HABITAT COMPLEXITY INFLUENCES THE GROWTH RATE OF JUVENILE GADIFORMES (Gadus morhua, Gadus ogac, Urophysis tenuis) IN NEWMAN SOUND, NEWFOUNDLAND

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Abstract

In Newman Sound, Newfoundland, juvenile fish settle in shallow near-shore waters and are often associated with eelgrass beds of intermediate structural complexity. Although it is well established that structurally complex habitats such as eelgrass provide a refuge for juvenile fish from larger predatory fish, little is known about the potential energetic reward associated with use of these complex habitats. The settlement and close association of age 0 and 1 juvenile fish (approximately 60-100 mm SL) with eelgrass habitat may be the result of an active compromise in which optimal foraging habitat is sacrificed for habitats with increased shelter from predators. In this study, I quantified the relative growth rates of fishes associated with three adjacent habitats of differing structural complexity (barren seafloor, eelgrass, and water column) at five sites in Newman Sound, Newfoundland. Juvenile Greenland cod (*Gadus ogac*), Atlantic cod (*G. morhua*), and white hake (*Urophysis tenuis*) were placed in 1 m^3 enclosures positioned over eelgrass, barren seafloor, and water column habitats in 2002 and 2003. Changes in standard fish length (mm SL) and volume (ml) were measured, and specific daily growth rates were determined and compared. Stomach contents were examined for habitat-related differences in the type and quantity of items consumed by enclosed fish at the termination of each experiment. Zooplankton samples were also collected biweekly during summer and fall in 2003 to determine if differences in prey concentration differed among the habitats.

Annual and seasonal variations in growth rates were documented among habitats and between the species. In fall 2002, there was no statistical difference in specific

growth rates (SGR) of Greenland cod among the habitats (barren = 0.068 % SL·day^{-1}, eelgrass = 0.074 % SL·day^{-1}, water column = 0.064 % SL·day^{-1}). SGR of Atlantic cod during winter from 2002 to 2003 did not differ significantly either (barren = 0.129 % SL·day^{-1}, eelgrass = 0.151 % SL·day^{-1}, deep water = 0.116 % SL·day^{-1}), but survival was significantly greater in deeper habitats (55 %) than in shallower habitats (20 %). In spring 2003, mean SGR (± SE) of Atlantic cod was significantly greater in eelgrass than barren seafloor or water column habitats (0.366 ± 0.026 % SL·day^{-1}, 0.327 ± 0.035 % SL·day^{-1}, and 0.065 ± 0.013 % SL·day^{-1} respectively). In summer 2003 juvenile white hake grew more rapidly in eelgrass (0.713 ± 0.062 % SL·day^{-1}) than in barren or water column habitats (0.483 ± 0.055 % SL·day^{-1} and 0.271 ± 0.040 % SL·day^{-1} respectively). In fall 2003, juvenile Greenland cod grew more rapidly in water column (0.449 ± 0.055 % SL·day^{-1}) habitats than in either barren (0.372 ± 0.028 % SL·day^{-1}) or eelgrass habitats (0.254 ± 0.013 % SL·day^{-1}). Diets were similar among habitats within experiments, but differed over time. Fish in eelgrass tended to have greater amount of food by weight in their stomachs at the time of sampling than fish in either barren or water column habitats (1.03 %, 0.88 % and 0.69 % respectively). Gadiformes in each habitat appeared to select for benthic or epibenthic prey. The concentration of available prey differed among the habitats. Eelgrass samples had the highest concentration of zooplankton (1.93 individuals·Liter^{-1}), followed by barren (1.33 individuals·Liter^{-1}) and water column samples (0.99 individuals·Liter^{-1}).

These data suggest that at certain times of the year, juvenile fish settle and occupy structurally complex habitats for energetic reward as measured by growth. At the scale

of these experiments, there were differences in the growth rates, food availability and zooplankton concentration between three habitats at my sites. Enclosure methodology can be a useful tool in determining relative differences between specific juvenile fish foraging habitats provided that confounding variables and artifacts of the experimental method are rigorously accounted for. Understanding the relationships between specific habitat components (e.g., vegetation) and fish growth aids our understanding of juvenile fish ecology, and may ultimately help restore depleted fish populations in the Northwest Atlantic through habitat conservation and protection.

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1.0 Introduction

An important component of fisheries research focuses on determining factors that influence survival of fish at various early life stages in an effort to accurately predict cohort size, fishery recruitment and, ultimately yield. Accurate estimation of cohort size helps scientists estimate the potential fishery recruitment for a given year to set preemptive limits on catch, or take other management action that prevents population declines. Recruitment signals of age 0 and 1 Gadiform cohorts can be detected by local inshore abundance surveys (Ings et al. 1997). These surveys can be used to estimate the size of newly-settled cohorts at the scale of a coastline, and ultimately to predict fishery recruitment from the amount of suitable habitat available (Schneider et al. 1997). The suitability of a habitat must first be identified and this changes with life-stage, and is likely influenced by inter- and intra-specific density dependent factors (Stenseth et al. 1999; Fromentin et al. 2001; Lekve et al. 2002; Laurel et al. 2004). It is therefore important to identify habitats that are used by fish at various life-stages, the spatial distribution of those habitats, and the characteristics that make them important to accurately estimate cohort size and fishery recruitment from small scale surveys.

A multitude of hypotheses exist as to why recruitment in marine fish stocks is highly variable (Anderson 1988). One leading hypothesis is that recruitment variability is dependent on survival at early life stages (Sissenwine 1984), and survival is a direct function of growth and mortality (Houde 1989; Pepin and Myers 1991). The growth and mortality of juvenile marine fish is complex, but is thought to be largely dependent on four factors: water temperature, body size, food availability and predation (Houde and

Zastrow 1993; Horn 1998; Mommsen 1998; Anderson and Gregory 2000). Water temperature influences metabolic processes in fish and directly influences growth rate (Mommsen 1998; Otterlei et al. 1999; Bjornsson and Steinarsson 2002). If food is not limiting, juvenile fish typically grow more quickly in warmer water within their range of thermal tolerance, but if the water temperature exceeds key thresholds, the maintenance food ration increases to a point that causes stress and depression of optimal growth rate, which can be lethal (Hawkins et al 1985; Sogard and Olla 2001). Most metabolic processes are also strongly related to body size (Brett 1979; Mommsen 1998; Otterlei et al. 1999). Growth rate in particular has been shown to decrease with increasing body size (Jobling 1988; Brander 1995; Otterlei et al. 1999), but growth efficiency (i.e., the energy used to metabolize food) is generally higher in younger, smaller fish with higher respiration rates (Peck et al. 2003a,b). For fish to maintain homeostasis and invest energy into growth, adequate food supplies must be available. Larger food rations generally result in faster growth and greater lipid deposition (Hawkins et al. 1985; Mommsen 1998; Peck et al. 2003a; Sogard and Spencer 2004). This rapid growth may improve survival because smaller fish are more susceptible to predation (Post and Evans 1988; Sogard 1997; Kristiansen et al. 2000).

The high growth – low mortality hypothesis supposes that fast growth is a selective advantage for juvenile fish in that it reduces the risk of size-dependent mortality to predation by allowing rapidly growing individuals to pass through the most vulnerable size classes more quickly than those with slower growth (Werner et al. 1983a,b; Hare & Cowen 1997; Sogard 1997). Growth rate has been correlated with year-class strength

(Peterman et al. 1988; Campana 1996) and ultimately fitness (Schluter 1994). Growth is dependent on a variety of endogenous and exogenous factors (Mommsen 1998) and Searcy et al. (1997) observed that habitat selection and measurements of growth were greatly influenced by water temperature, size selective mortality, and density dependent factors (i.e., conspecific abundance). Juvenile fish should therefore actively select and occupy those habitats that maximize their potential for growth (i.e., habitats with optimal thermal regimes and a high concentration of energy-rich food items). However, tradeoffs in habitat selection may exist in which occupation of the best foraging habitat might be sacrificed for habitats with increased shelter from predators.

It has been demonstrated in freshwater fish communities that young-of-the-year juveniles may actively select specific habitats in which to reside. For example, habitats that maximize foraging returns are selected for in the absence of predation risk, but optimal foraging habitat is sacrificed for structurally complex refuge habitat in the presence of actively foraging predators (Keast and Eadie 1983; Werner et al. 1983a,b). Additional possibilities for compromised habitat selection are also plausible. Inter- and intra-specific interactions may result in competition for limited resources and likely alter the energetic potential associated with a particular habitat (Searcy et al. 2007). As competitor density changes, the energetic reward associated with a habitat may also change. These changes may influence growth rate and ultimately the survival of the fish associated with that habitat (Mittelbach 1988; Bjornstad et al. 1999; Lekve 2002; Searcy et al. 2007). In addition, over-winter survival is thought to be size-dependant (Sogard 1997). Larger fish are able to store more lipids and have lower basal metabolic demands

relative to body size than smaller fish, and as a result have reduced energy demands (Mommsen 1998). Large fish are also thought to be more capable than smaller individuals of surviving periods of starvation that are believed to occur during winter as food abundance decreases (Henderson et al. 1988; Post and Evans 1989; Gotceitas et al. 1999; Hurst and Conover 2003; Garvy et al. 2004).

The fitness of any animal is largely determined by its ability to successfully reproduce and pass its genome on to successive generations. Gadiformes such as Atlantic cod (*Gadus morhua*), Greenland cod (*G. ogac*), and white hake (*Urophysis tenuis*) are distributed across much of the Northwest Atlantic among inshore (i.e., in bays and fjords, etc.) and offshore (i.e., Georges Bank and Grand Banks, etc.) habitats at all life stages (Bigelow and Schroeder 1953; Scott and Scott 1988). They have evolved reproductive strategies characterized by high fecundity; females can spawn millions of eggs to counter the high rates of mortality that occur at early life-stages (Bailey and Houde 1989). Along the northeast coast of Newfoundland, mature Gadiformes spawn during winter and spring at either offshore (Atlantic cod, white hake) or inshore (Atlantic cod, Greenland cod, white hake) spawning grounds (Scott and Scott 1988). Their eggs are either demersal (Greenland cod) or pelagic (Atlantic cod, white hake). Pelagic eggs float in the water column and are sometimes passively transported to inshore coastal areas (deYoung and Davidson 1994), but favorable conditions for transport are highly variable and are closely associated with spawning location of adult fish (Bradbury et al. 2000; Pepin and Helbig 1997). Research suggests that in certain years, pelagic drift does not occur (Anderson et al. 1995) and inshore spawning has also been reported (Smedbol and Wroblewski 1997).

Eggs hatch in the spring and summer, and larvae remain in the pelagic zone until they metamorphose into pelagic juveniles. Many juvenile Gadiform species settle inshore in pulses during the summer and fall to begin the demersal phase when they reach approximately 50-70 mm Standard Length (mm SL) (Templeman 1966, Fahay 1983, Methven and Bajdik 1994, Dalley and Anderson 1995; Laurel et al. 2003b). Settlement patterns for Gadiformes are quite diverse, but Greenland cod tend to settle and become demersal in early summer, followed by white hake in mid-summer, and Atlantic cod in early fall (Scott and Scott 1988; Gregory et al. 2004; Gregory et al. 2006; Ings et al., submitted; Renkawitz personal observation).

Structurally complex habitats are generally known to support greater diversity and a higher abundance of individuals than less complex habitats (Heck et al. 1989; Lindholm et al. 1999; Lazzari et al. 2003) although habitat usage can vary at spatial, temporal, diurnal, and ontogenetic scales. In Newfoundland, juvenile Gadiformes are typically distributed in shallow (<10 meters) near-shore waters. These areas contain complexes of eelgrass (*Zostera marina*), kelp, cobble, and boulders that are thought to increase survival by reducing predation risk (Keats et al. 1987; Gotceitas et al. 1995; Gotceitas et al. 1997; Gregory and Anderson 1997; Grant and Brown 1998b; Linehan et al. 2001; Laurel et al. 2003 a & b; Laurel et al. 2004). Mortality rates of newly settled age 0 to 1 Gadiformes are high (Peterman et al. 1988; Campana et al. 1989). Tethering studies using newly settled juveniles have identified fish such as Atlantic cod, Greenland cod, white hake and sculpin species as predators in nearshore habitats especially from dusk until dawn when larger fish move inshore to feed (Grant and Brown 1998a; Linehan et al. 2001; Laurel et

al. 2003a; personal observation). Other potential predators in these habitats include the avian (e.g., gulls, terns, mergansers, kingfishers, and cormorants) and the mammalian (e.g., otter) variety, all of which are known to forage on juvenile fish (Scott and Scott 1988; Palsson 1994; Renkawitz personal observation).

Eelgrass is a critical component of the marine ecosystem because it creates a highly structured and diverse habitat from shifting sand and silt, softens impacts of waves and currents, stabilizes the shoreline, and provides a low-flow environment that is favorable for deposition of organic matter and sediments (Fonseca et al. 1982; Short and Short 1993; Short and Burdick 1996; Abdelrhman 2003; Peterson et al. 2004; Hasegawa et al. 2007). Eelgrass absorbs and concentrates nutrients from the land and sea and transfers them to the sediment or to other animals (Buzzelli et al. 1989; Short and Short 1993; Short and Burdick 1996; Hasegawa et al. 2007). Eelgrass also enhances the survival of many invertebrates and the young of many marine fish species (Adams 1979a,b; Heck et al. 1981; Dean et al. 2000). It has also been shown to concentrate zooplankton on which juvenile fish forage (Gerking 1957; Hasegawa et al. 2007), thereby increasing the potential energetic reward associated with these habitats.

The presence of structure (e.g., vegetation, boulders, etc.) provides physical locations in which smaller fish can seek refuge from larger predatory fish until that threat of predation has passed. Observed habitat associations of juvenile Gadiformes vary at spatial, temporal, and ontogenetic scales (Schneider et al. 1987; Gibson et al. 1996; Gregory et al. 1997; Borg et al. 1997; Hartzenbeler et al. 2000; Gillanders et al. 2003; Cote et al. 2003; Laurel et. al 2004). The structural characteristics of aquatic vegetation

(i.e., species, density, height, patch size, biomass, etc.) have been shown to influence fish density and usage as potential foraging and refuge habitat (Carr 1994; Dean et al. 2000). In sea grass communities, faunal abundance and species diversity are positively correlated with structural complexity. Complexity is usually quantified as shoot biomass, leaf surface area, or areal extent based on the fractal geometry of sea grass patches. In Newman Sound, Bonavista Bay, Newfoundland, juvenile Gadiformes are associated with eelgrass of intermediate complexity as measured by fractal geometry (Wells 2002). Eelgrass habitats with low structural complexity are typically characterized as broad un-fragmented meadows with relatively smooth regular edges, while highly complex habitats are often fragmented and have highly convoluted or irregular edges. Eelgrass habitats of intermediate complexity are typically intermediately sized patches that are moderately fragmented, with a moderate amount of convoluted edges. Predation risk for age 0+ Gadiformes increases with water depth, and is lower in areas vegetated with eelgrass and other macroalgae compared to barren or unvegetated areas at the same depth (Linehan et al. 2001). Gorman (2004) demonstrated that predation risk was greatest at eelgrass edges and suggested that mortality is lower in eelgrass than in habitats without biogenic structure.

In the presence of predators, the lack of biogenic structure results in higher mortality rates (Linehan et al. 2001) and behavioral modifications that may reduce foraging efficiency of age 0 to 1 juvenile fish (Gotceitas et al. 1995). Alternatively, the foraging efficiency of juvenile fish in the absence of predators can be greater in habitats with low structural complexity, resulting in faster growth (Post and Evans 1988). Rates

of predation on zooplankton by small fish are greatest over barren substrates (Heck and Thoman 1981), and foraging efficiency significantly decreases with increasing plant density and vegetation type (Stoner 1982; Gotceitas and Colgan 1989; Dionne and Folt 1991; Levin and Hay 2003). However, prey biomass is often positively correlated with vegetation density (Macan, 1949; Gerking 1957), and it has also been suggested that for some species, association with vegetation results in greater food availability and increased growth rates (Crowder and Cooper 1982; Holbrook and Schmitt 1984; Sogard 1992; Tupper and Boutilier 1995). Additional experiments have demonstrated that consumption and growth rates of some juvenile fish are greatest in habitats of intermediate complexity and predation rates on zooplankton can be greater at seagrass edges than in either the center of seagrass beds or over barren substrates (Bullard and Hay 2002).

Many estimates of growth rate for free ranging juvenile Gadiformes in the North Atlantic exist, and they are highly variable depending on myriad factors. Hawkins et al. (1985) estimated the length and weight specific growth rate for age 0+ cod in a Scottish Fjord at 0.606 $\%\cdot day^{-1}$ and 2.58 $\%\cdot day^{-1}$ respectively. These rates varied seasonally and region specific growth rates might better approximate the conditions experienced by local populations of fish. Growth can be used as a proxy for the energetic profitability of a habitat (Schluter 1994) provided that other potentially biasing or confounding variables are sufficiently accounted for (Searcy et al. 2007). Whether growth rate varies as a function of habitat association for juvenile Gadiformes remains uncertain. For example, the growth rates of free ranging Gadiformes in nearshore coastal areas of Northeastern

Newfoundland is highly variable (i.e., seasonally, annually, etc.) but have recently been estimated at 0.38 %·day^{-1} from May to June and 1.0 %·day^{-1} from August to October (Gregory personal communication). However, little can be said about the growth potential of specific habitat types from most estimates of juvenile growth because these fish are able to move beyond habitat boundaries for food acquisition, must compete with inter- and intra-specifically for space, and actively avoid predators among other activities, all of which take energy away from growth. The primary objective of my investigation was to determine if juvenile Gadiformes that associate with a structurally complex habitat (i.e., eelgrass) experience faster growth rates than fish in habitats with little or no structural complexity, as would be expected if energy gain was a compromise between optimal foraging and optimal sheltering habitats (i.e., eelgrass). It is known that eelgrass provides improved shelter from predation (Linehan et al. 2001; Laurel et al 2003a), but it is not known if certain habitats are better foraging habitats than others for age 0 and 1 Gadiform juveniles. To answer this question I used experimental enclosures containing three species of newly settled age 0+ Gadiformes deployed in Newman Sound to remove the risk of predation, and to restrict foraging to two discrete benthic areas (barrens areas and eelgrass), and one water column habitat. The growth of these fish was monitored from 2002-2003. Restricting the foraging ranges to these habitats for the entire experiment was required to determine if a growth advantage was associated with a specific habitat because newly settled juveniles are known to move between and among habitat types temporally and diurnally. Estimates of growth associated with specific habitats are usually confounded by the very fact that free ranging juveniles may be

feeding in various habitats and at different rates during different times of the day (Grant and Brown 1998a; personal observation). The use of experimental enclosures attempts to remove confounding variables by limiting the foraging range of enclosed fish to discrete habitat types, removing the threat of predation, and by regulating the abundance of competitors in a given habitat.

Although information is available on the general diet of juvenile fish in Newfoundland (Keats et al. 1987; Keats and Steele 1992; Keats et al. 1993; Lomond et al. 1998; Lander 2000), comparatively little information is available on the diets associated with specific habitats. The secondary objective of this study was to determine if observed differences in growth rates among habitats were associated with differences in either the quality or quantity of food at a single point in time. To accomplish this, stomachs were removed from the fish in the enclosures and analyzed. Because growth rate is an important proxy of fitness (Schluter 1994), and food intake has been closely linked to growth rate (Jobling 1994; Elliott 1994; Hart and Salvanes 2000), differences in the quantity and quality of food consumed by Gadiformes may have been indicative of differences in the energetic potential among habitats.

Prey biomass is often positively correlated with vegetation density (Gerking 1957). Whether prey availability differs among habitats in Newfoundland is not yet known. The third objective of this study was to determine whether differences in growth rate among habitats were associated with differences in food availability. To accomplish this objective, a zooplankton pump was employed to sample the three discrete habitat types. Differences in zooplankton concentration may have reflected the quality of the

habitats for age 0+ Gadiformes during the early demersal phase from the perspective of food availability.

Several potential outcomes of this study were identified, each with unique implications. The absence of any difference in growth between the habitats might suggest that settlement of juvenile fish in areas with biogenic structure may be for reasons other than food acquisition and rapid growth. The observation of growth differences might result from either of two additional outcomes, each with three scenarios and unique biological explanations.

First, growth might be greater in any one of the habitats compared with the other two. Rapid growth of juveniles associated with only eelgrass would suggest that settlement and association with structurally complex habitats may be at least partially because it entails an energetic benefit, with the added benefit of greater shelter. Rapid growth associated with only the water column juveniles would suggest an energetic reward within the water column and imply that settlement to the seafloor and/or association with biogenic structure may be primarily for shelter. Rapid growth associated with only barren seafloor habitats would suggest that while settlement in open areas may be advantageous energetically, association with eelgrass may be for other factors such as shelter.

Second, growth rates could have been higher in any two habitats when compared to one habitat. Rapid growth associated with both benthic (barren seafloor and eelgrass) habitats may suggest an energetic benefit of association with the seafloor, coupled with the added benefit of structural complexity. Fish growth could have been greatest in the

barren seafloor habitats and the water column, suggesting that open areas may be more advantageous energetically, and that association with eelgrass habitats may represent a compromise in terms of habitat usage. Finally fish could have grown more rapidly in both the water column and the eelgrass habitats, suggesting that barren seafloor habitats are the least beneficial habitats from an energetic perspective, but that settlement and association with biogenic structure may be beneficial from an energetic perspective with the added benefit of greater shelter.

Statement of Co-authorship:

Habitat complexity influences the growth rate of juvenile Gadiformes (*Gadus morhua*, *Gadus ogac*, *Urophycis tenuis*) in Newman Sound, Newfoundland.

M.D. Renkawitz designed the research program, constructed the experimental equipment, organized the collection of all data, collected and processed all samples, performed all data analysis and prepared the manuscript. D.C. Schneider contributed conceptual ideas, suggested methods, and advised on statistical analyses. R.S. Gregory contributed conceptual ideas, advised on the field program, assisted in acquiring supplies and collecting samples. D.C. Schneider and R.S. Gregory served as mentors to M.D. Renkawitz and were instrumental in assuring the successful completion of this program. All co-authors contributed to the interpretation of the results and editing the manuscript.

