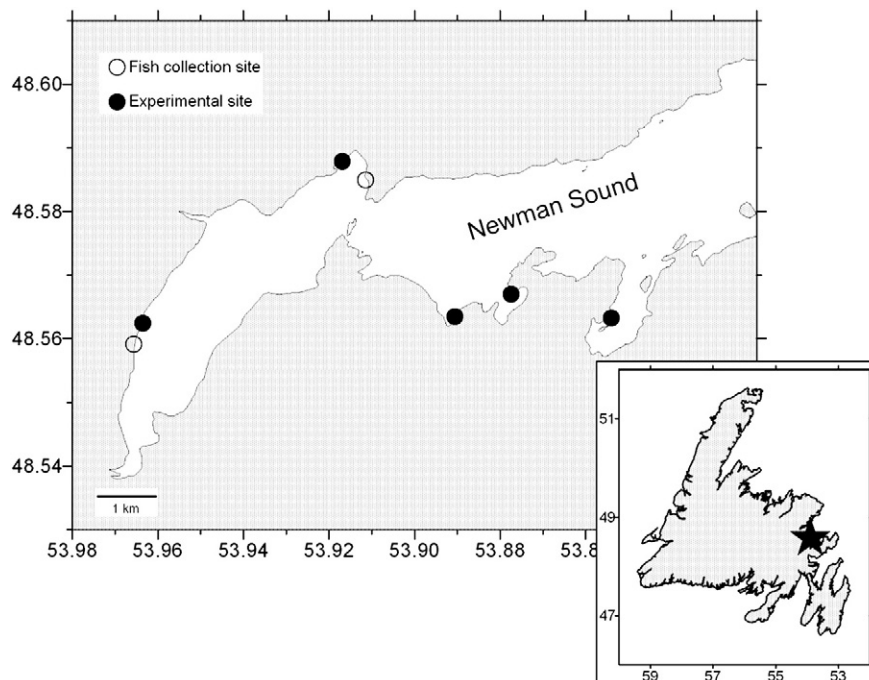

Fig. 1. Newman Sound, Bonavista Bay, Newfoundland. Study site used for fish collection, growth experiments and plankton sampling from 2002–2003.