2.0 Methods

To determine if an energetic reward was associated with certain habitats within Newman Sound, Bonavista Bay, Newfoundland, I constructed experimental fish enclosures and placed them in discrete habitats: eelgrass, barren seafloor, and the water column. I then placed juvenile fish inside the enclosures and monitored their growth over time. At the end of each experiment I removed and examined their stomach contents to qualify and quantify differences in foraging among the three habitats. I also collected zooplankton samples in each of the habitats to determine if there were differences in food availability among the habitats.

2.1 Study Area and Site Selection:

Newman Sound is located within Bonavista Bay off the northeast coast Newfoundland. Near-shore bottom habitat structure ranges in type and complexity from areas vegetated with eelgrass, Irish moss (*Chondrus crispus*), rockweed (*Fucus cottoni*), or knotted wrack (*Ascophyllum nodosum*) to unvegetated, fine-grained sediments and large boulder or cobble complexes. Based on several criteria I selected experimental sites in close proximity (<50 meters) to pre-established monitoring sites within Newman Sound. I chose sites that encompassed a large (i.e., approximately 20 m^2) area vegetated with eelgrass only, and an adjacent soft-sediment barren area at least 20 meters from the edge of any patch of vegetation. The height and density of the eelgrass blades were random and irregular at each of the sites but were not measured as part of this study. Eelgrass blade height was typically about 0.5 meters in the spring, and by fall blades were over 1.0 meter. Shoot density also appeared to increase seasonally until the end of

the fall when the top of the blades began to break off after stress from increased wave action or the onset of winter die-back caused a reduction in blade height and density (Renkawitz personal observation). Within the barren area, I chose locations without boulders or other obstructions that would have added structure to the area. These benthic habitats were also selected to represent the same depth of 4 meters at mean low tide. The final criterion that I used was that each site had to have a relatively deep area (~8 m at mean low tide) in close proximity (approximately 20 meters) to the eelgrass and barren habitats. I surveyed 12 sites for potential suitability from a boat using an aqua scope and depth sounder, and then observed promising sites more closely by SCUBA. I selected two sites in 2002, one in the inner sound (Stairs Cove) and one in the outer sound (Hefferns Cove). In 2003, I expanded the experiment to include five sites to increase replication, including two sites in the inner sound (Stairs Cove and Mistaken Cove), and three sites in the outer sound (Hefferns Cove, Minchin Cove and South Broad Cove) (Figure 1, Appendix 1). I marked the 6 areas at each site (two barren areas, two eelgrass areas, and two water column areas) where the enclosures were placed with moored marker floats for ease of relocation.

2.2 Experimental Enclosures:

2.2.1 Enclosure Construction:

I constructed a total of thirty 1.0 m^3 experimental enclosures and deployed them in three habitats at five sites in Newman Sound (Figure 2). Frames consisted of 2.5 cm schedule 40 PVC pipe filled with sand and PVC three-way elbow connectors affixed with plumber's adhesive at the corners. The distance from the outside edge of one elbow

connection to the outside edge of the opposite elbow connection measured 1.0 m. After the frames were complete, I wrapped them with 6.35-mm flexible black polyethylene mesh on all 6 sides, and secured them to the frame with 35.5 cm black cable ties. I used twelve cable ties on each length of PVC pipe and wrapped them around twice to increase their holding strength. I cut a 38.0 cm x 33.0 cm opening into the top of each enclosure. I made wooden frames from 2.5 cm x 7.6 cm pine strapping, and joined them together with 5 cm x 15 cm strips of tin at the corners that were attached with 1.27 cm brass screws. I then secured the frame to the opening in the enclosure with 35.5 cm cable ties. I cut a piece of mesh to fit another 2.5 cm x 7.6 cm wooden access panel (exactly same materials and dimensions as the frame) and secured it with staples. Then I 'sandwiched' the mesh between the frames and the access panel and secured it to the frame of the enclosure with eight 3.8 cm brass screws. Next, I tied a knot in the middle of two 4 meter lengths of 6.35 mm twisted yellow polypropylene rope, forming a small loop at the top with four ends of rope hanging at the bottom. I attached each of these four ends half way down each of the four vertical frame sections (PVC pipe) of the enclosure with four additional 35.5 cm cable ties to form a bridle.

On 2/3 of the enclosures (eelgrass and barren seafloor enclosures), I tied a 15.27 cm orange foam float to one end of a 5 meter length of 1.27 cm green twisted polypropylene rope and tied the other end to the loop in the bridle to form a float-line. I secured each knot with a 15.27 cable tie to prevent it from coming untied. This 'float-line' or 'tagline' acted as a visible marker for each enclosure, and was used in the

retrieval process. I marked each of the floats and the enclosures with an individual alpha-numeric code for immediate recognition.

On the remaining 1/3 of the enclosures (water column enclosures), I tied a 2 meter length of twisted green polypropylene rope to the loop in the bridle and secured it with a 15.27 cm cable tie. At the other end of the rope, I tied an inflated 30.48 cm orange polyball float and secured the knot with a 15.27 cm cable tie. I fashioned an additional bridle and secured it in the same manner as the first to the four vertical pipe sections of the enclosure in the opposite direction of the first bridle. I tied an 8 meter length of 1.27 cm twisted green polypropylene rope to the loop in the bridal hanging down and secured it with a 15.27 cm cable tie. I tied the other end to two concrete mooring blocks (each weighing approximately 10 kg), and secured the knot with a 15.27 cm cable tie.

2.2.2 Deployment and Retrieval:

Before the study began, I transported six enclosures to each of the sites by boat and placed them onshore. Because of the size of the enclosures, only one could be safely handled at a time on the boat. I filled a fish tote by bucket with clean seawater and placed it on the deck of the boat to act as a "live well". Once on site, I placed one corner of the enclosure in the live well, giving about 20 – 25 cm of water depth for the fish to swim in. After I measured the length and volume of the fish, I placed fish into the bottom corner of the enclosure which was submerged in the water of the live well. Then I attached the access panel to the frame with brass screws using a screwdriver. Two people then picked up the enclosure, gently placing it over the side of the boat and letting it fall slowly in the water until it settled into position near the moored habitat marker. The

barren enclosures rested on barren seafloor, while eelgrass enclosures rested on top of the eelgrass within eelgrass beds. I left the enclosures in place for between 20 and 210 days depending on the experiment (See Section 2.4).

Upon retrieval, I hauled each enclosure up slowly using the tagline. When it came to the surface, two people picked it up by the frame and placed one corner gently into the live well with clean saltwater. I used the live well to reduce the stress of sampling to the fish, with the goal of enhancing survival for repeated measurements of the same fish over the duration of each experiment. Then I removed the access panel to gain access to the fish which I removed with a dip net. While measurements were being made on the fish, I removed all bio-fouling vegetation and debris from the exterior and interior of the enclosure if any was present, checked the enclosures for damage, and made repairs when necessary. After measuring the fish, I returned them to the enclosure, secured the access panel, and re-deployed it.

2.3 Fish Collection:

Beach Seining:

I collected fish using a modified 25 meter Danish beach seine that swept 880 m^2 of seafloor and up to 2 meters in the water column (Schneider et al. 1997; modified from Lear et al. 1980). Fish were collected at one of two sites in Newman Sound (Figure 1) and all fish for each experiment were collected at the same site on the same day and transported to experimental sites in a live-well in clean salt water. Water temperature and salinity differences within Newman Sound are negligible and moving fish from one location to another likely had little influence on the results because all fish were exposed

to exactly the same stress (i.e., seining, transportation, and deployment within experimental enclosures). The headrope length was 24.4 m and had foam floats spaced about every three meters to suspend the headrope in the water column to a height of 2 meters; the net fished the bottom 2 meters of the water column. The footrope was 26.2 meters long, and was weighted along its length with 3 mm diameter steel chain and 0.9 cm diameter leadline to ensure contact with the bottom. The wings and belly were made with 19 mm knotless nylon stretch mesh, while the codend was comprised of 12.7 mm knotless nylon stretch mesh.

Deployment from a motorized 6-meter open boat began at a fixed point along shore. One person stood at this point holding the hauling line. The boat backed astern perpendicular to the shore while the hauling line was let out to a distance of 55 meters. While in reverse, the boat was then turned hard to starboard, letting out the net parallel to the shore for 16 meters. When the net was in the water, the boat swung forward, and pulled into shore bow first while letting out the second hauling line.

Once the net had sunk to the bottom, two people pulled the net to shore by the hauling lines in a coordinated, rhythmic, hand-over-hand manner. Pace and timing were facilitated by using knots placed every 10 meters along the hauling rope. The two hauling points remained separate until the seine approached shore. When the bridles on the wings appeared at the surface, the two people began moving toward each other while pulling on the hauling lines to prevent escapement. Once the bridles were together, a third person hauled on the net by the footrope, while the two other people held the headrope up to ensure that no fish were inadvertently left in the wings of the net. Once

the net was brought in completely, all of the fish were collected in the codend. I transferred the contents from the net into fish totes that had been filled with clean seawater just before the net came ashore in order to minimize stress to the fish.

After fish were in the tote, I placed the target species in a 20 L bucket filled with clean seawater. I placed the bycatch in an additional seawater filled tote, and released them alive where they were caught after the catch was sorted. I made every effort to use similarly sized fish for a given species (Table 1a) to limit the effect of size related bias of growth estimates. If an insufficient number was caught, I seined the same site again in order to obtain at least 30 specimens of a similar size for each species.

2.4 Growth Experiments:

2.4.1 Fish Marking Scheme and Anesthetic

When multiple fish were placed in an enclosure (i.e., for the fall 2002 pilot study and 2002 to 2003 over-wintering study only), I marked similarly sized (Table 1a) individuals with Visual Implant Elastomer tags (VIE™, Northeast Marine Technologies) to provide unique identifiers (Guy et al. 1996; Bruyndoncx et al. 2002; NMT 2002; Olsen et al. 2004). To reduce stress to the fish during the marking process, I anesthesized them prior to injecting the elastomer tag (Guy et al. 1996, Peake 1998). To accomplish this, I placed captured fish in a bucket of clean seawater and then moved them into an adjacent bucket that contained two 5g dose packets of Eno™, a commercially available product (containing 2.32g sodium bicarbonate, 0.5g sodium carbonate (anhydrous), and 2.18g citric acid) that was used for an anesthetic, dissolved in 9.5 liters of seawater. After 20 to

30 seconds, when fish lost equilibrium and ceased normal swimming motion, I considered them anesthetized.

Each of the five fish per enclosure were administered an individual fluorescent green VIE mark at one of five body locations for individual recognition (Figure 3). I mixed the VIE the day of use according to the instructions provided by the manufacturer and maintained it on ice until used (NMT 2002). After sedation, I inserted the needle beneath the skin at one of five locations parallel to the base of the dorsal fin (Figure 2), and depressed the plunger to extrude about 2-3 mm of elastomer. After the marks were applied I placed the fish in recovery buckets with clean seawater until they revived, which took about 30 to 60 seconds. Any fish that were lethargic or did not appear healthy after that time were removed and replaced with an alternate fish. Once all 5 acceptable fish were marked and recovered, I transferred them to the enclosure, and the enclosure was deployed.

2.4.2 Growth Monitoring

I included three species of juvenile Gadiformes in the growth experiments from 2002-2003: Greenland cod, Atlantic cod and white hake. I identified Greenland cod and Atlantic cod according to Methven and McGowan (1998) and white hake were identified according to Methven (1985). When possible, I targeted fish within 5 mm SL of each other but inclusion of some fish outside this size range was unavoidable because of availability (Table 1a).

Age 0+ Greenland cod and age 0+ Atlantic cod were the focus of the fall 2002 pilot experiment and the 2002-2003 over winter growth experiment respectively. I

selected two sites for each experiment (Mistaken Cove and Stairs Cove in the pilot experiment, Mistaken Cove and Minchin Cove in the over-winter experiment), each with three defined habitat types: barren, eelgrass, and water column. After collection, I held fish in seawater-filled totes on the shoreline. I arbitrarily selected five fish and placed them in a separate bucket containing seawater. Each fish was anesthetized, marked, measured to the nearest mm SL (Table 1a), and then placed in a recovery bucket with clean seawater. Upon recovery, the five marked fish were placed in an enclosure, the access panel was secured, and each enclosure was transported to and deployed at the designated habitat. At the end of both experiments, I measured each fish to the nearest mm SL, euthanized, and preserved them (See Section 2.6.1 for methods) for additional measurements and stomach content analysis.

In 2003 I used age 1+ Atlantic cod in the spring, age 0+ white hake in the summer, and age 0+ Greenland cod in the fall for the experiments. I changed the methods slightly for these three experiments in 2003. I placed only one fish in each of the enclosures, thus eliminating the need for anesthetic and VIE marking. In these experiments, I increased the number of sites to five, with two sites in the inner sound (Stairs Cove and Mistaken Cove) and three sites in the outer sound (Hefferns Cove, Minchin Cove and South Broad Cove). I also increased the total number of enclosures to 30 (five sites, six at each site [two in each of three habitats]).

At the beginning of the experiments, the volumetric displacement (to the nearest 0.5 ml) and length of each fish was measured to the nearest mm SL (Table 1a). Volumetric displacement involved partially filling a 100 ml graduated cylinder with a

known volume of seawater, adding the fish, and observing the displacement of water to the meniscus. One person took both measurements for each fish throughout the experiments to reduce measurement error. Enclosures were checked periodically (i.e., every one or two weeks, or at the mid point of each experiment) to insure fish were still alive in the enclosures. Fish were removed, measured and replaced when necessary (See Sections 2.4.3 and 2.4.5). At the end of the experiments, lengths and volumes were again measured. I then euthanized each fish and preserved them for stomach content analysis and additional Morphometric measurements.

2.4.3 2002 Greenland Cod Pilot Experiment

I collected age 0+ Greenland cod at Piper Beach on October 3, 2002 and placed five fish in each enclosure at Mistaken Cove the same day (Table 1a). On October 5, 2002, I collected fish at Stairs Cove and placed them in the enclosures at Stairs Cove the same day. On October 25, 2002, I removed the fish from Stairs Cove and Mistaken Cove enclosures after 20 and 22 days, respectively.

2.4.4 2002-2003 Atlantic Cod Winter Growth Experiment

From the fall of 2002 to the spring of 2003, I used age 0+ Atlantic cod in the over-wintering growth experiment. For this study, I selected Mistaken Cove in the inner sound and Minchin Cove in the outer sound. I collected age 0+ Atlantic cod on October 25, 2002 at Stairs Cove, and transported them in a live well to each site via boat. I transported enclosures individually to the designated habitat location, placed five fish in each enclosure (Table 1) before deployment.

I recorded the locations of all enclosure locations with a handheld Global Positioning System (GPS) unit which had an accuracy of approximately five meters. On December 5, 2002 I checked the enclosures to guarantee all fish were still present in each of the enclosures. After doing this, I then removed the floats and polyballs from the enclosures to prevent any movement or loss of the enclosures during the winter due to shifting ice during ice-over in Newman Sound. The previously floating enclosures in the water column sank to a depth of 8 meters and rested on the barren seafloor, while the benthic enclosures remained at a depth of 4 meters. This allowed for comparisons between water depth and survival over the winter, after retrieval of the enclosures and measuring the fish on May 28, 2003.

2.4.5 Spring 2003 Atlantic Cod Growth Experiment

In the spring of 2003, the presence of suitably sized age 0+ juveniles of any species were in short supply, and age 1+ Atlantic cod were substituted. I collected all age 1+ Atlantic cod from Piper Beach. On June 11, 2003, I collected fish and transported them to Heffems Cove and Minchin Cove in a live well, stocked the enclosures with one fish each, and deployed them (Table 1a). On June 13, 2003, I collected fish and transported them to Stairs Cove and Mistaken Cove, stocked and deployed the enclosures. On June 14, 2003 I collected fish and transported them in a live-well to South Broad Cove for stocking and deployment.

I recovered all of the enclosures at each of the five sites on July 8, 2003. I measured the fish, cleaned, inspected and redeployed each enclosure. Several of the enclosures did not contain any fish. The reason for this loss of fish is speculative, but

may have been the result of natural mortality or possible escapement, and is treated more fully in the discussion. On July 9, 2003 I collected age 1+ Atlantic cod at Piper Beach placed them in those enclosures that did not contain any fish the previous day; Atlantic cod were replaced in several enclosures at Stairs Cove (one water column), Mistaken Cove (one water column), Hefferns Cove (one barren seafloor), Minchin Cove (one eelgrass, one water column). On July 24, 2003 I removed the fish from all the enclosures.

2.4.6 Summer 2003 White Hake Growth Experiment

On July 29, 2003, I collected age 0+ white hake from Piper Beach and transported them to each site where one fish was deployed in each of the enclosures (Table 1a). On August 18, 2003, I checked and measured fish from the inner sound sites and on August 19, 2003, I checked and measured fish at the outer sound sites. All enclosures contained fish, so no restocking was necessary. On September 9, 2003 I removed all white hake from the enclosures.

2.4.7 Fall 2003 Greenland Cod Growth Experiment

I collected age 0+ Greenland cod on September 9, 2003 from Piper Beach, and transported them via live well to each of the sites and the enclosures were deployed in each of the habitats, each containing one fish (Table 1a). On September 23, 2003 and October 7, 2003 I checked enclosures and measured the fish, replacing them where necessary (i.e., missing fish due to escapement or mortality) from age 0+ Greenland cod collected at Piper Beach the same day. On September 23, 2003 fish were replaced at Stairs Cove (one barren, one eelgrass), Mistaken Cove (one barren, one water column),

Hefferns Cove (one barren seafloor, two eelgrass), Minchin Cove (one eelgrass, two water column), South Broad Cove (one barren, one water column), and on October 7, 2006, fish were replaced at Stairs Cove (one water column), Mistaken Cove (one eelgrass), Hefferns Cove (one barren), South Broad Cove (one barren seafloor, one water column). I removed the fish from the enclosures on October 20, 2003.

2.4.8 Data Analysis:

Relative growth rate (RGR) was calculated by the following formulae for (1) length measured in standard length (mm SL) and (2) volume (ml):

$$RGR_{Length} = 100[(SL_x - SL_i)\,(SL_i)^{-1}]\,(t_x - t_i)^{-1} \quad (1)$$

and

$$RGR_{Volume} = 100[(Vol_x - Vol_i)\,(Vol_i)^{-1}]\,(t_x - t_i)^{-1} \quad (2)$$

where SL_x and SL_i were the standard lengths (mm) of fish at times t_x and t_i respectively. Vol_x and Vol_i were the the volumes (ml) of fish at times t_x and t_i respectively. Specific growth rates (SGR) as a percentage of growth per day were adapted from Gotceitas et al. (1999) and calculated for (3) length and (4) volume as follows:

$$SGR_{Length} = 100[\ln(SL_x) - \ln(SL_i)]\,(t_x - t_i)^{-1} \quad (3)$$

and

$$SGR_{Volume} = 100[\ln(Vol_x) - \ln(Vol_i)]\,(t_x - t_i)^{-1} \quad (4)$$

The SL_i and Vol_i were the initial standard length (mm SL) and volume (ml) respectively, at initial time t_i (days). SL_x and Vol_x were the standard length (mm SL) and volume (ml) at a given time in days (t_x) respectively.

Data were analyzed by an analysis of variance (ANOVA) using the general linear model (GLM) procedure in MINITAB 13 (Minitab, Inc. 1999). The null and alternate hypotheses tested in each of the five experiments to determine if there was variation in the growth rates among habitats were as follows:

$$H_0: \beta_{Barren} = \beta_{Eelgrass} = \beta_{Water\ Column} \quad (5a)$$

$$H_A: \beta_{Barren} \neq \beta_{Eelgrass} \neq \beta_{Water\ Column} \quad (5b)$$

The null hypothesis (5a) states that the mean growth rates were the same in each habitat, whereas the alternative hypothesis (5b) states that the mean growth rates in the three habitats were not equal to each other. Type I error tolerance (α) was 0.05 for all analyses in these experiments. All residuals were examined for homogeneity, independence and normality to meet the assumptions for calculating p-values from F-ratios.

For the 0+ Greenland cod pilot and 0+ Atlantic cod over winter growth experiments, the model relating growth rate, $SGR_{(Length)}$, at two sites, three habitats, two enclosures per habitat, containing five marked fish within each enclosure was as follows:

$$SGR_{(Length)} = \beta_0 + \beta_{Site} * \text{Site} + \beta_{Habitat} * \text{Habitat} + \beta_{Enclosure} * \text{Enclosure} + \beta_{Mark(Enclosure)} + \text{Mark(Enclosure)} + \textit{Error} \quad (6)$$

To remove the potentially confounding variables associated with having multiple fish per enclosure (i.e., unequal numbers of fish/enclosure due to mortalities resulting in unequal competition for food, aggressive interactions, territorial defense, etc.), the number of fish per enclosure was reduced to one, and three additional sites were added for the three experiments in 2003. The model used to relate standard growth rate, SGR,

in these experiments conducted at five sites, among three habitats, two enclosures per habitat, and their interactions was as follows:

$$SGR_{(Length)} = \beta_0 + \beta_{Site} * Site + \beta_{Habitat} * Habitat + \beta_{Enclosure} * Enclosure + \beta_{(Site*Habitat)} * (Site*Habitat) + \beta_{(Site*Enclosure)} * (Site*Enclosure) + \beta_{(Habitat*Enclosure)} * (Habitat*Enclosure) + \beta_{(Site*Habitat*Enclosure)} * (Site*Habitat*Enclosure) + Error \quad (7)$$

In 2003, situations where fish were missing from the enclosure due to mortality or potential escapement were encountered, and replacement fish were added to the enclosure. To balance the analysis, the length and volume of these fish were estimated using site specific regression equations for each time interval. To calculate the regressions, only the data collected from fish that were recovered were used. Estimated observations were then removed from the degrees of freedom, and the ANOVA tables were re-calculated. This was considered to be a conservative method of balancing the analysis, in that fast growth was not overestimated, and slow growth was not underestimated. If anything, this method would result in a Type II error: failure to reject the null hypothesis (i.e., failing to reject that there was equal variation in growth rates between the habitats when there were actually differences in growth rates).

To determine if the initial lengths or volumes of fish stocked in the enclosures differed among the three habitats, one way ANOVAs were conducted using the GLM procedure in MINITAB 13 for each of the five experiments. The following model, equation 8, was used to test the relationship between the initial lengths and volumes among three habitats:

$$\text{Length (or Volume)}_{Initial} = \beta_0 + \beta_{Habitat} * Habitat + Error \quad (8)$$

The null and alternative hypotheses tested were,

$$H_0: \beta_{Barren} = \beta_{Eelgrass} = \beta_{Water\ Column} \quad (9a)$$

$$H_A: \beta_{Barren} \neq \beta_{Eelgrass} \neq \beta_{Water\ Column} \quad (9b)$$

that lengths and volumes were the same among habitats or they were not the same among habitats, respectively.

To determine if the initial length and volume had an influence on the overall specific growth rates in each of the five experiments, multiple regressions were conducted using MINITAB 13. To estimate density dependence free of part-whole correlation it was necessary to obtain a statistic free of spurious correlation (Pearson 1897). To do this, the following regression equations were used for length (10a) and volume (10b), as derived in Appendix II:

$$\ln SL_x = (t_x - t_i)^1 (\alpha) + (SL_i) (t_x - t_i)^1 \beta + \ln SL_i + Error \quad (10a)$$

and

$$\ln Vol_x = (t_x - t_i)^1 (\alpha) + (Vol_i) (t_x - t_i)^1 \beta + \ln Vol_i + Error \quad (10b)$$

The estimate of the slope parameter, the β coefficient for the term $SL_i (t_x - t_i)^1$, was evaluated against the following null and alternative hypotheses:

$$H_0: \beta = 0 \quad (11a)$$

$$H_A: \beta \neq 0 \quad (11b)$$

The resultant statistic and p-value were not inflated by spurious correlation, and the estimate of β was considered not significant if the confidence limits included 0.

2.5 Water Temperature:

2.5.1 Collection

Temperature data were collected at the study sites in 2003, but not 2002. In 2003, I deployed two Vemco™ mini-loggers at each site that recorded the temperature once every hour to the nearest 0.1 °C. In order to obtain a crude temperature "profile", one temperature recorder was attached to the inside of a suspended enclosure (water column), and one was attached to the inside of a seafloor enclosure (benthic) at each of the five sites. The temperature range and accuracy of the units was -4 °C to 20 °C, and ± 0.2 °C respectively.

2.5.2 Data Analysis

Data were analyzed by a fixed factor analysis of covariance (ANCOVA) using the GLM procedure in MINITAB 13. The null (H_0) and alternate (H_A) hypotheses (that there were no differences in the variances in the temperatures among the different habitats and that there were differences in the variances in temperatures among habitats) were as follows:

$$H_0: \beta_{Benthic} = \beta_{Water\ Column} \quad (12a)$$

$$H_A: \beta_{Benthic} \neq \beta_{Water\ Column} \quad (12b)$$

The model used to relate mean daily temperature at 5 sites, 2 habitats and their interactions for each of the 3 growth experiments, with time as the covariate:

$$\text{Mean Daily Temperature} = \beta_0 + \beta_{Time} * \text{Time} + \beta_{Site} * \text{Site} + B_{Habitat} * \text{Habitat} + B_{(Site*Habitat)} * (\text{Site*Habitat}) + \textit{Error} \quad (13)$$

The analysis of the temperature data was broken into three corresponding with the growth experiments in order to meet the assumptions of normality, independence and

homogeneity of residuals. Non-significant interactions with the covariate were removed from the model according to Engqvist (2004) and the model was recalculated.

2.6 Stomach Content Analysis:

To quantify the dietary composition of enclosed juvenile fish at the end of the growth experiments among three habitats in Newman Sound, Newfoundland, each fish was euthanized and preserved at the conclusion of the experiment and stomach contents were identified and enumerated to the lowest taxonomic level possible.

2.6.1 Sample Preservation

All fish recovered from the enclosures were euthanized by inducing cranial hemorrhaging. An identifying tag was attached to each fish, which included site, alpha numeric enclosure number, standard length, and VIE mark if applicable. They were then preserved in 500 ml mason jars with 5% buffered formalin in seawater. After two days, they were rinsed five times with fresh water and transferred to 95% ethanol.

2.6.2 Morphometric Measurements

Measurements of length, volume, and weight were made of the preserved fish with a measuring board, to the nearest millimeter (mm SL), a volumetric flask to the nearest half milliliter (ml), and an electronic balance to the nearest thousandth of a gram (g) respectively. Horizontal and vertical gape widths were measured with Vernier calipers to the nearest hundredth of a millimeter.

2.6.3 Stomach Removal

A straight incision was made with a scalpel from just below the head to the anus along the ventral surface of the body of the fish. The entire digestive tract was removed

from the fish from the beginning of the esophagus to the anus. Next the gall bladder and all caeca were removed from the pyloric region of the stomach. The esophagus was held closed to ensure contents did not fall out inadvertently. Once the digestive tract was isolated, the intestine was removed by cutting the pyloric sphincter distally. The full stomach was then blotted dry to remove any excess preservative and weighed (0.001 g). Then the volume was measured (0.1 ml) and recorded. Each stomach was then dissected, and the contents were placed in small 10 ml jars of 95% ethanol. The inside of the stomach surface was then rinsed three times with ethanol in a squirt bottle and examined under a dissecting microscope to insure nothing remained in the stomach. The empty stomach was then blotted dry again (inside and out) to remove any remaining liquid, and weighed (0.001 g). The empty stomach volume was then measured (±0.01 ml). The total content weight and volume were then calculated by subtracting the full stomach weight and volume by the empty weight and volume.

2.6.4 Stomach Content Processing

The stomach contents were then pipetted from the jar onto a channeled dissecting tray. Contents were sorted and counted using fine-tipped forceps and dissecting probes. As the contents were counted, they were dictated into a tape recorder, and the recorded information was transcribed afterward to reduce the potential for double counting individuals that may occur by having to look away from the eyepieces to record data. Contents were identified to the lowest taxonomic group possible using a variety of sources and dichotomous keys (Smith 1964; Russell-Hunter 1969; Gosner 1971; Kozloff 1990, Dussart 1995, Anderson 2001). However, because of the advanced digestion of

some of the contents, it was sometimes impossible to even guess at the taxonomic group, and the item was labeled as "unknown".

2.6.5 Data Analysis

To quantify differences in the amount of prey consumed in the different habitats, total stomach weight as a percent of the body weight was calculated by the following formula to adjust for body size (Hyslop 1980):

$$C_{Rel} = [(SW_F - SW_E) / W_B] \times 100 \quad (14)$$

C_{Rel} was the relative stomach content weight (as a percent of the body weight), SW_F was the full stomach weight (g), SW_E was the weight of the empty stomach (g), and W_B was the total body weight of the fish (g). Each prey item was enumerated to the lowest taxonomic level possible. While simple counts tend to overestimate the importance of small prey in the diet (Hyslop 1980), they can give a better indication of the amount of energy exerted in the search and capture of prey, which is energy diverted from growth and metabolism (Ball 1961, Hyslop 1980).

Data were analyzed by analysis of variance (ANOVA) using the GLM procedure in MINITAB 13 to test for similarities (15a) and differences (15b) in the variances in the total number of items and the stomach content weights of the fish among the three habitats using the following hypothesis pair:

$$H_0: \beta_{Barren} = \beta_{Eelgrass} = \beta_{Water\ Column} \quad (15a)$$

$$H_A: \beta_{Barren} \neq \beta_{Eelgrass} \neq \beta_{Water\ Column} \quad (15b)$$

These hypotheses were used in conjunction with the following models:

$$\text{Total \# of Prey Items} = \beta_0 + \beta_{Habitat} * \text{Habitat} + \textit{Error} \quad (16)$$

&

$$\text{Relative Stomach Content Weight} = \beta_0 + \beta_{\text{Habitat}} * \text{Habitat} + \textit{Error} \quad (17)$$

2.7 Zooplankton Exclusion Experiment

To determine if the enclosures were actively enhancing or excluding potential prey items (type and size) a plankton sampling experiment was conducted in 2003 at Mistaken Cove using an enclosure simulator (See Appendix I for coordinates). Internal and external samples were taken from the enclosure using methods described below on three different occasions. Samples were preserved, processed and analyzed.

2.7.1 Enclosure Simulator

A modified 0.5 m^3 enclosure was constructed using similar methods and materials as the experimental fish enclosures. Instead of constructing an access panel at the top of the enclosure, a 2.54 cm diameter hole was cut in the center of the top mesh. A 6-meter long section of 2.54 cm diameter clear plastic tubing was fed through the hole until it was exactly in the center of the cube. The tube was then secured using hose clamps and twine to ensure that the tube opening remained in the center of the cube.

2.7.2 Apparatus setup and Deployment

The three sampling events occurred on August 20, 2003, September 04, 2003 and September 16, 2003, at Mistaken Cove (See Appendix I for coordinates) over a patch of barren substrate in four meters of water. The sampling window was established during full daylight, within two hours before and after low tide to avoid potentially confounding effect with the tide. A total of 20 samples were taken during each of the three sampling days (10 inside, 10 outside).

Sampling was conducted from a boat moored in four meters of water (Figure 4). The modified sampling cube was lowered into the water along with a 6 meter length of 2.54 cm diameter clear plastic tube with a mooring weight secured 0.25 meters below the opening to sample water inside and outside the cube. Next a reversible-flow water pump (calibrated to pump at a rate of 0.25 liters per second) was bolted to the sampling platform. A 1.5 meter 2.54 cm diameter clear plastic tube was attached to the outflow end of the pump and secured. The ends of the intake sampling tubes were connected to the inflow end of the pump and secured, and were alternated during the sampling window to alternate taking samples from inside and outside the enclosure.

The pump was primed with unfiltered surface water and allowed to purge for 60 seconds to flush surface water from the system. Upon the commencement of sampling, the outflow tube was placed over a 500 micron mesh filter for 120 seconds (30 liters of filtered seawater). A squirt bottle was filled with pre-filtered seawater and was used to transfer organisms from the inside of the filter into a 500 ml canning jar containing 5% buffered formalin and filtered seawater. After the tissue was fixed for two days, the sample was rinsed and transferred to 95% ethanol solution.

2.7.3 Sample Processing

Samples were processed as described in Section 2.6.4.

2.7.4 Data Analysis

Data were analyzed using MINITAB 13. The Kolmogorov-Smirnov Goodness of Fit Test (KS-Test) for small samples was used to determine if the samples collected were from the same underlying distribution. Two hypothesis pairs were tested to determine if

(1) zooplankton concentrations inside and outside the enclosure were from the same sampling distribution and (2) to determine if the number of taxa per sample inside and outside the enclosure were from the same sampling distribution (equations 18a,b):

$$H_0: [\text{Inside}] = [\text{Outside}] \quad (18a)$$

$$H_A: [\text{Inside}] \neq [\text{Outside}] \quad (18b)$$

The KS-Test is non parametric, and no assumptions about the normality of the distribution were required.

2.8 Zooplankton Sampling Among Habitats

To characterize and monitor prey availability at five sites in Newman Sound, zooplankton pump sampling events occurred bi-weekly between August 19, 2003 and October 21, 2003.

2.8.1 Apparatus Setup and Deployment:

Five zooplankton pump sampling events were conducted approximately bi-weekly between August 19, 2003 and October 21, 2003, at each of the five study sites (See Appendix I for coordinates). Sampling was conducted using the same materials and methods as in section 2.7.2 with slight modifications (Figure 4). The boat was not moored, and instead was left running to maintain position over the habitat being sampled. Heavy winds and rough seas made this strategy necessary, especially during the final three sampling events in the fall. The enclosure simulator was not used, and a single 6-meter long 2.54 cm diameter clear plastic tube with a weighted end was used for sampling. For sampling the benthic habitats (i.e., barren seafloor and eelgrass), the weighted end was lowered until the mooring weight touched the seafloor insuring that the

intake opening remained 0.5m above the seafloor. Sampling in eelgrass habitats occurred within the eelgrass beds, among the eelgrass blades. For water column sampling, the weighted end of the tube was lowered until the intake was 2.5 m below the surface of the water (the depth of the middle of the water column enclosures).

Sampling was conducted in pairs: two samples were collected at each habitat before moving to the next habitat in a random order. Between each sample, the pump was allowed to purge for 60 seconds to ensure that residual water from the previous sample was expelled from the water pump system before a new sample was taken. A total of 30 samples was taken during each of the five sampling events and preserved for processing in the lab.

2.8.2 Sample Processing

Samples were preserved and processed using the same methods as in the preceding sections 2.7.2 and 2.7.3.

2.8.3 Indices of Diversity

In addition to zooplankton concentration (# items / liter) and the number of taxa per sample, three indices of diversity and evenness were calculated and analyzed: the Simpson Index, the Berger-Parker Index, and the Shannon-Wiener Index.

The Simpson's diversity index (D), was calculated as follows (Krebs 1989; Begon et al. 1996):

$$D = 1 / \sum_{i=1}^{s} \rho_i^2 \qquad (19)$$

where ρ_i is the fraction of all organisms which belong to the i-th species. Because $\rho_i^2 = n_i (n_i - 1) / [N (N-1)]$, it was substituted in the above equation to give:

$$D = 1 / \sum_{i=1}^{S} n_i (n_i - 1) / [N (N-1)] \quad (20)$$

In this equation, S was the total number of species in the sample (richness), n_i was the total number of individuals in species *i* counted, and N was the total of all individuals counted. This index estimates the probability that any two individuals chosen at random belong to different species, and is ranked on a scale of 0 (most diverse) to 1 (least diverse). To make this relationship more intuitive, the reciprocal of D was taken for graphical and statistical analysis.

The Berger-Parker diversity index (d) was calculated as follows (Krebs 1989; Begon et al. 1996):

$$d = N_{max} / N \quad (21)$$

In this equation, N_{max} was the number of individuals in the most abundant species for a sample, and N was the total number of individuals counted. This index is a measure of how common the most abundant species is in a sample. It is ranked on a scale of 0 to 1 with 0 being the most diverse, and 1 being the least diverse. Again, the reciprocal of d was taken for statistical and graphical purposes to make this measure of diversity more intuitive.

The Shannon-Wiener diversity index (H') was calculated as follows (Krebs 1989; Begon et al. 1996):

$$H' = -\sum_{i=1}^{S} (\rho_i)(\ln \rho_i) \quad (22)$$

In this equation S was the total number of species in the sample (richness) and ρ_i was the proportion of the richness made up by a given species. H' measures the value of species as a function of their frequency in the community. Low values (i.e., 0) indicate low diversity, while higher values indicate greater diversity.

2.8.4 Data Analysis

The data for zooplankton concentration and taxa number per sample, the Simpson's, Berger-Parker, and Shannon-Wiener Indices were all analyzed using Minitab 13. An analysis of co-variance (ANCOVA) was conducted using the general linear model (GLM) routine to test the same null and alternate hypotheses for each measure of diversity, zooplankton and taxa concentration: the difference among the habitats were equal, or alternatively were not equal, as follows:

$$H_0: \beta_{Barren} = \beta_{Eelgrass} = \beta_{Water\ Column} \quad (23a)$$

$$H_A: \beta_{Barren} \neq \beta_{Eelgrass} \neq \beta_{Water\ Column} \quad (23b)$$

The model used to compare each of the index values among five sites, among three habitats, between two replicates per habitat, and their interactions, with time (date) as the covariate, was as follows:

$$\text{Index Value} = \beta_0 + \beta_{Date} * \text{Date} + \beta_{Site} * \text{Site} + \beta_{Habitat} * \text{Habitat} + \beta_{Replicate} * \text{Replicate} + \beta_{(Site*Habitat)} * (\text{Site*Habitat}) + \beta_{(Site*Replicate)} * (\text{Site*Replicate}) + \beta_{(Habitat*Replicate)} * (\text{Habitat*Replicate}) + \beta_{(Site*Habitat*Replicate)} * (\text{Site*Habitat*Replicate}) + \textit{Error} \quad (24)$$

Taxa numbers per sample and all three indices of diversity met the model assumptions for computing p-values from F-ratios. However, zooplankton concentration did not meet these assumptions. Zooplankton concentration data were natural log (ln) transformed to stabilize the variances to meet model assumptions.

3.0 Results

3.1 Water Temperature

The mean daily water temperatures in water column and benthic habitats in Newman Sound were virtually identical during each of the growth experiments in 2003 (Figure 5). There was no statistical difference between the temperatures at the sites or among the habitats during each of the experiments either (Appendix III (a) Spring: (ANCOVA $p = 0.748$, $n = 425$, $F_{1,406} = 0.10$), (b) Summer: (ANCOVA $p = 0.887$, $n = 429$, $F_{1,410} = 0.02$), (c) Fall: (ANCOVA $p = 0.826$, $n = 419$, $F_{1,400} = 0.05$).

Mean daily water temperatures were warmest during the white hake experiment (July 29, 2003 to September 9, 2003; $\overline{x} = 14.16 \pm 1.30$ °C), followed by temperatures during the Greenland cod experiment (September 9, 2003 and October 20, 2003; $\overline{x} = 10.32 \pm 0.54$ °C), and finally temperatures during the Atlantic cod experiment (June 11, 2003 to July 24, 2003; $\overline{x} = 9.03 \pm 2.59$ °C) (Table 2). During the Atlantic cod experiment in the spring, there were several episodic events in which the water column temperatures rose above the benthic temperatures by over 1°C for two or three days before equalizing again. Two episodic events (one in late September and one in mid-October) also occurred in which water rapidly decreased by 6-8 °C over one to three days however these changes were the same in each habitat at all sites.

3.2 Zooplankton Inclusion-Exclusion Experiment

The results of the Kolmogorov-Smirnov test (K-S Test) for each of the three sampling events at Mistaken Cove in Newman Sound, Newfoundland reveal that there were no significant differences in either the number of taxa per sample or the

zooplankton concentration (# / liter) in the pump samples taken inside and outside an experimental enclosure (Table 3). The composition of taxa and proportions of individuals within a given taxon between each of the three sampling events fluctuated slightly, but no obvious trends were evident and differences likely reflected natural temporal variability in zooplankton abundance and distribution (Figure 6). The taxa and zooplankton samples taken from inside and outside the experimental enclosure were from the same distribution. Therefore, the enclosure likely did not exclude potential zooplankton prey items from entering the enclosure, or attract any potential prey items during the sampling window.

3.3 Growth Experiments

3.3.1 2002 Greenland Cod Pilot Experiment

Of the 60 Greenland cod stocked in the enclosures, 75 % were recovered after 22 days (Table 1b). All of the recovered fish retained their VIE marks. There were no differences in the percentage of fish recovered between sites or among the three habitats. The initial lengths of fish during stocking of enclosures did not differ among the habitats (Appendix IV, One-way ANOVA, $p = 0.845$, $F_{[2,57]} = 0.17$). Results of a multiple regression revealed that initial length did not influence the overall length-specific growth rate ($\beta \pm 95$ % C.I. $= 0.00033 \pm 0.00207$), $t_{[43]} = 0.31$, $p = 0.756$). The relative growth of the enclosed fish in the three habitats was very similar over time (Figure 7a). Growth rates were extremely low (the slope of the regression equation) and were also similar for fish in each habitat (Table 4). Mean standard growth was also similar for all fish enclosed in the three habitats (Table 1b). Fish in the barren mud enclosures grew at a

mean rate (± SE) of 0.068 ± 0.016 %·day^{-1}, fish in eelgrass enclosures grew at a mean rate of 0.074 ± 0.021 %·day^{-1}, and fish in water column enclosures grew at a mean rate of 0.064 ± 0.024 %·day^{-1}, but no significant differences were detected among the habitats (Appendix V, $p = 0.138$, $n = 107$, $F_{[2,94]} = 2.02$).

3.3.2 2002 – 2003 Atlantic Cod Winter Growth Experiment

All 10 enclosures used in the over-winter experiment were recovered in the spring of 2003 (Table 1b). Of the 60 fish stocked in the enclosures, only 32 % were recovered after 210 days, and all of those recovered retained their VIE marks. Over twice as many fish were recovered from the deep water enclosures as from either the eelgrass or barren seafloor enclosures (Table 1b) and this difference was significant (Appendix VI, $p = 0.017$, $n = 60$, $F_{[2,57]} = 4.39$). In addition, significantly more fish were recovered from a depth of 8 meters than from a depth of 4 meters (55 % and 20 % respectively; Appendix VI, $p = 0.005$, $n = 60$, $F_{[1,58]} = 8.35$). There were no differences in the initial lengths of fish stocked into the enclosures among the three habitats (Appendix III, $p = 0.515$, $F_{[2,52]} = 0.67$). Initial length did not have a significant influence on overall specific growth rate based on the results of a multiple regression ($\beta \pm 95$ % C.I. $= 0.00052 \pm 0.00081$), $t_{[17]} = 1.24$, $p = 0.231$). Initial length also had no effect on over winter survival (One-way ANOVA, $p = 0.244$, $n = 60$, $F_{[16,59]} = 1.29$). Slight differences in relative growth rates of the fish between the three habitats were detected (Figure 7b). Fish in eelgrass enclosures grew at an average (± SE) rate of 0.151 ± 0.015 %·day^{-1}, fish in barren seafloor enclosures grew 0.129 ± 0.017 %·day^{-1} and fish in deep water enclosures grew 0.116 ± 0.015 %·day^{-1} (Table 1b), however, these differences were not significant (Appendix V, p

= 0.121, n = 19, $F_{[2,6]} = 3.06$). Nonetheless, mean (± SE) growth rate did differ significantly by site, in that the mean growth rate was significantly greater at Mistaken Cove (0.141 ± 0.012 %·day^{-1}) than at Minchin Cove (0.102 ± 0.014 %·day^{-1}; Appendix V, p = 0.026, n = 19, $F_{[1,6]} = 8.68$).

3.3.3 Spring 2003 Atlantic Cod Growth Experiment

Approximately 83 % of the Atlantic cod used in this experiment were recovered after 43 days (Table 1b), and there was no obvious indication that recovery rate was dependant on site or habitat. The initial sizes of fish stocked in the enclosures did not differ significantly among the three habitats (Appendix IV, Length [p = 0.482, $F_{[2,27]}$ = 0.75], Volume [p = 0.511, $F_{[2,27]} = 0.69$]). Results of multiple regressions indicated that there was no influence of initial length (β ± 95 % C.I. = 0.00122 ± 0.00280), t (29) = 0.93, p = 0.358) or initial volume (β ± 95 % C.I. = 0.01598 ± 0.01645), t (29) = 1.90, p = 0.068) on the overall specific growth rates. Length- and volume-specific growth rates were similar for barren seafloor and eelgrass habitats, but were much lower for the water column habitats (Table 4). Significant differences were detected between length specific growth rates among the three habitats (Appendix VII, p < 0.001, n = 75, $F_{[2,45]} = 9.18$). The mean standard growth rates (± SE) were higher for Atlantic cod in eelgrass (0.366 ± 0.026 %·day^{-1}) than in barren seafloor (0.327 ± 0.035 %·day^{-1}), and both were much greater than growth rates in water column (0.065 ± 0.013 %·day^{-1}) (Table 1b). Relative growth rates followed a similar pattern (Figure 8a). The mean volume specific growth rates (± SE) showed that cod enclosed in benthic habitats had higher growth rate (barren seafloor, 1.350 ± 0.171 %·day^{-1}; eelgrass, 1.321 ± 0.121 %·day^{-1}) than those enclosed in

water column, 0.235 ± 0.123 %·day^{-1} respectively) (Table 1b), and relative growth followed a similar pattern (Figure 8b). These differences were also significant (Appendix VII, $p = 0.003$, $n = 75$, $F_{[2,45]} = 6.64$).

3.3.4 Summer 2003 White Hake Growth Experiment

One hundred percent of the fish used in the summer 2003 white hake growth experiment were recovered after 42 days (Table 1b), all of which were present from the onset of the experiment. The initial sizes of fish stocked in the enclosures did not differ significantly among the three habitats (Appendix IV, Length [$p = 0.345$, $F_{[2,27]} = 1.11$], Volume [$p = 0.139$, $F_{[2,27]} = 2.12$]). Results of multiple regressions indicated that there was no influence of the initial length ($\beta \pm 95$ % C.I. = 0.00031 ± 0.00506), t (29) = 0.12, $p = 0.905$) or the initial volume ($\beta \pm 95$ % C.I. = 0.00925 ± 0.01679), t (29) = 1.08, $p = 0.289$) on the overall growth rates. The growth rates in length and volume were greatest in eelgrass followed by the barren seafloor and water column habitats (Table 4). After the first three weeks, the relative growth of enclosed barren and eelgrass fish were similar, but by week six a clear difference had emerged (Figure 9). White hake enclosed in the water column had consistent growth, however at a slower rate than fish enclosed in the two benthic habitats. From day 20 to day 42, however, it appeared as if growth in all habitats may have slowed somewhat as the water temperature suddenly dropped. Overall, fish enclosed in eelgrass habitats had the greatest growth, followed by fish in barren seafloor and water column habitats (Table 1b). The mean SGR (± SE) of white hake in eelgrass was greatest at 0.713 ± 0.062 % in length·day^{-1} and 2.224 ± 0.249 % in volume·day^{-1}. The mean SGR (± SE) in barren seafloor habitats was 0.483 ± 0.055 % in

length·day^{-1} and 1.754 ± 0.188 % in volume·day^{-1}, and SGR was lowest in the water column at 0.271 ± 0.040 % in length·day^{-1} and 0.753 ± 0.140 % in volume·day^{-1}. These SGR were significantly different among the three habitats for both length (Appendix VIII, $p = 0.009$, $n = 90$, $F_{[2,60]} = 5.09$) and volume (Appendix VIII, $p = 0.005$, $n = 90$, $F_{[2,60]} = 5.82$).

3.4.5 Fall 2003 Greenland Cod Growth Experiment

Eighty percent of the fish used in this experiment were recovered after 41 days (Table 1b). Many fish in the enclosures developed lesions on the anal fin and the caudal peduncle. In some cases, these lesions caused the edges of the fin to turn white and the fins to split. In more severe cases, the fins were completely absent, and the fishes' body was raw and irritated where the fin was attached at the caudal peduncle. The presence of these lesions was not confined to a specific site or habitat and they were also found on free ranging fish caught at various seining events, indicating that there may have been a pathogen or harmful bacteria in the water in Newman Sound during this experiment. The lesions were not an artifact of the methods used in this experiment, but may have influenced the growth rates experienced by the enclosed fish. The initial sizes of fish stocked in the enclosures did not differ significantly among the three habitats (Appendix IV, Length [$p = 0.080$, $F_{[2,27]} = 2.77$], Volume [$p = 0.193$, $F_{[2,27]} = 1.75$]). Initial length and initial volume did not influence the overall length- or volume-specific growth rates based on the results of multiple regressions [initial length: ($\beta \pm 95$ % C.I. = 0.00200 ± 0.00251), t (29) = 1.77, $p = 0.088$); initial volume: ($\beta \pm 95$ % C.I. = 0.00445 ± 0.00983), t (29) = 0.89, $p = 0.383$, respectively)]. Slopes of the regressions for length and volume of

fish in water column habitats were greatest, followed by barren seafloor and eelgrass habitats (Table 4; Figure 10). Mean SGR (± SE) for fish enclosed in water column enclosures was rapid for the entire 6 week interval in terms of length (0.449 ± 0.055 %·day^{-1}) and volume (1.288 ± 0.237 %·day^{-1}) (Table 1b). Mean SGR (± SE) of fish enclosed in barren mud habitats in terms of length (0.372 ± 0.028 %·day^{-1}) and volume (1.104 ± 0.144 %·day^{-1}), were also greater than the SGR of fish in eelgrass for length (0.254 ± 0.013 %·day^{-1}) and volume (0.950 ± 0.072 %·day^{-1}). Significant differences in SGR_{Length} were detected among the three habitats (Appendix IX, $p = 0.002$, $n = 96$, $F_{[2,66]} = 6.95$). However differences in SGR_{Volume} of fish among habitats were not significant at $\alpha = 0.05$ level (Appendix IX, $p = 0.087$, $n = 96$, $F_{[2,66]} = 2.53$). The mean absolute change in length and volume followed similar patterns as SGR and RGR (Table 1). Fish in the water column grew at the greatest rate, followed by fish in barren seafloor and eelgrass habitats.

3.4 Diet of Enclosed Juvenile Gadiformes

3.4.1 2002 – 2003 Atlantic Cod Winter Diet

The stomachs of the 19 Atlantic cod that survived the over-winter growth experiment were removed and analyzed: five were from barren seafloor enclosures, three were from eelgrass enclosures, and 11 were from the deep water enclosures. Every stomach contained food that ranged from well digested to fresh, suggesting that the fish were feeding up to and right before they were removed from the enclosures. There were no obvious differences in the state of digestion of the stomach contents among the three habitats. There was a great deal of variation in the number of prey items found in the

stomachs of enclosed fish (Figure 11). Total numbers of each prey group among habitats are presented in Appendix X. Mean number (± SD) of prey items for fish enclosed in barren seafloor habitats was 384.40 ± 329.00, whereas fish from eelgrass enclosures contained only 160.33 ± 126.53 items, and fish from deep water enclosures contained 295.18 ± 276.30 items (Table 5). No major differences in the median number of prey items in the stomachs were detected. Results of a one-way ANOVA reveal that the total number of items in the stomachs did not differ significantly among the habitats (Appendix XI, $p = 0.627$, $n = 19$, $F_{[2,16]} = 0.48$). There was large variation in stomach content weight as a percent of the total body weight (Figure 11). The mean percent (± SD) stomach content weights of fish scaled to body size from the three habitats were similar (barren seafloor = 1.45 ± 0.79, eelgrass = 1.16 ± 1.47, deep water = 1.23 ± 0.47, Table 5). The median content weight was lower in the eelgrass fish than in the barren seafloor and deep water enclosed fish, but differences were not statistically significant (Appendix XII, $p = 0.795$, $n = 19$, $F_{[2,16]} = 0.23$).

Proportionally, there were also no obvious major differences in the prey taxa consumed between habitats. Calanoid copepods comprised about 50-75 % of the diet in each of the three habitats (Figure 12). Of that proportion, 100 % were *Pseudocalanus* sp. in barren mud and eelgrass stomachs, whereas in deep water 90 % were *Pseudocalanus* sp. and 10 % were *Temora* sp. Of the approximately 25 % of the diet that were cyclopoid copepods, all of these were *Oithona* sp. in barren seafloor and eelgrass; and 96 % were *Oithona* sp. and 4 % were *Oncaea* sp. in deep water stomachs. Harpacticoid copepods

(*Microsetella* sp.) comprised approximately 21 % of the diet in deepwater and barren seafloor habitats, but only 15 % of the diet of fish in eelgrass.

Euphausiids comprised about 5 % of the diet in eelgrass and deep water fish diets, and about 3 % barren diets. Amphipods (caprellids and gammarids) comprised about 2 % of the diet of eelgrass fish and less than 1 % of the barren and deep water diets. Of the total number of euphausiids consumed, 47 % were found in deep water stomachs, 30 % were found in barren stomachs and 23 % were found in the stomachs of eelgrass fish.

3.4.2 Spring 2003 Atlantic Cod Diet

The stomachs of the 25 age 1+ Atlantic cod that survived the spring growth experiment were removed and analyzed (Table 1a; nine from barren, nine from eelgrass, seven from the water column). There was no obvious difference in the state of digestion between the stomach contents from the three habitats, and all of the stomachs contained food items. Most of the stomachs were full of fresh prey, suggesting that the cod were actively feeding right before they were sampled. There was a high degree of variation in the number of food items found in the stomachs (Figure 13). The mean number (± SD) of prey items was much greater in fish from barren seafloor (587.00 ± 532.00) habitats than eelgrass (313.40 ± 268.70) or water column (65.00 ± 26.50) habitats (Table 5). The median number of prey items also differed among the habitats. A one-way ANOVA was conducted on natural log transformed values of total prey items. Transformation was necessary to stabilize the variances and meet the model assumptions (i.e., normality and homogeneity of residuals). Results were significant (Appendix XI, $p = 0.003$, $n = 25$, $F_{[2,22]} = 7.56$). Mean stomach content weights (± SD) scaled to body weight (%) were

also highly variable within and among habitats (Figure 13). Stomach content weights of fish from barren seafloor (1.36 ± 0.68) and eelgrass (1.19 ± 0.74) habitats were similar, and were both much greater than the stomach content weights from the water column (0.44 ± 0.15) habitats (Table 5). Results of a one-way ANOVA conducted on natural log-transformed values of the percent weight of the stomach contents met the model assumptions and the differences were significant ($p = 0.018$, $n = 25$, $F_{[2,22]} = 4.81$).

The observed proportion of prey items consumed differed slightly between the two benthic habitats and the water column habitat (Figure 14; Appendix X). The diet of barren mud and eelgrass fish was dominated by approximately 70 % harpacticoid copepods (4 % *Zaus* sp. and 96 % *Microsetella* sp. in barren, 1 % *Zaus* sp. and 99 % *Microsetella* sp. in eelgrass), while harpacticoids only comprised 23 % of the water column diet (all *Microsetella* sp.). Cyclopoids comprised a higher proportion of the water column diet (24 %; 92 % *Oithona* sp. and 8% *Oncaea* sp.) followed by barren seafloor (20 %; 58 % *Oithona* sp. and 42 % *Oncaea* sp.) and eelgrass diets (1 %; 98 % *Oithona* sp. and 2 % *Oncaea* sp.). Calanoids represented a higher proportion of the water column diet (23 %; 35 % *Acartia* sp., 29 % *Temora* sp., 36 % *Calanus* sp.) than the barren (8 %; 48 % *Acartia* sp. and 52 % *Temora* sp.) or eelgrass diet (8 %; 24 % *Acartia* sp. and 52 % *Temora* sp. 24 % *Calanus* sp.).

Euphausiids occurred at a higher proportion in the diet of fish in eelgrass (2 %) compared to the diet of fish in barren seafloor and water column habitats (both less than 1 %). Of the total euphausiids consumed, most were consumed by fish enclosed in eelgrass (65 %) followed by barren seafloor (34 %) and water column (1 %) habitats. Amphipods

comprised the highest proportion in the diet of water column (8 %) followed by eelgrass (3 %) and barren seafloor (1 %) fish. Of the total amphipods consumed however, most were consumed in eelgrass, followed by barren seafloor and water column habitats (48 %, 34 %, and 18 % respectively).

3.4.3 Summer White Hake Diet

The stomachs of the 30 age 0+ white hake that were used in the spring growth experiment were removed and analyzed (10 from each of the three habitats). There was abundant well-digested material along with some fairly fresh items in the stomachs, showing that the white hake had fed earlier in the day and had also fed recently relative to the time of sampling. All of the stomachs contained food items. The numbers of prey items in each of the stomachs was variable (Figure 15). The mean number of food items (± SD) in stomachs was greatest in fish from the eelgrass habitat (61.30 ± 44.80), followed by barren mud (23.50 ± 26.10) and water column (18.90 ± 18.04) fish (Table 5). Stomachs from eelgrass enclosures had the highest median number of items, and stomachs from barren seafloor and eelgrass enclosures had about the same median number of items. The results of a one-way ANOVA, which did not require data transformation, show that the total number of items in the stomachs differed significantly among the habitats (Appendix XI, $p = 0.011$, $n = 30$, $F_{[2,27]} = 5.39$). The stomach weights of individual fish among and within the habitats were also variable (Figure 15). The mean stomach content weight as a percent of the body weight (± SD) was also greatest in fish from eelgrass (0.69 ± 0.52) enclosures, followed by fish from the water column (0.47 ± 0.39) and barren seafloor (0.29 ± 0.25) enclosures (Table 5). The median stomach

weights followed the same pattern. A one-way ANOVA revealed that the stomach content weight differed significantly among the habitats as well (Appendix XII, $p = 0.004$, $n = 30$, $F_{[2,27]} = 7.01$).

The dietary composition of experimental fish also differed among habitats, but no one taxonomic group dominated the diets among treatments (Figure 16; Appendix X). Even though calanoids are typically found in the water column, they comprised 34 % of the barren seafloor diet (70 % *Pseudocalanus* sp., 29 % *Calanus* sp., less than 1 % *Temora* sp.), 31 % of the eelgrass diet (87 % *Pseudocalanus* sp., 12 % *Calanus* sp., less than 1 % *Acartia* sp.), and only 4 % of the water column diet (60 % *Acartia* sp., 40 % *Calanus* sp.). Harpacticoids comprised 11 % of the eelgrass diet and 2 % of the barren seafloor and 2 % of the water column diet (all were *Microsetella* sp.). Fish from the water column also had a large proportion (29 %) of bivalves (clams and mussels with hard shells) in their stomachs compared to barren and eelgrass fish (2 % and 0 % respectively). Polychaetes, (both late larval and post larval) comprised 6 % of the barren seafloor and water column diet and only 3 % of the eelgrass diet, but by number eelgrass fish had the most in their stomachs.

Amphipods comprised a large proportion of all of the diets (33 % barren seafloor, 25 % eelgrass, 20 % water column). Euphausiids were found in the highest proportion in stomachs of fish in the water column (32 %), followed by fish in eelgrass (24 %) and barren seafloor habitats (14 %). By number, eelgrass fish had the most euphausiids in their stomachs. 57 % of the amphipods consumed were found in the stomachs of fish in eelgrass habitats, 30 % were in the stomachs of barren seafloor fish and 13 % were in the

stomachs of water column fish. In addition, 61 % of the euphausiids consumed were in the stomachs of fish in eelgrass, 25 % were in the stomachs of water column fish, while 15 % were in the stomachs of barren seafloor fish.

3.4.4 Fall 2003 Greenland Cod Diet

The stomachs of the 24 age 0+ Greenland cod that survived the spring growth experiment were removed and analyzed (Table 1a; six from barren, nine from eelgrass, nine from the water column). Every stomach collected contained food items. There was some well digested material, but the majority was very fresh and hence recently captured. While the number of prey items consumed varied within and between each habitat (Figure 17), differences were not significant (Appendix XI, one-way ANOVA, $p = 0.256$, $n = 24$, $F_{[2,21]} = 1.45$). The stomachs collected from water column fish had the highest mean (± SD) number of prey items (154.22 ± 104.07), followed by stomachs from eelgrass (145.78 ± 90.82) and barren seafloor (79.83 ± 44.15) fish (Table 5). The median number of prey items followed a similar pattern. However, the weight of the stomach contents as a percentage of the body weight did not follow this pattern (Figure 17). The mean percent weight (± SD) was much greater in stomachs collected from fish in eelgrass (0.90 ± 0.26) than from stomachs collected from water column (0.54 ± 0.39) or barren seafloor (0.41 ± 0.24) fish (Table 5). The total weight of the stomach contents differed significantly among the habitats (Appendix XII, one-way ANOVA, $p = 0.014$, $n = 24$, $F_{[2,21]} = 5.28$).

Diets were similar among the habitats (Figure 18; Appendix X). Calanoid copepods were the dominant food item by proportion in barren seafloor (65 % calanoids;

of total calanoids the breakdown was 22% *Acartia* sp., 42 % *Temora* sp., 2 % *Calanus* sp., 34 % *Pseudocalanus* sp.), eelgrass (75 % calanoids; of total calanoids the breakdown was 22 % *Acartia* sp., 40 % *Temora* sp., 3 % *Calanus* sp., 35 % *Pseudocalanus* sp.), and water column diets (60% calanoids; of total calanoids the breakdown was 45 % *Temora* sp., 2 % *Calanus* sp., 53 % *Pseudocalanus* sp.). In contrast to barren seafloor and eelgrass where Acartia was important, this taxon was effectively absent from stomachs of fishes in the water column treatment. Cladocerans (*Evadne* sp. and *Podon* sp.) were also present in larger proportions in water column (24 %), than in barren seafloor (7 %) and eelgrass (5 %) diets. Cyclopoids comprised 8 % of the water column diet, 6 % of the barren mud diet, and less than 1 % of the eelgrass diet, whereas harpacticoids made up 6 % of the barren seafloor diet, 4 % of the eelgrass diet and less than 1 % of the water column diet. Euphausiids comprised 8 % of the barren diet, 7 % of the eelgrass diet and only 3 % of the water column diet, while amphipods comprised 5 % of both barren and eelgrass diets and less than 1% of the water column diet. Of the total euphausiids consumed, 73 % were consumed by fish in eelgrass, 20 % by fish in barren seafloor and 7 % by fish in water column enclosures. Similarly, of the total euphausiids consumed, 57 % were consumed by fish in eelgrass enclosures, while 23 % and 20 % were consumed by fish enclosed in water column and barren habitats, respectively.

3.5 Zooplankton Sampling Among Habitats

Zooplankton concentration and the number of taxa per sample appeared stable among habitats from August 19th to September 25th, and then fluctuated slightly until October 21st (Figure 19a). Zooplankton concentrations were consistently higher in barren

and eelgrass samples than in water column samples between August 19th and September 25th. However, zooplankton samples with substantially large concentrations were collected from all six Stairs Cove samples from October 8th and 2 eelgrass samples from Mistaken Cove on October 21st. When these outliers were removed from the data (Figure 19b) or by natural log transformation to stabilize the variances (Figure 19c), the mean zooplankton concentrations were approximately equal on October 11th and October 21st. An ANCOVA relating site, habitat, replicate and time (covariate) to ln transformed zooplankton concentrations met the criteria of normality, independence and homogeneity and revealed that statistical differences existed between the habitats (Appendix XIIIa, $p = 0.001$, $n = 150$, $F_{[2,119]} = 6.96$). There were differences in zooplankton concentration among sites. Overall, Stairs Cove had the highest mean (± SD) zooplankton concentration (24.74 ± 3.60 zooplankton liter^{-1}), followed by Mistaken Cove (15.11 ± 0.77 zooplankton liter^{-1}), South Broad Cove (11.97 ± 0.86 zooplankton liter^{-1}), Hefferns Cove (10.09 ± 1.02 zooplankton liter^{-1}), and Minchin Cove (9.64 ± 1.18 zooplankton liter^{-1}). In addition, the number of taxa per sample differed among the habitats and over time (Appendix XIIIb, $p = 0.006$, $n = 150$, $F_{[2,119]} = 5.32$). In general samples from barren areas had the highest number of taxa per sample followed by eelgrass and water column samples (Figure 19).

Overall, mean zooplankton concentrations were significantly greater in samples from the two benthic habitats than the water column (Table 6; $p = 0.009$, $F_{[1,129]} = 7.01$). Calanoids (*Acartia* sp, *Temora* sp., *Calanus* sp., and *Microsetella* sp.) were the most abundant taxa in each of the three habitats, with the greatest concentrations in eelgrass

samples, followed by barren seafloor and water column samples (Table 6). Of the other major copepod taxa observed more frequently, harpacticoids (*Microsetella* sp. and *Zaus* sp.) were most abundant in the barren samples, while cyclopoids (*Oithona* sp. and *Oncaea* sp.) were most abundant in barren seafloor and water column samples. Cladocerans (*Evadne* sp. and *Podon* sp.) were most abundant in eelgrass samples. Of the larger items in the zooplankton, polychaete and amphipod concentrations were greater in barren and eelgrass samples than in water column samples. Overall, euphausiid, isopod, chaetognath and mysiid concentrations were greater in eelgrass samples than in barren seafloor or water column samples.

There was a large degree of variation in the concentration of various taxa in the samples over time (Table 7). Mean zooplankton concentrations remained fairly stable during the first 2-3 sampling events for most taxa followed by a strong negative trend after September 10, 2003 (Figure 20a-r). No obvious succession of dominant zooplankton taxa over time was detected, despite the general negative trend in zooplankton concentration for all taxa. However, as most taxa declined in concentration in samples from October 8, 2003, chaetognath, cumacean, gastropod and harpacticoid concentrations increased slightly in the samples, but by the final sampling event on October 21, 2003 they had stabilized.

The diversity of samples collected from all three habitats was intermediate according to the Simpson's Index, intermediate to low according to the Berger-Parker Index, and low according to the Shannon-Wiener Index (Figure 21a-c; Table 7). Results of fully fixed factor ANCOVAs indicated that there were no statistical differences in the

diversity among the habitats within sampling dates in samples collected in Newman Sound according to all three diversity indices (Simpson's Index: Appendix XIII(c), $p = 0.306$, $n = 150$, $F_{[2,119]} = 1.20$; Berger-Parker Index: Appendix XIII(d), $p = 0.282$, $n = 150$, $F_{[2,119]} = 1.28$; Shannon-Wiener Index: Appendix XIII(e), $p = 0.209$, $n = 150$, $F_{[2,119]} = 1.59$). Graphically, slight fluctuations in diversity were evident (Figure 21). The three indices showed that the barren seafloor samples were more diverse than eelgrass and water column samples from August 18, 2003 to September 9, 2006 (Figure 21a-c), and on September 5, 2006 the diversities were similar in all three habitats. On October 8, 2006, diversity was again greatest for the barren seafloor samples measured with the Berger-Parker and Simpson's Indices, but the diversity of samples was similar according to the Shannon-Wiener Index. The benthic samples collected on October 21, 2006 were again more diverse than the water column samples for all three indices. All three diversity indices differed significantly with time, suggesting an overall negative trend in zooplankton diversity in the samples collected from August 19, 2003 to October 21, 2003 in Newman Sound (Simpson's Index: Appendix XIII(c), $p = < 0.001$, $n = 150$, $F_{[2,119]} = 15.02$; Berger Parker Index: Appendix XIII(d), $p = 0.015$, $n = 150$, $F_{[2,119]} = 6.09$; Shannon-Wiener Index: Appendix XIII(e), $p = < 0.001$, $n = 150$, $F_{[2,119]} = 20.47$).

4.0 Discussion

My objective in this study was to test three related hypotheses: (1) juvenile Gadiformes that occupied habitats with structural complexity (i.e., eelgrass) experienced faster growth than similarly sized juveniles that remained in the water column or occupied barren habitats; (2) differences in growth rates among habitats were associated with differences in either the quality or quantity of prey items consumed; (3) differences in growth rate among habitats were associated with differences in food availability. As expected, juveniles ingested higher concentrations of benthic prey taxa (harpacticoids, amphipods, mysids, isopods, polychaetes, bivalves) near the seafloor than in the water column. Juvenile Gadiformes also ingested higher concentrations of calanoid copepods in eelgrass than in barren seafloor habitats. Atlantic cod and white hake foraged selectively on benthic prey relative to the assemblage available to them in the water flowing through the enclosures. However, the diets of all three species differed little between structured and unstructured benthic habitat, compared to diet of similarly sized fish enclosed in the water column. Juvenile cod consumed more calanoids when in the water column enclosures, while consuming more harpacticoids and other benthic taxa when in the barren and eelgrass enclosures. Surprisingly, calanoid copepods were not a significant component in the diet of white hake in water column enclosures. Greenland cod consumed large numbers of calanoids when in either of the benthic or the water column enclosures, and cladocerans were a major prey item for this species when in the water column enclosures. Atlantic cod and white hake grew faster in eelgrass than in barren seafloor substrate or in the water column. Greenland cod grew faster in water

column enclosures than in eelgrass or barren seafloor enclosures, a difference consistent with the greater importance of calanoid copepods in their diet. The observed differences in growth rate could not be attributed to thermal differences or to the structuring effects of the enclosures, suggesting that different habitats in Newman Sound, Newfoundland supported different relative potential for growth in juvenile Gadiformes.

4.1 Water Temperature

Maximum growth and food conversion rate in fish is closely related to water temperature optima, and fish tend to reside at these temperatures to optimize physiological activity (Jobling 1981). These temperature optima change ontogenetically as fish mature. Smaller fish often prefer warmer water than older conspecifics when food is not limiting (Lafrance et al. 2005). For example, for Atlantic cod, the optimal temperature for growth decreases with increasing fish mass, from 17°C for a 2 gram fish to 7°C for a 200 gram fish (Bjornsson et al. 2001). Whereas differences in temperature are known to cause differences in growth rate in juvenile fish, the observed differences in growth rates in my study were not due to temperature because water temperatures were virtually identical throughout Newman Sound and were not significantly different between the habitats during experiments in 2003.

There were periods during the spring when water column temperatures were slightly warmer than benthic temperatures, which could have been the result of a combination of solar radiation and limited wind-induced mixing of surface and bottom water, but these differences in temperature were not statistically significant, and likely did not cause differences in growth rates. The rapid warming and cooling events during

the three experiments may have been caused by either wind-driven downwelling or upwelling events respectively, which can increase the supply of zooplankton and larval fish in fjords (Schneider and Methven 1988; Ings 2006). The study sites within Newman Sound appeared to be well mixed and isothermal in 2003, and temperature was likely not a significant factor for growth rate patterns of enclosed juvenile Gadiformes in the three habitats.

4.2 Enclosure Method

Caging studies have artifacts, in that the behavior of enclosed individuals differs from that of free-ranging individuals and the effects can vary across large and small spatial scales (Frost et al. 1988; Hall et al. 1990; Englund and Olsson 1996). In this study, physical structure (the enclosure itself) was introduced into otherwise unstructured habitats (barren seafloor and water column) and habitat structure was altered in eelgrass habitat (i.e., the physical placement of the enclosure in the eelgrass beds modified the structure of the habitat). Enclosed juveniles did not have access to potential prey in or on the seafloor, or to prey directly associated with eelgrass blades because the enclosure was not buried in the sediment and the eelgrass blades were not in the enclosure; fish could only forage on whatever entered the enclosures from the surrounding habitat. Fish behavior and the behavior of potential prey items (zooplankton) may have been influenced as a result. Englund (1997) suggested that in small-scale predator caging studies, the patterns observed reflect the effects of prey behavior and movements (i.e., prey densities are influenced by prey movements and behaviors). The observed effects in large-scale experiments are primarily the result of the influence of the predator (i.e.,

predation influenced prey densities). In addition, removal of the risk of predation does not necessarily remove the perceived risk of predation, and enclosed fish might have still been influenced by actively foraging predators outside the enclosure. In fact, Gregory (1994) reported that feeding rate of juvenile salmon declined in a potentially risky environment even in the absence of a direct predator threat. However the types of predators do not differ significantly between sites or among habitats in Newman Sound (Linehan et al. 2001; Laurel et al. 2003) so all enclosed fish were likely exposed to similar perceived predation threats further limiting the structuring effects of the enclosures. In my study, the principle artifacts were associated with the physical structure of the enclosure, which was identical across all three habitats. As a result, the structuring effects of the enclosures were likely the same in each of the habitats, and the resulting differences in growth rates and diets are not considered confounded.

Large enclosures are preferable to smaller enclosures in ecological studies because they reduce the effect of the enclosure by better approximating the natural ecosystem (Parsons, 1978). Stephenson et al. (1984) found that in large enclosures (>1000 m^3), a distinctive 'edge zone' extended about 1 m from the walls in which macro-zooplankton abundance was greater than in the middle of the enclosures; this zone was absent in medium (125 m^3) and small (20 m^3) enclosures. In addition micro-zooplankton patchiness within the enclosure decreased with decreasing enclosure size (Stephenson et al. 1984). The size of the enclosures used in this study was necessary to reduce the structuring effect as much as possible while still being small enough to recover cages and

sample the enclosed fish. The effect of internal zooplankton patchiness may have also been reduced by the structural uniformity of the enclosures.

The enclosures used in my experiments were an effective method of confining juvenile fish to a specific habitat. Sogard (1992) buried the edges of the enclosure into the sediment to give fish access to the substrate in growth experiments. There would have been several problems with doing this in my experiment. First, the enclosures would have then been different from each other, making comparisons between them difficult because of the addition of potential confounding variables (i.e., benthic enclosures would have had five sides, water column would have had six). Second, because of the depth of water in which the enclosures were located, stocking and removing the fish would have required SCUBA, which would have increased the chance of escapement and greatly increased the logistical difficulty in terms of personnel and time.

Sogard (1992) also placed natural vegetation in enclosures at vegetated sites. I chose not to include living eelgrass in my experiments for the logistical reasons, and chose not to include synthetic vegetation in an attempt to avoid confounding variables with the physical structure of the enclosures (i.e., I wanted to keep them all exactly the same). In tank studies, Gotceitas and Brown (1993) demonstrated that in the absence of predators, juvenile cod preferred open sandy habitats as opposed to sheltered habitats, presumably to enhance foraging efficiency. Main (1987) demonstrated that increased structure, in addition to predator avoidance strategies, reduces risk of predation on the small caridean shrimp, *Tozeuma carolinense*, by pinfish, *Lagodon rhomboides*. It has

also been shown that potential prey items (e.g., amphipods) of juvenile fish exhibit anti-predator responses and associate with dense structure when injury-released chemical cues from other amphipods are detected (Wisenden et al. 1999). However the inclusion of complex structure (living vegetation) in other enclosure experiments does not suggest that reduced foraging efficiency is likely (Sogard 1997). In fact Keats and Steele (1993) noted that juvenile fish often feed on amphipods and harpacticoid copepods that are directly associated with marine vegetation. Incorporating vegetation in eelgrass enclosures in my experiments may have resulted in a more accurate estimate of growth rate differences between structured and unstructured habitats because the fish would have had access to naturally occurring substrates (i.e., better approximating the natural ecosystem) that they would encounter as free ranging fish. This approach was not possible for my experiments because eelgrass is rooted in the sediment, adding to the logistical constraints associated with burying the edges of the enclosures. I did consider adding artificial eelgrass in the enclosures, however, this would have introduced an additional confounding variable (i.e., artificial eelgrass blades) that the study was not designed to test. Instead, my enclosures were all constructed exactly the same (i.e., 6 sides with no additional internal structure) so that each had the same structural artifacts. Due to the placement of enclosures in larger patches of eelgrass, blades of eelgrass surrounded the each of the enclosures in this habitat, allowing for animals associated with the eelgrass blades to pass through the enclosures readily. Similarly, in the barren seafloor enclosures, enclosed fish did not have direct access to the sediment to forage in or on, rather they could forage on animals that entered the enclosures actively or

passively from the surrounding habitat. The same treatment was experienced by fish in water column enclosures (i.e., they could only forage on animals that entered the enclosure from the surrounding habitat). Therefore the estimates of habitat quality as inferred from growth rates may have been a more conservative estimate rather than an exact value of habitat quality. Nevertheless, these estimates are robust and indicate real differences in growth experienced by juvenile Gadiformes among the three habitats.

The presence of predators influences the foraging behavior of some juvenile fish (Milinski and Heller 1978; Post and Evans 1988), and dietary studies are useful to quantify food preferences and trends (Link 2004). Experimental enclosures for juvenile fish foraging studies can be used to illustrate relative differences in the energetic potential and food availability among various habitats by excluding predators and eliminating predation risk (Rozas and Odum 1988; Sogard 1997). A significant limitation of enclosure methodology for such studies is that fish are restricted to consuming only items that enter the enclosure, which is problematic if the enclosure prevents items from entering. The enclosures in my study did not appear to exclude prey items based on zooplankton inclusion-exclusion experiment. While the benthic sediments were not sampled explicitly, fish in seafloor enclosures did not have direct access to foraging in the sediment, and relied solely on animals that entered the enclosure from the surrounding habitat for food. The plankton sampling methods used in this study were robust enough to detect differences in the concentration of zooplankton among the habitats, and likely reflected real differences in the availability of prey items among the habitats. English (1982) demonstrated that growth rates (percent per day) of enclosed

Chinook salmon differed among "in situ" enclosures with different mesh sizes, small, medium and large (1, 9, and 19mm respectively). Fish with low concentrations of larger prey items available were able to grow more rapidly than fish with high concentrations of small zooplankton available. The 6.35 mm mesh I used did not appear to exclude larger potential prey items from entering the enclosures and may have therefore have given a more accurate estimate of the relative energetic potential of the habitats based on the relative growth rates. I was surprised to find that small fish (a 48 mm SL newly settled *G. morhua* and three unmeasured *P. gunnellus*) were able to pass through the mesh and were present within the enclosures during four enclosure recoveries. The effect of these potential competitors on the growth rates of the enclosed study fish was not obvious and I considered it negligible for several reasons; they were small enough to be consumed by the larger study fish, they had likely settled very recently and were probably only beginning to switch to a demersal diet, and they were all from eelgrass enclosures during the white hake experiment, where the most rapid growth rates of all the experiments were measured. The presence of such high protein sources for larger age 0 or 1 juvenile Gadiformes in the eelgrass habitats is further evidence, albeit anecdotal, of relative differences in foraging quality among habitats.

The presence of mussel spat in stomachs of fish enclosed in water column habitats is suggestive of the structuring effects of enclosures. While there was no evidence that the mesh became fouled with animals (aquaculture mesh is designed to limit this possibility), the polypropylene ropes were fouled with mussel spat and amphipods. These individuals might have become dislodged from the ropes, and may have fallen

through the mesh and become more available for the enclosed fish to consume from time to time, but because the structuring effect was the same for all enclosures (i.e., they all had ropes extending to the surface) the effect on growth rate and diet among habitats was considered the same.

A common source of bias in dietary analysis of fish is the failure to acknowledge, recognize, and detect regurgitation of the stomach contents (Bowman 1984; Staniland et al. 2001). Stomachs in this study did not show any obvious signs of regurgitation. In each of the experiments, some stomachs were full, with thin and smooth to lightly-ridged internal stomach walls, both of which are indicators of gut fullness. They had fairly well digested material in the posterior end of the stomach, and very fresh material in the anterior end of the stomach. Some of the stomachs examined had thicker stomach walls with heavier internal ridging and relatively fewer food items, with either well-digested food or a mixture of well-digested and fairly fresh food, which are indicators of reduced consumption of food items and gut fullness. If characteristically full stomach indicators were detected with little or no food items in the stomach, regurgitation would have been suspected, but this was not the case. Therefore regurgitation likely did not occur, and the contents represented the actual foraging conditions of the enclosed fish at the time they were sampled.

4.3 Growth & Diet Experiments

The fitness of an animal is determined by its ability to successfully reproduce and pass on its genes to successive generations. The survival of an individual to reproductive maturity requires the balancing of conflicting demands; an individual must eat to develop

and mature, but avoid being eaten before it has a chance to reproduce. Predation is often size-selective and individuals that are able to optimize their potential for growth when they are small likely have a selective advantage over those individuals that do not. The problem is that the most energetically rewarding foraging habitat might also jeopardize the survival of an individual because of the risk of predation (Werner and Gilliam 1984; Lima and Dill 1990; Walters and Juanes 1993). Conversely, those habitats that provide the greatest shelter from potential predators might also have very low energetic reward associated with them. In order to actively select habitats in which to forage and seek shelter, individuals must be able to evaluate their environment. They must be able to recognize the energetic potential of habitats and actively select those areas that optimize growth. This includes evaluating factors such as foraging quality (i.e., food availability, type and quality) and inter- and intraspecific competition for resources (i.e., territory and food) both of which influence the energetic potential of a given habitat. In addition they must recognize the potential threat of predation and select areas that will most effectively mediate those threats (Werner and Gilliam 1984; Lima and Dill 1990; Walters and Juanes 1993).

The growth-mortality hypothesis proposes that faster growth is a selective advantage in that it enables fish to pass through certain size-dependant predation windows faster than slower growing conspecifics (Werner and Gilliam 1984; Hare and Cowen 1997; Sogard 1997). According to this hypothesis, fast-growing juveniles should increase their chances of survival by escaping predation threats more quickly than slower-growing individuals. However there are counterarguments to this supposition

(Walters and Juanes 1993). Rapid growth requires a constant supply of high protein food (Mommsen 1998). While growth is dependent on a variety of endogenous and exogenous factors, it first requires energy allocation to foraging and processing food items, in addition to other activities, each with associated metabolic costs (Soofiani and Hawkins 1982; Soofiani and Priede 1985; Mommsen 1998; Mathers et al. 1993; Lankford et al. 2001; Cutts et al. 2002; von Herbing and White 2002; Munch and Conover 2003). All food items do not have the same protein and energetic value (Thayer et al. 1973; Steimle and Terranova 1985; Hislop et al. 1991; Bowen et al. 1995); therefore, fish that preferentially seek out habitats that support high-energy food items and forage on those items in the early juvenile stage will likely maximize growth and therefore potentially increase their probability of survival.

Areas of eelgrass have been shown to support greater species diversity and abundance of fish and crustaceans than adjacent unvegetated areas (Heck and Wetstone, 1977; Heck et al. 1989; Lazzari and Tupper 2002; Lazzari et al. 2003). In tank and field studies it has been suggested that juvenile Gadiformes occupy structurally complex habitats (eelgrass, kelp, rock reef, cobble) during the day and disperse at night to potentially reduce the risk of size-selective predation threats as newly-settled juveniles (Keats et al. 1987; Gotceitas and Colgan 1989; Gotceitas and Brown 1993; Methven and Bajdik 1994; Gocceitas et al. 1997; Gregory and Anderson 1997; Grant and Brown 1998a,b; Anderson and Gregory 2000; Linehan et al. 2001; Laurel et al. 2003 a,b; Laurel et al. 2004). Lindholm et al. (1999) demonstrated habitat-mediated survivorship in cod, and suggested that increasing structural complexity reduces the reaction distance of

predators because of the obstruction of visual cues. It has also been suggested that predation risk and the association with habitats that reduce that risk, changes ontogenetically (Gregory and Anderson 1997; Cote et al. 2001; Cote et al. 2003; Lafrance et al. 2005).

Comparatively little information exists on the energetic consequences of associating with certain habitats in juvenile Gadiformes. It has been demonstrated that submerged aquatic vegetation can support more invertebrates and zooplankton than unvegetated areas of equal size (Gerking 1962; Menzie 1980). In addition to demonstrating that predation pressure was reduced in vegetated areas, Rozas and Odum (1988) showed that banded killifish (*Fundulus diaphanus*) enclosed in vegetated areas ate items associated with that vegetation, whereas individuals enclosed in unvegetated areas had empty stomachs. In addition, blue spotted sunfish (*Enneacanthus gloriosus*) and mummichogs (*Fundulus heteroclitus*) enclosed in vegetated areas ate much larger prey items than those held in unvegetated enclosures. This pattern suggests that in addition to increased shelter, foraging in vegetated areas increases the energetic reward of juvenile fish, and that this benefit might result in faster growth and ultimately higher survival.

In enclosure experiments in a New Jersey estuary, Sogard (1992) demonstrated that there was significant variability in the short-term growth rates in juvenile fish across an estuarine nursery, and attributed them to natural variability in habitat quality. It was also suggested that habitat association could be the result of species-specific behavior. It was demonstrated that free-ranging goby (*Gobisoma bosci*) were most highly associated with eelgrass beds, even though eelgrass supported the lowest growth rate for enclosed

individuals. This finding suggests a compromise in habitat selection in which areas that reduce predation risk are selected over areas that optimize growth. In experiments with winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*), Sogard (1992) demonstrated that free-ranging individuals were most closely associated with vegetated substrates which supported the highest rate of growth compared to other habitats. She found that tautog were absent from barren substrates, suggesting active avoidance of barren areas, potentially because of the elevated predation risk associated with a low structure environment. In these experiments, the vegetated habitats that supported the greatest energetic reward, also potentially reduced the predation risk for those species. In field observations of free-ranging Atlantic cod, Tupper and Boutlier (1995) found that fish associated with eelgrass had the greatest growth rate when compared to those associated with cobble and rock reef habitats, but predation was also substantially higher in the eelgrass habitat. The fish in their study were free ranging individuals which had access to multiple foraging habitats, refuge habitats, and had to interact with competitors and predators. Therefore the actual energetic potential of the habitats could not be inferred by the growth rate alone, but required consideration of predation risk effects as well.

Food greatly influences the growth and survival of juvenile marine fish (Jobling 1994; Elliott 1994; Hart and Salvanes 2000) and survival at early life stages has been shown to determine cohort size (Anderson and Gregory 2000) which can be used to estimate fishery recruitment (Peterman et al. 1988; Campana et al. 1989; Ings et al. 1995). Fish should maximize their potential for growth by selecting high-energy food

items. If food availability and quality varies with habitat, fish should select those areas with the highest density of high-quality prey items. Because growth rate is an important proxy of fitness (Schluter 1994), and food intake has been closely linked to growth rate (Jobling 1994; Elliott 1994; Hart and Salvanes 2000), differences in the quantity and quality of food consumed by Gadiformes at a given time could be indicative of differences in the energetic potential among the habitats in which they reside. The use of enclosure methodology in my investigation allowed the direct comparison of growth rates and prey consumption of age 0 and 1 juvenile Gadiformes (at the sizes tested) confined to three discrete habitats (i.e., barren seafloor, eelgrass and the water column), from which reasons for the observed association of juvenile fish with eelgrass could be inferred (Cerri and Fraser 1983).

4.3.1 Greenland Cod Growth (2002)

The similarity of growth rates among treatments in this experiment suggested that there was little benefit energetically associated with specific habitats. In addition, the growth rate of the enclosed fish in my experiment was extremely low at approximately 0.07 $\%\cdot day^{-1}$ overall compared to free ranging individuals of similar size which grow at a rate of approximately 1 $\%\cdot day^{-1}$ in Newman sound during fall (Gregory, pers. com.). Energetic and behavioral principles could have played a role. If food was limiting, the density of fish within the enclosures may have been high enough to influence growth by limiting the metabolic scope of the individuals (Searcy et al. 2007). Metabolic scope is the amount of energy available for activity beyond basal metabolic processes (Claireaux et al. 2000). Competitive interactions between the five fish in the enclosure potentially

used much of the scope, thereby leaving little energy remaining for growth (Mommsen 1998). While fish were not observed in situ (i.e., in the enclosures in Newman Sound 2003), groups of 30 age 0 juveniles were observed in a land based holding tank (approximately 2 m^3) for a separate study and the fish appeared to be randomly distributed throughout the tank (Renkawitz personal observation). In 2003 fish were occasionally observed by SCUBA, and were also found to move very freely throughout the enclosures, presumably in search of food. In other tank studies similar observations have been made (Gotceitas et al. 1995; Gotceitas et al. 1999) suggesting that competition among juvenile Gadiformes might not result in aggressive competition for limited resources (i.e., food or space) in Newman Sound because no evidence that the system is close to carrying capacity exists (Schneider personal communication). Alternatively, the more likely explanation is that the duration of this experiment may not have been long enough for differences in growth between the habitats to have emerged.

4.3.2 Atlantic Cod Winter Growth and Diet (2002-2003)

While slight differences in the growth rates among the over-wintering habitats were measured (e.g., shallow eelgrass and shallow barren habitats supported faster growth than deep water habitats), the differences were not significant. Overall the items consumed by enclosed juvenile Atlantic cod were generally consistent with previous dietary observations (Bowman 1981; Keats et al. 1986; Keats and Steele 1992; Keats et al. 1993; Grant and Brown 1998; Lomond et al. 1998; Lander 2000). Copepods were the dominant prey items, and were found in similar proportions in the stomachs across the three habitats, suggesting that the distribution of zooplankton at Mistaken Cove and

Hefferns Cove were fairly homogenous at various depths at the time of sampling. A high degree of variation existed between the stomach weight among individuals and the number of items in the stomachs among individuals that successfully survived over winter within and between the habitats, but no statistical differences were detected between habitats. The potential energetic benefit associated with eelgrass may have been limited for Atlantic cod after the winter eelgrass die off in the spring (Hasegawa et al. 2007), even though the decomposition of eelgrass may have continued to fuel the microbial food web (Short and Short 1993), but this is only speculative and no direct evidence that this occurred exists.

I observed no influence of size on growth rate or survival of Atlantic cod in my over-winter growth experiment in Newman Sound for juveniles ranging from 61 - 81 mm SL. Contrary to my findings, Gotceitas et al. (1999) demonstrated that the growth rate of small age 0 Atlantic cod (approximately 60 mm SL) was significantly greater than larger age 0 cod (approximately 80 mm SL), but that significantly more large juveniles survived the winter compared to smaller individuals. However, these results may not have been free of spurious significant associations. First-winter mortality is thought to be dependent on fish size (Post and Evans 1989). Smaller juveniles are typically more vulnerable to predation than larger conspecifics over the winter (Garvey et al. 1998; Garvey et al. 2004). Sogard and Olla (2000) demonstrated that age 0+ walleye pollock, *Theragra chalcogramma*, which achieved a larger size and condition during the first summer, had a greater probability of survival. Fat reserves generally scale linearly with mass (Henderson et al.1988). Larger fish are able to store more lipids, have lower basal

metabolic demands relative to body size than smaller fish and are therefore more capable of surviving the periods of starvation that are believed to occur over the winter as food becomes more scarce (Post and Evans 1989; Shuter and Post 1990, Gotceitas et al. 1999; Hurst and Conover 2003; Garvy et al. 2004). Henderson et al. (1988) demonstrated that larger, earlier spawned sand smelt (*Atherina boyeri*) were able to lay down more fat than smaller, later spawned conspecifics and were more likely to survive the period of fasting over the winter. However, the factors that have been shown to influence mortality over the winter for some species, might not influence the survival of juvenile cod over the winter.

The inner-sound site at Mistaken Cove supported greater overall growth than at the Minchin Cove site. Sogard (1992) cited site differences in growth between habitats during experiments within a New Jersey estuary, and suggested that certain sites may have had more favorable environmental conditions for growth. There were no differences between the stomachs samples from Mistaken Cove and Minchin Cove in my study suggesting similar foraging conditions. However, the stomachs were only sampled at the end of the experiment, and represent the foraging conditions at the moment of sampling, not over the duration of the experiment, so differential foraging conditions could not be ruled out.

It has been suggested that predation during winter rather than starvation is the mechanism that influences survival over the winter and ultimately recruitment (Santucci and Wahl 2003; Garvey et al. 2004). In the absence of predators in my experiment, it was expected that survival over the winter would have been higher than it actually was,

irrespective of water depth. Significantly more fish were recovered from deep water enclosures (55 % survival) than were recovered from shallow water enclosures (20 % survival). Growth rates between the depths were not significantly different, suggesting that the same amount of energy was being consumed. Several reasons for this result are possible. First, fish in shallow water may have been more likely to come in contact with ice crystals that formed near the water surface than fish in deep water. This could potentially result in flash freezing and death.

Alternatively, fish in deeper water may have had a higher likelihood of survival over the winter than shallow fish because of differences in food availability. Gotceitas et al. (1999) found that food ration did not influence over-winter survival. In my study, the number of amphipods and euphausiids consumed in deeper water were greater than in either shallow barren seafloor or shallow eelgrass habitats, indicating that these items may have been more available in deeper habitats. Stomach weights were also less variable in deeper water than in shallower water, suggesting that at the time of sampling, the availability of prey items may have been more consistent in deeper water. Greater availability of larger prey items in deeper water may have resulted in fewer periods of starvation over the winter for several reasons. If food was more abundant in deeper water, there may have been less competition for resources. If food was scarce in shallow water, competitive interactions (e.g., for food, territories, etc.) with other fish may have resulted in the inability to maintain basal metabolic activity resulting in starvation and death. The effect of these situations would result in greater apparent survival of fish in deeper water, as was apparent in my experiments. However, this explanation is

speculative, and additional information is needed on food availability during the winter in Newman Sound to explain these results more completely in terms of over winter survival.

4.3.3 Atlantic Cod Growth and Diet (Spring 2003)

Enclosed age 1+ Atlantic cod grew at a significantly faster rate (in length and volume) and consumed more prey in eelgrass and barren seafloor substrates than in water column habitats, suggesting an increased energetic reward with benthic habitats. Growth rates of free-ranging cod in Newman Sound were estimated at 0.38% day^{-1} in 2003, (Gregory et al. 2006) which was generally consistent with the mean growth rate (± SE) of fish enclosed in eelgrass habitats in my study 0.366 ± 0.026% day^{-1}.

The stomach contents were also consistent with previous dietary observations of various species in Newfoundland (Keats et al.1986; Keats and Steele 1992; Keats et al. 1993; Grant and Brown 1998; Lomond et al. 1998; Lander 2000). The dietary composition of fishes in barren seafloor and eelgrass habitats was fairly similar, and stomach content weights in these habitats were virtually identical. Cod in water column enclosures consumed far fewer items, but consumed more copepods than fish in benthic enclosures. More items were consumed in barren than eelgrass enclosures, but larger items (e.g., amphipods) were consumed in eelgrass. Fish in all habitats generally foraged selectively on benthic organisms (e.g., harpacticoids) relative to what was available. This preference is consistent with the dietary shift from water column to benthic prey that occurs between 85 and 100 mm SL in age 1+ Atlantic cod (Lomond et al. 1998). The juveniles in my study were 85-91 mm SL at the end of the experiment. Harpacticoid densities are typically highest on, under or near the sediment surface (Hicks and Coull

1983; Hicks 1994). The principle food items consumed by fish enclosed in experimental benthic enclosures (with barren and vegetated substrates) are also harpacticoids and amphipods (Sogard 1992). Zooplankton biomass has been shown to scale with vegetation density (Macon 1949; Gerking 1957; Howard and Short 1986). Keats and Steele (1993) found amphipods and harpacticoid copepods (as well as polychaetes, mysids and isopods) to be the primary items in the diet of age 0+ ocean pout (*Macrozoarces americanus*) in Newman Sound, and found these zooplankton to be strongly associated with algal canopies. The results from my study suggest that Atlantic cod rely on similar zooplankton species during the early demersal stage. The substantial overlap in the diets of different juvenile fish species might increase the competition for resources which may further influence the quality of foraging habitats. This difference in perceived quality may further influence habitat selection by juvenile fish.

In Newman Sound it has been demonstrated that the structural complexity of eelgrass provides more shelter for juvenile fish compared to habitats with low complexity such as barren seafloor and water column habitats (Linehan et al. 2001; Laurel et al. 2003). My study has suggested there is also an energetic benefit associated with benthic habitats compared to water column habitats, but that the tradeoff between structured and unstructured habitats for juvenile cod may be minimal. Contrary to these results, Tupper and Boutilier (1995) suggested that post-settlement growth rates of free-ranging cod were significantly greater in eelgrass habitats than in barren areas, but that predation risk was also higher in eelgrass. Sogard (1997) demonstrated with enclosure experiments that goby experience similar rates of growth in sand and in vegetation and suggested that the

absence of free-ranging goby from sandy habitats and their close association with vegetated habitats was primarily as a shelter from predation. The results of my experiment suggested, given the similar energetic reward between the benthic habitats, that the close association of juvenile Atlantic cod with eelgrass is not the result of a compromise in habitat selection. Rather it provides comparable potential for growth as other benthic habitats, with the added benefit of being a refuge from predation (Linehan et al. 2001).

4.3.4 White Hake Growth and Diet (Summer 2003)

White hake are known to be a very fast-growing species (Scott and Scott 1988). The growth rates of these fish were substantially greater than other fish species in my experiments in Newman Sound. At Pleasant Bay, Massachusetts, Fahay and Able (1989) reported the growth rate of newly settled free-ranging white hake to be approximately 1.02 mm SL day^{-1}. In my study, fish enclosed in eelgrass habitats experienced significantly greater growth rates and consumed more prey items than fish in either barren mud or water column habitats. The mean growth rate (± SE) of white hake enclosed in eelgrass habitats in my study was 0.713 ± 0.062% length·day-1 which was greater than the growth rates of free-ranging white hake in Newman Sound in 2003 (0.54% length·day-1, Gregory, unpublished data). Free-ranging white hake growth rates were similar to those enclosed in the barren mud habitat in my study (0.483 ± 0.055 % length·day-1). As with other Gadiformes, white hake tend to abruptly shift their feeding as they metamorphose from larvae to demersal juveniles (Koeller et al. 1989). The diverse diet of free-ranging white hake has been found to include copepods, cladocerans,

amphipods, euphausiids, nematodes, mysiids, polychaetes, and decapods among others items (Coates et al. 1982; Durbin et al. 1983; Bowman and Michaels 1984; Bowman 1986; Scott and Scott 1988; Garrison and Link 2000). In my study, similar items were found in the stomachs of enclosed age 0+ juvenile white hake. Foraging in each habitat appeared to be selective when compared to the availability of prey items. Generally, no one taxon dominated the overall diet and composition was similar between benthic habitats (barren seafloor and eelgrass). The diet in water column habitats differed from that in benthic habitats. The most notable difference was the near absence of calanoids from the water column diet compared to the benthic diet. The presence of mussel spat in the diet of the water column hake was suggestive of a structuring effect of the enclosure, but because this effect was similar for each habitat (i.e., the same amount of spat was on each of the ropes in each habitat), it did not have an effect on the relative differences seen in growth between the three habitats. Most large prey items (amphipods and euphausiids) were consumed by fish in eelgrass, suggesting that a greater density of large prey items that may have been more valuable energetically were associated with that habitat (Thayer et al. 1973; Steimle and Terranova 1985). Foraging in habitats with more valuable items may increase the growth rate of a species, and ultimately increase survival because less time needs to be spent foraging and more can be spent on predator vigilance (Hugie and Dill 1994). These results suggest that in Newman Sound, Newfoundland, white hake that associate with eelgrass in the summer, in addition to experiencing increased refuge from predation (Linehan et al. 2001), have an energetic advantage over fish that associate with barren seafloor or water column habitats.

4.3.5 Greenland Cod Growth and Diet (Fall 2003)

The growth rates were greater for Greenland cod in water column treatments than in barren seafloor or eelgrass in the fall of 2003. These data suggest that there was an energetic reward for fish in water column enclosures. The growth rate of free-ranging Greenland cod in Newman Sound during 2003 was estimated at 0.97% length·day^{-1} (Gregory et al. 2006) while the highest mean growth rate in my experiment was in the water column, and was only 0.449 ± 0.055 % length·day^{-1}. The discrepancy in these rates suggest that cod in each of the habitats were not growing as rapidly as free-ranging individuals, which might be the result of limited foraging range of enclosed juveniles compared to free-ranging individuals.

There is little published information on the diet of age 0+ Greenland cod. However, the diets of larger (>300 mm SL) coexisting Greenland and Atlantic cod have been shown to be very similar (Nielsen and Andersen 2001). If this similarity is assumed to hold true for age 0+ Greenland cod, then a rapid dietary shift from water column to benthic prey between 50 and 100 mm SL is also likely to occur as it does in Atlantic cod (Lomond et al. 1988). Therefore I expected the diet to be very similar between the species (i.e., consisting mainly of harpacticoids, gammarids, mysids and amphipods with some copepods). While these items were present in the stomachs of Greenland cod at the end of my experiments, calanoids were the dominant prey item in all stomach, suggesting that the shift from water column prey to benthic prey may occur at larger sizes in juvenile Greenland cod than in juvenile Atlantic cod and white hake. A shift from water column to benthic prey type at a larger size could be why fish in water column enclosures grew

more rapidly than those that were in the benthic environment (i.e., they had not yet switched to feeding selectively on benthic prey items). The association of Greenland cod with eelgrass may therefore be an active compromise in habitat usage, in which sheltered biogenic structure is opted for over habitats that optimize growth.

4.3.6 Summary

The growth mortality hypothesis states that rapid growth in early life stages confers a selective advantage over slower-growing conspecifics by allowing more rapid passage through size-dependant mortality windows, thereby resulting in increased individual fitness. The experiments in Newman Sound suggest that faster growth may be experienced by fish that occupy specific habitats. In this study, I determined that juvenile Atlantic cod and white hake fed selectively on benthic organisms. Biogenic structure (i.e., eelgrass) increased the feeding efficiency and growth rate of Atlantic cod and white hake beyond the structuring effects of the enclosures. This finding suggests that these species associate with eelgrass to optimize their growth rate. Conversely, Greenland cod grew fastest in the water column, suggesting that their association with eelgrass is a compromise in habitat use, and does not optimize growth. Gadiformes may therefore increase their growth and decrease their predation risk in structurally-complex eelgrass habitats at certain times of the year.

4.4 Zooplankton Sampling Among Habitats

4.4.1 Habitat Differences

Density-dependence in fish populations has been demonstrated at large and small scales. Small-scale experiments that reveal the causal mechanisms of density-dependent

processes can be used to describe large-scale population level events (Johnson 2006). Biological and environmental gradients have been demonstrated to influence the abundance and distribution of juvenile fish (Horne and Campana 1989; Gregory and Anderson 1997). Zooplankton, especially copepods, are important food items in the diet of juvenile fish in marine food webs (Turner 2004). The variability of zooplankton is strongly linked to oceanographic processes that influence diatom/phytoplankton distribution and abundance (Robinson 1994). Cowen et al. (2000) suggest that cohort biomass of fish can be regulated by density-dependent reductions in prey resources at late larval and early juvenile stages; the relatively large abundance of juvenile fish in relation to the abundance of zooplankton can limit the size of a give year-class (Runge 1988). Inter and intra-specific competition with other juvenile fish can further exacerbate the problems associated with variable prey availability and can be particularly difficult for species that experience changes in foraging behaviors with ontogenetic dietary shifts such as those that occur in juvenile Gadiformes (Bergman and Greenberg 1994).

Zooplankton diversity, concentration, distribution, and population stability are highly variable (Petchy et al. 2002; Kane 2003; Steiner et al. 2005), and the mechanisms that drive their variation can be influenced by environmental stressors of natural and anthropogenic origin (Robinson 1994; Marcus 2004). Fluctuations in concentration and composition occur at spatial, temporal, tidal, and diurnal scales among others. In this study, all samples were collected biweekly within two hours of high tide during daylight hours to standardize the measurements to the extent possible. Undoubtedly, many changes in concentration and composition at the sites in Newman Sound were not

documented by the sampling methodology, but the standardized method allowed for direct comparison over time among habitats. Zooplankton concentrations in my study were 'moderate' (i.e., typically between 1-100 animals/liter) according to Pace et al. (1991). Contrary to expectations, the overall zooplankton concentration and the number of taxa per sample in Newman Sound remained relatively constant from August to October 2003, with a slight overall decrease in both zooplankton concentration and number of taxa toward the end of the experiment. The presence of high abundances of copepods and the simultaneous absence of other dominant species in my study was consistent with the findings of Vidjak et al. (2006). While the concentration of individual taxa fluctuated bi-weekly, no clear pattern of seasonal succession was observed in which one taxon clearly dominated and was then replaced by another. Rather, the various taxa were consistently represented in the samples throughout my experiment.

Zooplankton concentration was greater in eelgrass than in barren seafloor and in water column habitats, suggesting that the energetic potential of eelgrass habitats may be greater than that of barren and water column habitats. Benthic, epi-benthic and pelagic zooplankton were all sampled with the plankton pump method employed, and because fish did not have access to foraging in the sediment, sediment samples were not collected to look at the availability of animals in the sediment. A review by Orth et al. (1984) suggests that seagrass beds, when compared to nearby unvegetated areas, support a much more dense and diverse assemblage of vertebrate and invertebrate species. Copepods were the dominant zooplankton taxa in Newman Sound. They were found in the greatest numbers among eelgrass, suggesting that the presence of biogenic structure actively or

passively concentrates organisms. Larger zooplankton such as amphipods, euphausiids, isopods, and mysiids generally occurred at greater concentrations in the benthic habitat samples than in the water column habitat samples suggesting that these larger, higher energy food items were more available to juveniles associated with the seafloor than to those that remained in water column habitats. The presence of taxa that are generally considered to be primarily benthic (harpacticoids, polychaetes, bivalves, etc.; Hicks and Coull 1983; Hicks 1984) in water column zooplankton samples, suggests that benthic invertebrates were sometimes available to water column juveniles, even if those juveniles were not foraging in benthic environments. Analysis of stomach samples from Gadiformes enclosed in water column environments confirmed this to be the case.

4.4.2 Summary

Seagrass beds generally contain dense and rich invertebrate assemblages compared to nearby unvegetated areas (Orth et al. 1984). Although they are highly productive, faunal communities associated with eelgrass often experience large fluctuations and seasonal changes in species abundance (Pihl and Rosenberg 1982; Petchy et al. 2002). Based on zooplankton samples from barren seafloor, eelgrass, and water column habitats in Newman Sound, it appears that benthic habitats may offer greater energetic potential than water column habitats for juvenile fish, suggesting that post-larval settlement may be partially in response to energy (food) acquisition for certain species. These results also suggest that eelgrass habitats support a greater concentration of potential prey items and that the association of juvenile fish with these more structured biogenic habitats may be in response to energy acquisition in addition to increased refuge

from potential predators (Linehan et al. 2001), but the energetic benefit may vary seasonally.

Communities with greater diversity often have more trophic pathways along which density-dependent population control mechanisms can operate, and are usually more stable (Adams 1979a,b; Steiner et al. 2005). Generally, systems with short trophic pathways are fragile, and changes in the abundance of one species may often have drastic consequences for secondary and tertiary consumers such as juvenile Gadiformes. In habitats with high structural complexity such as eelgrass, mangroves, and salt marshes where no single species dominates the zooplankton community and trophic pathways are therefore complex, the loss or change in abundance of a single species is not likely to have as pronounced an effect on the community as a whole (Steiner et al. 2005). Juvenile Gadiformes may rely on the structural complexity of inshore habitats (e.g., eelgrass) for diverse sources of food and shelter in Newman Sound during the early demersal phase. These factors have been suggested to influence survival at early life stages and may ultimately limit recruitment into various fisheries. Loss of diverse, structurally complex habitats in coastal waters may be an impediment to the effective rebuilding of fish stocks in the future (Short and Burdick 1996). Preservation and conservation of eelgrass habitats may help maximize juvenile cohort size in a given year by facilitating higher growth rates and higher survival at early juvenile stages. Understanding the complexity of early life stages and the habitat characteristics that influence growth and survival of fish may aid conservation efforts and enable managers to more effectively rebuild depleted fish stocks in the Northwest Atlantic.

5.0 Conclusions

Fishery recruitment depends on survival of early juvenile cohorts (Sissenwine 1984) and survival is thought to be largely a function of water temperature, body size, food availability, and predation. Juvenile fish should therefore select habitats that increase growth and decrease predation to improve survival.

With experiments in Newman Sound, Newfoundland, I determined that growth rates of juvenile Atlantic cod and white hake were fastest in eelgrass, and that growth rates of Greenland cod were fastest in the water column beyond any structuring effect of the enclosures. These result suggest that in addition to reducing predation risk (Linehan et al. 2001; Laurel et al. 2003), some species of juvenile Gadiformes may also optimize growth in eelgrass (i.e., Atlantic cod, white hake). Others grow faster outside of eelgrass (i.e., Greenland cod), indicating that association with biogenic structure is primarily for shelter instead. I also showed that juvenile Atlantic cod and white hake appear to select benthic and epibenthic prey items whereas juvenile Greenland cod appear to select epibenthic or water column prey when restricted to barren, eelgrass and water column habitats. This difference may have resulted from selective species-specific predation behavior relative to the assemblage flowing through the enclosures. Finally I demonstrated that biogenic structure (i.e., eelgrass) increased the availability of zooplankton beyond any structuring effect of the enclosures.

These results contribute to our understanding of the complex recruitment puzzle in Newman Sound, Newfoundland. It would be useful in the future to establish if the patterns observed in this study hold at larger spatial and temporal scales (i.e., in a large

scale mesocosm study with individually marked juveniles and no predators) with various numbers of conspecifics to elucidate the density-dependent variables that may influence growth and ultimately survival. In addition, the cost-benefit of foraging directly on animals associated with various substrates (i.e., in the sediment or on eelgrass blades) could be explored in greater detail to determine if foraging success of age 0-1 juveniles is compromised under certain conditions. The enclosure methodology could be utilized directly to measure growth rates and survival of newly settled juveniles at various water depths (i.e. 5, 10, 15, and 30 meters) to determine if the high abundance of Gadiformes nearshore correlates with growth, or if growth is actually greater in deeper water. This may further inform researchers as to why many Gadiformes appear to settle among inshore habitats in shallower water as opposed to deeper offshore water in Newman Sound. An additional usage of this methodology would be to deploy enclosures in eelgrass habitats with varying structural complexity to determine if a growth advantage is experienced at low, intermediate or high levels based on the fractal geometry of the habitat patch. Yet another direction would be to alter the number of fish in enclosures to investigate density-dependent factors that influence growth in discrete habitats. Each of these research directions would contribute substantially to our understanding of the underlying causes of settlement, habitat selection, growth, and survival during the early demersal life stage of age 0 and 1 juvenile Gadiformes.

Determining the characteristics that make some habitats more important than others is essential in defining critical habitat for a species. Adams (1976b) wrote that "eelgrass beds are efficient systems for converting consumed energy and solar radiation

into fish." My results suggest that eelgrass is an important habitat for juvenile marine fish at early life stages because it promotes rapid growth compared to other habitats. Globally, the natural and anthropogenic threats to eelgrass abundance and distribution are many, and disturbance of these habitats may influence the stability of the aquatic food webs associated with them (Short and Short 2003; Steiner et al. 2005). The factors that influence important habitats likely also influence the size of a given cohort of marine fish. In this study, I have contributed new knowledge on the importance of eelgrass to juvenile Gadiformes, which will aid habitat protection efforts and fisheries managers when strategies are developed to restore depleted fish stocks in the Northwest Atlantic.

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Table 1. **(a)** Experimental design used in five growth experiments using three species of fish confined to 1.0 m^3 enclosures among three habitats in Newman Sound, Newfoundland from 2002-2003. The number of fish per enclosure decreased from five to one, and the number of enclosures and sites used increased from the experiments 2002 to the experiments in 2003. **(b)** Recovery rates, lengths, volumes, and growth (absolute growth and SGR) are presented for five experiments, three enclosed species, among three habitats in Newman Sound, Newfoundland from 2002-2003.

a)

Experiment	Species	No. of sites	Habitat	No. of Enclosures	No. Fish / Enclosure	Total Fish	Mean Initial Len. (±SD) (mmSL)	Max / Min Initial Len. (mmSL)	Mean Initial Vol. (±SD) (ml)	Max / Min Initial Vol. (ml)	Duration (days)
Pilot (Oct. 3, 2002 - Oct. 25, 2002)	*G.ogac*	2	Barren	2	5	20	91.15 ± 6.00	107/83	-	-	22
			Eelgrass	2	5	20	91.75 ± 7.13	109/80	-	-	22
			Water Column	2	5	20	90.55 ± 6.44	104/83	-	-	22
Winter (Oct. 25, 2002 - May 28, 2003)	*G.morhua*	2	Barren	2	5	20	72.07 ± 4.65	79/62	-	-	210
			Eelgrass	2	5	20	70.40 ± 3.76	77/62	-	-	210
			Deep Water	2	5	20	71.55 ± 4.95	81/61	-	-	210
Spring (June 11, 2003 - July 24, 2003)	*G.morhua*	5	Barren	2	1	10	73.20 ± 4.32	79/67	3.40 ± 1.02	5.0 / 2.0	43
			Eelgrass	2	1	10	72.60 ± 3.37	78/68	3.50 ± 0.82	5.0 / 2.5	43
			Water Column	2	1	10	76.30 ± 2.36	80/73	3.80 ± 0.42	4.5 / 3.0	43
Summer (July 29, 2003 - Sept 9, 2003)	*U.tenuis*	5	Barren	2	1	10	66.90 ± 2.47	72/64	2.50 ± 0.41	3.0 / 2.0	42
			Eelgrass	2	1	10	67.60 ± 3.89	73/60	2.70 ± 0.75	4.0 / 2.0	42
			Water Column	2	1	10	72.20 ± 3.19	79/68	3.65 ± 0.85	5.5 / 3.0	42
Fall (Sept. 9, 2003 - Oct. 20, 2003)	*G.ogac*	5	Barren	2	1	10	76.90 ± 4.46	87/73	4.75 ± 1.09	7.5 / 4.0	41
			Eelgrass	2	1	10	79.60 ± 6.07	89/71	5.25 ± 1.50	7.5 / 3.0	41
			Water Column	2	1	10	74.30 ± 4.37	83/69	4.30 ± 0.68	5.0 / 3.0	41

b)

Experiment	Species	Habitat	% Fish Recovered	No. fish Recovered	Mean Final Len. (±SD) (mmSL)	Max / Min Final Len. (mmSL)	Mean Final Vol. (±SD) (ml)	Max / Min Final Vol. (ml)	Mean Growth: mm/day (±SE)	Mean Growth: ml/day (±SE)	SGR_{Length}: % length/day (±SE)	SGR_{Volume}: % volume/day (±SE)
Pilot (Oct. 3, 2002 - Oct. 25, 2002)	*G.ogac*	Barren	75	15	93.27 ± 6.72	110/85	-	-	0.062 ± 0.015	-	0.068 ± 0.016	-
		Eelgrass	85	17	92.41 ± 6.24	101/82	-	-	0.068 ± 0.019	-	0.074 ± 0.021	-
		Water Column	65	13	91.39 ± 7.85	105/83	-	-	0.062 ± 0.020	-	0.064 ± 0.024	-
Winter (Oct. 25, 2002 - May 28, 2003)	*G.morhua*	Barren	25	5	95.00 ± 10.84	110/83	-	-	0.109 ± 0.018	-	0.129 ± 0.017	-
		Eelgrass	15	3	94.67 ± 7.02	102/88	-	-	0.122 ± 0.014	-	0.151 ± 0.015	-
		Deep Water	55	11	91.27 ± 7.28	102/80	-	-	0.094 ± 0.012	-	0.116 ± 0.015	-
Spring (June 11, 2003 - July 24, 2003)	*G.morhua*	Barren	90	9	83.90 ± 4.04	89/77	5.80 ± 1.11	8.0/4.5	0.255 ± 0.027	0.057 ± 0.005	0.327 ± 0.035	1.350 ± 0.171
		Eelgrass	90	9	84.80 ± 5.01	91/78	6.05 ± 1.12	8.0/4.5	0.288 ± 0.022	0.060 ± 0.006	0.366 ± 0.026	1.321 ± 0.121
		Water Column	70	7	78.40 ± 2.22	85/75	4.20 ± 0.59	5.0/3.0	0.050 ± 0.010	0.010 ± 0.005	0.065 ± 0.013	0.235 ± 0.123
Summer (July 29, 2003 - Sept 9, 2003)	*U.tenuis*	Barren	100	10	82.10 ± 6.67	94/73	5.30 ± 1.46	8.0/3.5	0.362 ± 0.046	0.067 ± 0.001	0.483 ± 0.055	1.754 ± 0.188
		Eelgrass	100	10	91.20 ± 6.78	99/83	6.70 ± 1.06	8.0/5.0	0.562 ± 0.052	0.095 ± 0.010	0.713 ± 0.062	2.224 ± 0.249
		Water Column	100	10	81.00 ± 5.73	90/75	5.05 ± 1.30	7.0/3.0	0.210 ± 0.033	0.033 ± 0.006	0.271 ± 0.040	0.753 ± 0.140
Fall (Sept. 9, 2003 - Oct. 20, 2003)	*G.ogac*	Barren	60	6	89.60 ± 6.15	102/80	7.40 ± 1.22	9.5/5.0	0.310 ± 0.024	0.065 ± 0.008	0.372 ± 0.028	1.104 ± 0.144
		Eelgrass	90	9	88.30 ± 6.41	97/77	7.65 ± 1.90	11.0/5.0	0.212 ± 0.010	0.059 ± 0.004	0.254 ± 0.013	0.950 ± 0.072
		Water Column	90	9	89.50 ± 8.46	101/73	7.40 ± 1.82	10.0/4.0	0.371 ± 0.049	0.076 ± 0.014	0.449 ± 0.055	1.288 ± 0.237

Table 2. Mean daily water temperature (°C, $\bar{x}$ ± SD) in benthic and pelagic habitats at five sites during three growth experiments utilizing three species of juvenile Gadiformes in Newman Sound, Newfoundland between June 11 and October 20, 2003. Atlantic cod (*G. morhua*) was used in the spring (June 11, 2003 – July 24, 2003), followed by white hake (*U. tenuis*) in the summer (July 29, 2003 – September 9, 2003), and Greenland cod (*G. ogac*) in the fall (September 9, 2003 – October 20, 2003). Temperatures were not different between sites and among habitats within each experimental time frame.

Experiment Date	Habitat Type	Mean Daily Water Temperature (°C, mean ± SD)				
		Stairs Cove	Mistaken Cove	Hefferen's Cove	Minchin Cove	South Broad Cove
June 11, 2003 -	Benthic	9.23 ± 2.15	9.24 ± 2.66	8.30 ± 2.60	8.43 ± 2.88	8.94 ± 2.57
July 24, 2003	Pelagic	9.05 ± 2.17	10.00 ± 2.55	8.99 ± 2.64	9.07 ± 2.89	9.15 ± 2.55
July 29, 2003 -	Benthic	14.20 ± 1.34	14.38 ± 1.29	13.82 ± 1.26	13.88 ± 1.29	14.03 ± 1.28
Sept. 9, 2003	Pelagic	14.00 ± 1.34	14.63 ± 1.23	14.22 ± 1.20	14.27 ± 1.35	14.13 ± 1.25
Sept. 9, 2003 -	Benthic	10.39 ± 0.39	10.43 ± 0.66	10.15 ± 0.54	10.23 ± 0.69	10.34 ± 0.43
Oct. 20, 2003	Pelagic	10.09 ± 0.40	10.57 ± 0.56	10.28 ± 0.53	10.35 ± 0.71	10.39 ± 0.42

Table 3. The Kolmogorov-Smirnov test results comparing mean zooplankton concentration (# items·liter^{-1}) and mean number of taxa per sample inside and outside an experimental enclosure on three dates in 2003 indicate there was no difference in zooplankton concentration or the number of taxa per sample between those taken inside and outside the enclosure. This test failed to reject the null hypothesis for each sampling event, which was consistent with the hypothesis that each set of data came from the same underlying distribution.

Date	Category	Location	Mean (± SE)	Sample Size	D-Statistic	P-Value
20-Aug-03	Zooplankton Concentration (#/L)	Inside	11.42 ± 0.93	20	0.097	0.403
		Outside	10.78 ± 0.65			
	Taxa per Sample	Inside	0.30 ± 0.01	20	0.099	>0.999
		Outside	0.29 ± 0.01			
4-Sep-03	Zooplankton Concentration (#/L)	Inside	10.53 ± 0.97	20	0.122	0.404
		Outside	9.72 ± 0.68			
	Taxa per Sample	Inside	0.26 ± 0.02	20	0.091	>0.999
		Outside	0.24 ± 0.01			
16-Sep-03	Zooplankton Concentration(#/L)	Inside	13.36 ± 1.29	20	0.172	0.813
		Outside	15.05 ± 1.56			
	Taxa per Sample	Inside	0.23 ± 0.01	20	0.068	0.813
		Outside	0.23 ± 0.01			

Table 4. Regression equations for five growth experiments describing the SGR_{Length} and SGR_{Volume}, in mm SL ($\ln SL_x - \ln SL_i$), and in ml ($\ln V_x - \ln V_i$) respectively, over time for three Gadiform species enclosed in three distinct habitat types in Newman Sound, Newfoundland from 2002 to 2003. Regressions are based on the equation $y = b_0 + b_1x + \text{error}$, where y is the change in ln length or ln volume at time x (days). The slope (b_1) and intercept (b_0) are displayed with their standard errors, along with the F ratio and the r^2 value (expressed as a %) for the regressions.

Experiment	Metric	Habitat	b_1	±SE	b_0	±SE	F	r^2
Pilot (Oct. 3, 2002 - Oct. 25, 2002)	length	Barren	0.0004	0.0002	0.0001	0.0030	3.64	9.9
		Eelgrass	0.0011	0.0003	0.0000	0.0039	16.34	33.1
		Water Column	0.0004	0.0001	0.0002	0.0017	7.99	20.5
Over Winter (Oct. 25, 2002- May 28, 2003)	length	Barren	0.0013	0.0002	0.0000	0.0259	54.88	87.3
		Eelgrass	0.0015	0.0002	0.0000	0.0227	96.45	96.0
		Water Column	0.0012	0.0001	0.0000	0.0217	62.40	75.7
Atlantic Cod (June 11, 2003 - July 24, 2003)	length	Barren	0.0033	0.0003	-0.0019	0.0086	120.15	81.1
		Eelgrass	0.0036	0.0002	-0.0019	0.0069	230.03	89.1
		Water Column	0.0006	0.0001	-0.0006	0.0030	35.90	56.2
	volume	Barren	0.0133	0.0015	-0.0162	0.0429	79.05	73.8
		Eelgrass	0.0129	0.0012	-0.0098	0.0345	116.34	80.6
		Water Column	0.0023	0.0012	0.0132	0.0333	3.87	12.1
White Hake (July 29, 2003 - Sept. 9, 2003)	length	Barren	0.0048	0.0006	0.0118	0.0149	75.93	73.1
		Eelgrass	0.0071	0.0006	-0.0004	0.0162	141.12	83.4
		Water Column	0.0027	0.0004	0.0028	0.0102	50.73	64.4
	volume	Barren	0.0173	0.0022	0.0788	0.0585	63.61	69.4
		Eelgrass	0.0222	0.0030	0.0600	0.0813	54.30	66.0
		Water Column	0.0075	0.0013	0.0186	0.0075	31.68	53.1
Greenland Cod (Sept. 9, 2003 - Oct. 20, 2003)	length	Barren	0.0040	0.0003	-0.0070	0.0078	172.88	82.0
		Eelgrass	0.0025	0.0001	0.0005	0.0036	320.58	89.4
		Water Column	0.0045	0.0005	0.0130	0.0123	86.74	69.5
	volume	Barren	0.0117	0.0013	0.0192	0.0348	75.32	66.5
		Eelgrass	0.0091	0.0008	0.0158	0.0198	138.77	78.5
		Water Column	0.0120	0.0023	0.0673	0.0120	26.67	41.2

Table 5. The mean number of prey items (± SD) and the mean stomach content weights (± SD, scaled to body weight as a %) of three Gadiform species recovered from experimental enclosures from 3 discrete habitats in Newman Sound, Newfoundland. All fish were recovered during daylight hours.

Species	Sampling Date	Number of Fish Examined	Habitat	Mean (±SD) Number of Prey Items	Mean (±SD) Stomach Content Weight (%)
Atlantic cod	May 23, 2003	5	barren	384.00 ± 329.00	1.4540 ± 0.7900
		3	eelgrass	160.33 ± 126.53	1.1160 ± 1.0740
		11	deep water	295.18 ± 276.30	1.2260 ± 0.4660
Atlantic cod	July 24, 2003	9	barren	587.00 ± 532.00	1.3600 ± 0.6830
		9	eelgrass	313.40 ± 268.70	1.1910 ± 0.7430
		7	water column	65.00 ± 26.50	0.4428 ± 0.1486
white hake	September 9, 2003	10	barren	23.50 ± 20.10	0.2863 ± 0.2519
		10	eelgrass	61.30 ± 44.80	0.6870 ± 0.5180
		10	water column	18.90 ± 18.04	0.4700 ± 0.3860
Greenland cod	October 20, 2003	6	barren	79.80 ± 44.20	0.4104 ± 0.2397
		9	eelgrass	145.80 ± 90.80	0.9017 ± 0.2583
		9	water column	154.20 ± 104.10	0.5350 ± 0.3920

Table 6. Overall mean taxa concentration (#·Liter^{-1}, ± SE) of samples collected within three habitats at five sites during five sampling events between August 19, 2003 and October 21, 2003.

Taxon	Barren	Eelgrass	Water Column
Amphipoda	0.384 ± 0.027	0.378 ± 0.022	0.192 ± 0.016
Appendiculariae	0.097 ± 0.009	0.076 ± 0.007	0.100 ± 0.008
Bivalva	1.177 ± 0.130	1.632 ± 0.253	0.440 ± 0.086
Branchiura	0.002 ± 0.001	-	0.002 ± 0.001
Calanoida	19.992 ± 1.645	31.471 ± 2.641	14.921 ± 0.785
Chaetognatha	0.001 ± 0.000	0.013 ± 0.005	0.002 ± 0.001
Cladocera	1.048 ± 0.142	1.559 ± 0.213	1.170 ± 0.121
Cumacea	0.006 ± 0.002	0.012 ± 0.003	-
Cyclopoida	0.865 ± 0.090	0.603 ± 0.056	0.796 ± 0.154
Egg	0.107 ± 0.018	0.061 ± 0.011	0.054 ± 0.008
Euphausiacea	0.177 ± 0.018	0.237 ± 0.023	0.111 ± 0.013
Gastropoda	0.055 ± 0.005	0.052 ± 0.006	0.059 ± 0.008
Harpactacoida	2.189 ± 0.196	2.037 ± 0.201	1.693 ± 0.307
Hydroida	0.189 ± 0.073	0.073 ± 0.034	0.004 ± 0.002
Isopoda	0.030 ± 0.005	0.050 ± 0.007	0.003 ± 0.001
Mysida	0.009 ± 0.003	0.021 ± 0.005	-
Nauplii	0.124 ± 0.017	0.209 ± 0.025	0.130 ± 0.020
Fish Scales	0.031 ± 0.006	0.043 ± 0.014	0.021 ± 0.008
Polychaeta	0.158 ± 0.019	0.158 ± 0.016	0.042 ± 0.004
Porifera	-	0.003 ± 0.002	-

Table 7. Mean (± SE) **a)** zooplankton concentration (#·L^{-1}), **b)** number of taxa per sample, **c)** Simpson's Index value, **d)** Shannon – Wiener Index value, and **e)** Berger-Parker Index value of diversity of zooplankton samples taken in three habitats at five sites from August 19, 2003 to October 21, 2003 in Newman Sound, Newfoundland.

a) zooplankton concentration (#/L ± SE)

Date	Barren	Eelgrass	Pelagic
August 19, 2003	30.52 ± 3.80	38.21 ± 3.15	19.51 ± 2.43
September 10, 2003	26.82 ± 3.39	33.38 ± 2.85	17.81 ± 2.18
September 25, 2003	34.40 ± 3.84	39.56 ± 3.55	25.67 ± 1.87
October 8, 2003	36.35 ± 12.89	45.08 ± 18.09	29.80 ± 8.63
October 21, 2003	5.89 ± 1.70	38.20 ± 18.47	8.15 ± 2.00

b) taxa concentration (#/sample ± SE)

Date	Barren	Eelgrass	Pelagic
August 19, 2003	10.6 ± 0.5	9.6 ± 0.5	8.7 ± 0.6
September 10, 2003	11.3 ± 0.5	10.5 ± 0.5	9.5 ± 0.6
September 25, 2003	8.4 ± 0.4	9.0 ± 0.4	7.5 ± 0.5
October 8, 2003	12.1 ± 0.7	13.5 ± 0.4	9.0 ± 0.6
October 21, 2003	3.1 ± 0.5	3.6 ± 0.6	1.8 ± 0.3

c) Simpson's Index (±SE)

Date	Barren	Eelgrass	Pelagic
August 19, 2003	0.53 ± 0.04	0.45 ± 0.03	0.41 ± 0.04
September 10, 2003	0.42 ± 0.04	0.32 ± 0.04	0.34 ± 0.04
September 25, 2003	0.32 ± 0.05	0.28 ± 0.04	0.27 ± 0.06
October 8, 2003	0.55 ± 0.07	0.51 ± 0.06	0.62 ± 0.03
October 21, 2003	0.17 ± 0.05	0.17 ± 0.04	0.09 ± 0.04

d) Shannon - Wiener Index (±SE)

Date	Barren	Eelgrass	Pelagic
August 19, 2003	1.18 ± 0.08	0.99 ± 0.07	0.89 ± 0.07
September 10, 2003	0.99 ± 0.09	0.79 ± 0.07	0.79 ± 0.08
September 25, 2003	0.71 ± 0.09	0.67 ± 0.07	0.62 ± 0.11
October 8, 2003	1.22 ± 0.15	1.16 ± 0.14	1.25 ± 0.08
October 21, 2003	0.35 ± 0.09	0.36 ± 0.07	0.17 ± 0.06

e) Berger - Parker Index (±SE)

Date	Barren	Eelgrass	Pelagic
August 19, 2003	0.65 ± 0.03	0.71 ± 0.03	0.74 ± 0.03
September 10, 2003	0.74 ± 0.04	0.81 ± 0.02	0.80 ± 0.03
September 25, 2003	0.80 ± 0.04	0.84 ± 0.03	0.83 ± 0.04
October 8, 2003	0.57 ± 0.07	0.65 ± 0.06	0.54 ± 0.04
October 21, 2003	0.90 ± 0.03	0.90 ± 0.02	0.95 ± 0.02

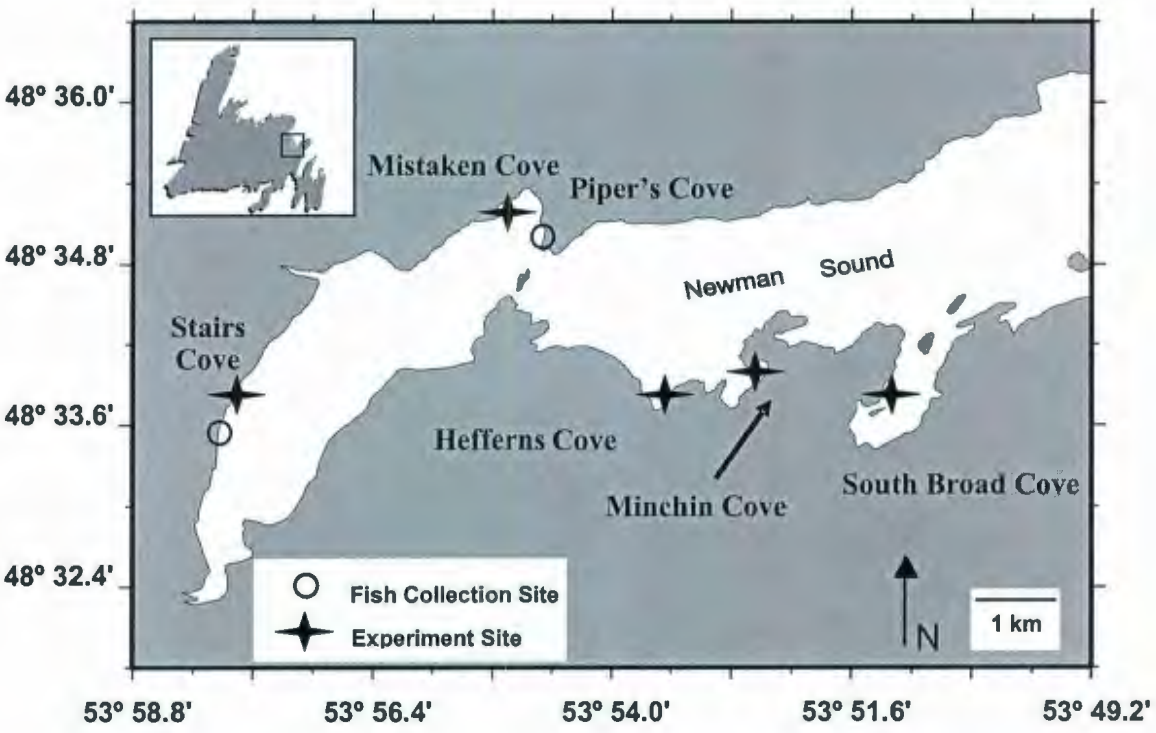


Figure 1. A map of Newman Sound located in Terra Nova National Park, Bonavista Bay, Newfoundland illustrating the study site and specific locations used for fish collection, the growth experiments and plankton sampling from 2002-2003. Stairs Cove and Mistaken Cove were located in the inner sound, while Hefferns Cove, Minchin Cove and South Broad Cove were located in the outer sound.

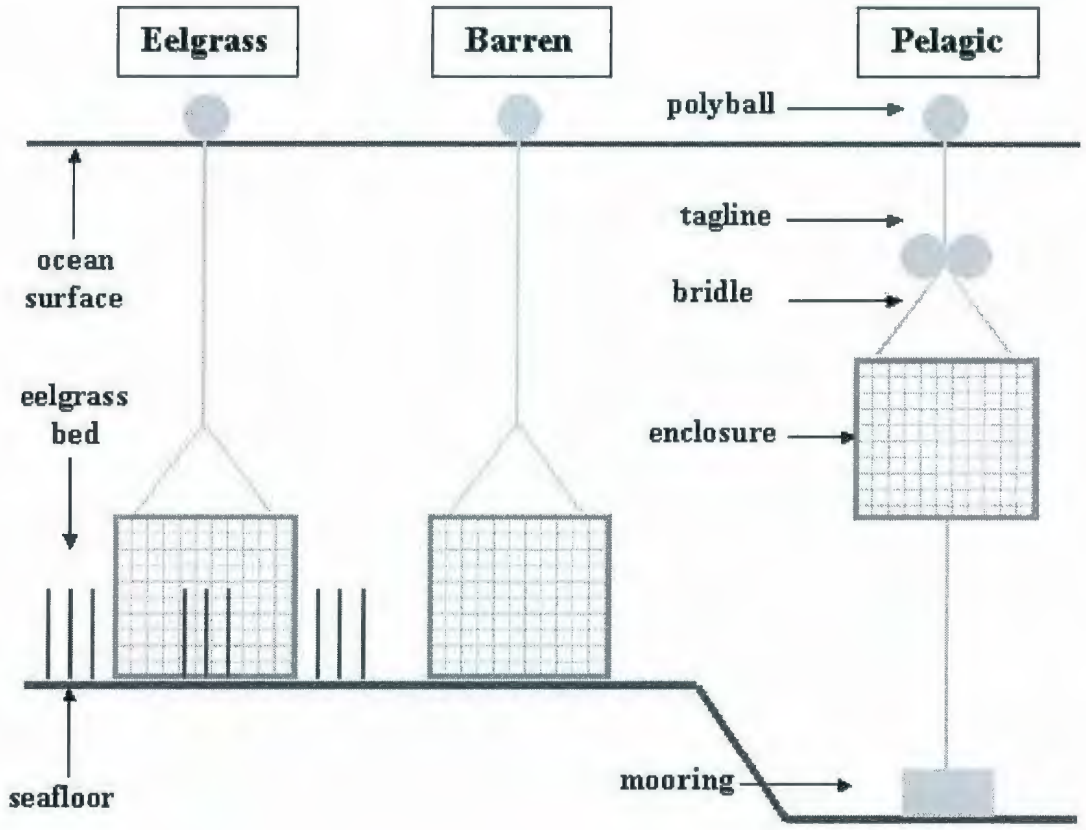


Figure 2. Experimental fish enclosures were deployed in three habitats in Newman Sound, Newfoundland to measure the growth rates of juvenile Atlantic cod, Greenland cod, and white hake during 2002-2003. Enclosures were constructed out of aquaculture mesh on all 6 sides. Barren and eelgrass enclosures were located in water 4 meters deep, while pelagic enclosures were moored in 8 meters of water, and the top of the enclosures were 2.5 meters below the surface of the water. The taglines were used to locate and haul the enclosures to the surface to gain access to the fish and for routine maintenance.

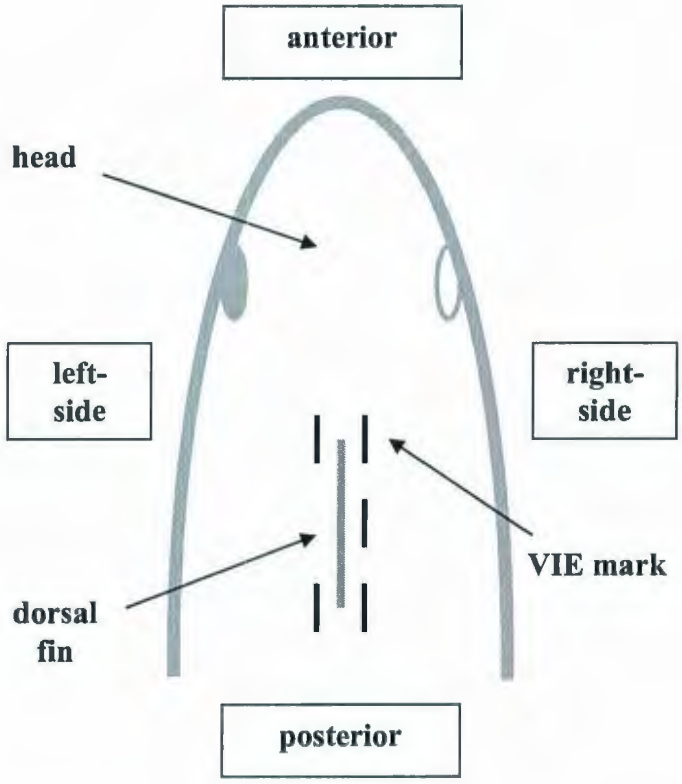


Figure 3. A schematic illustrating the locations of dorsally administered Visible Implant Elastomer (VIE) marks for *G. ogac* and *G. morhua* during the 2002 pilot and 2002-2003 over winter studies respectively. For individual recognition of multiple fish per enclosure, each fish was administered a 3 mm by 1 mm green mark in one of five locations relative to the first dorsal fin: left-anterior, left-posterior, right-anterior, right-middle and right-posterior.

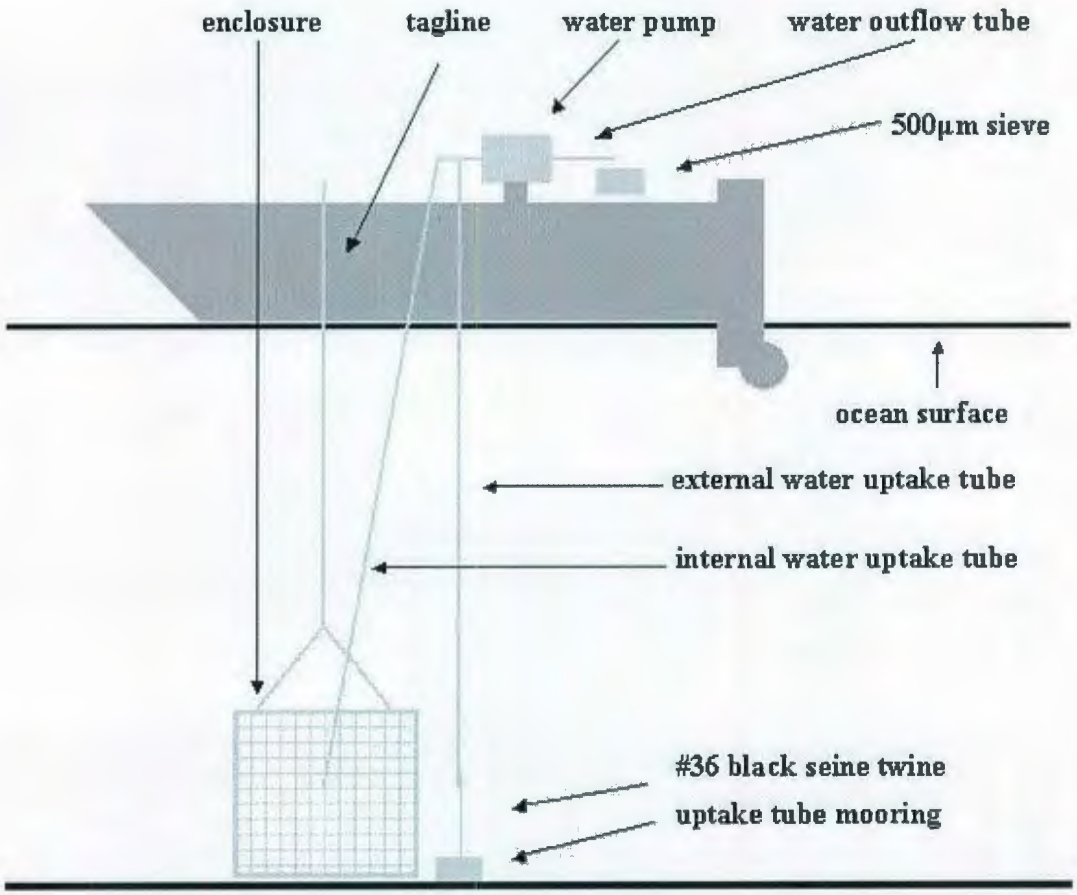


Figure 4. A schematic of the plankton pump setup used for the enclosure-exclusion experiment and for sampling barren, eelgrass and pelagic habitats. For the enclosure-inclusion experiment samples were collected by alternating between the internal uptake tube and the external uptake to collect water samples inside and outside the enclosure. Before sampling began, the pump was allowed to purge. For the routine habitat sampling, the enclosure and internal water uptake tube were not used. After the 2 minute interval, the samples were removed from the sieve with a squirt bottle containing pre-filtered water and preserved in glass canning jars.

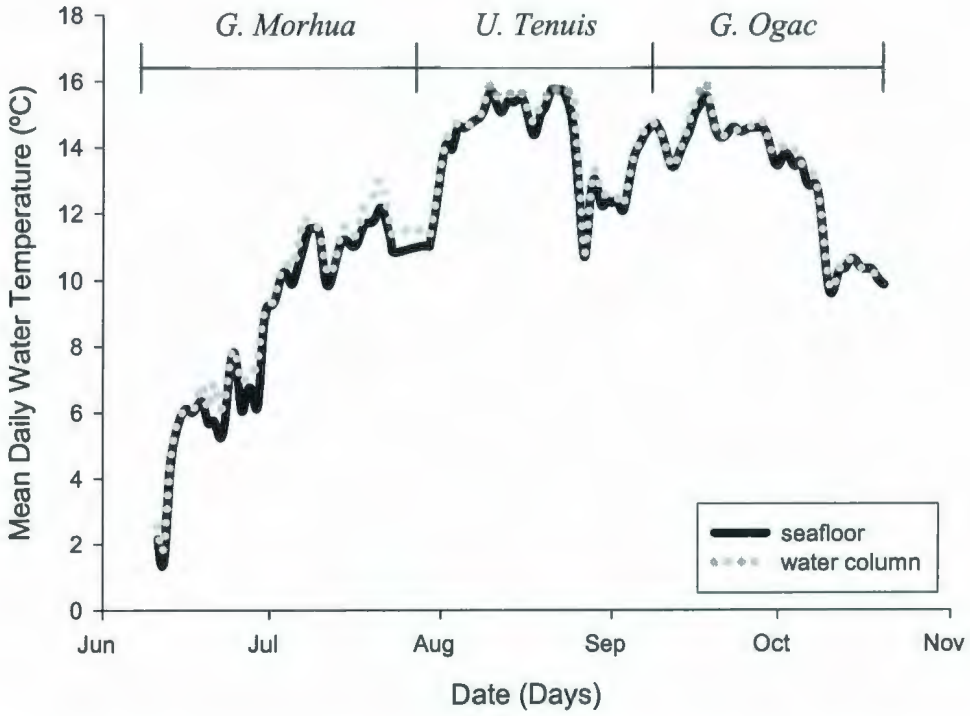
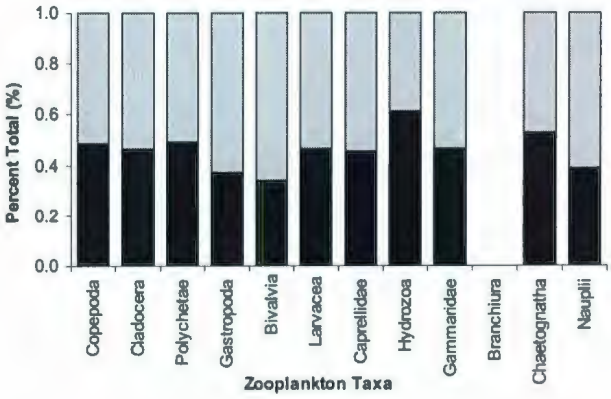


Figure 5. Mean daily water temperature (°C) profile at 5 sites from June – October 2003 in Newman Sound, Newfoundland during enclosure experiments using Atlantic cod, white hake, and Greenland cod. Vemco® mini-loggers were placed in benthic and pelagic (i.e., water column) enclosures for the entire duration of the experiments. Pelagic temperatures were measured 2.5 m below the sea surface, and benthic temperatures were measured 0.5 m off the seafloor. Temperatures were not significantly different between sites or habitats.

a)



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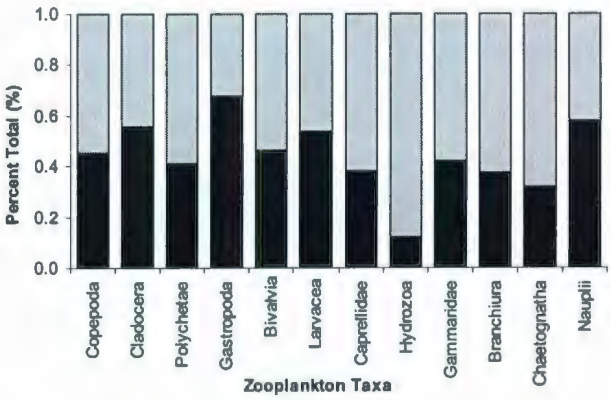

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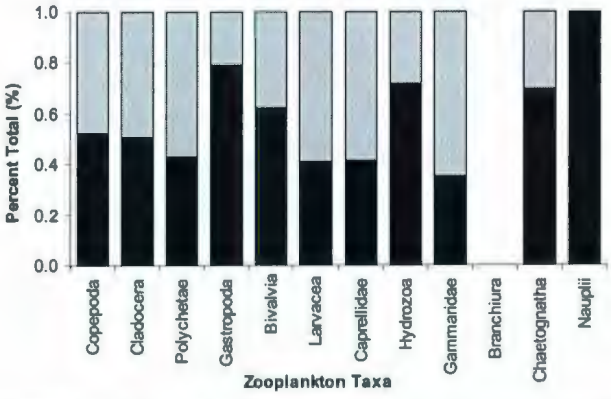


Figure 6. Percent total of 12 prey groups in 60 total plankton pump samples collected inside (solid black bar) and outside (solid grey bar) an experimental enclosure on **(a)** August 20, 2003 (n=20 samples), **(b)** September 4, 2003 (n=20 samples), and **(c)** September 16, 2003 (n=20 samples) at Mistaken Cove in Newman Sound, Newfoundland. There were no differences in prey concentration or the type of prey groups observed inside and outside the experimental enclosures. At each sampling event, 10 samples were taken inside and 10 samples were taken outside of an experimental enclosure.

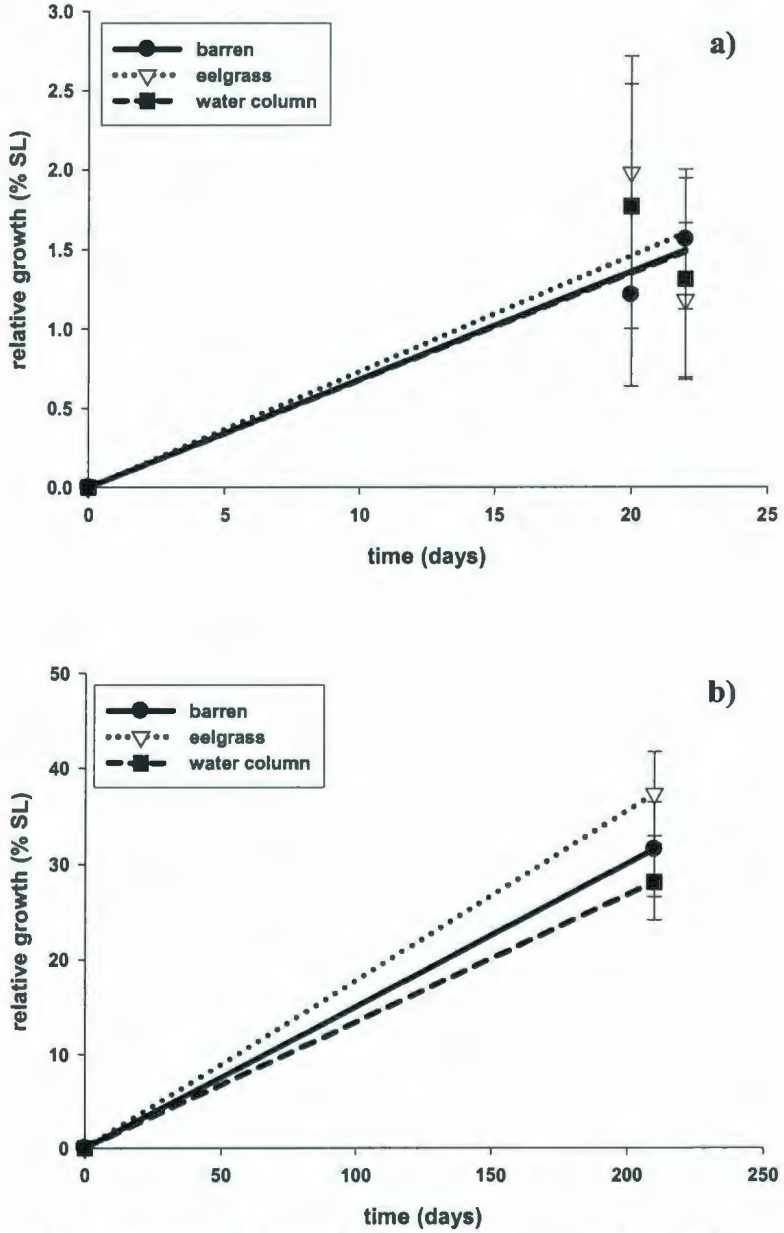


Figure 7. Mean (± SE) relative growth (% standard length in mm) of **(a)** Greenland cod, *G. ogac*, from October 3 – October 25, 2002 enclosed in barren, eelgrass and water column habitats and **(b)** over wintered Atlantic cod, *G. morhua*, from October 25, 2002 – May 23, 2003 enclosed in shallow (4 meters, barren and eelgrass) and deep water (8 meters) habitats at two sites in Newman Sound, Newfoundland. The y-axis represents relative growth in mm SL (%), while the x-axis represents time (days). Regressions for growth in each habitat are illustrated by the lines on each figure.

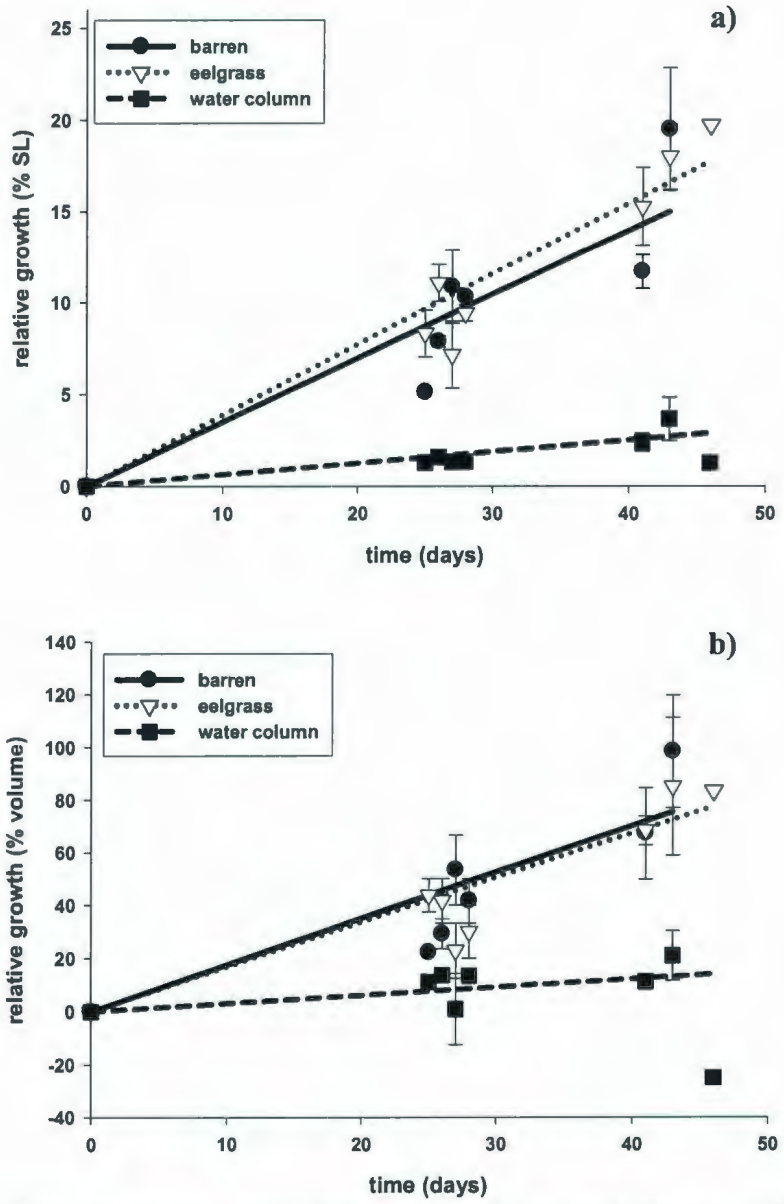
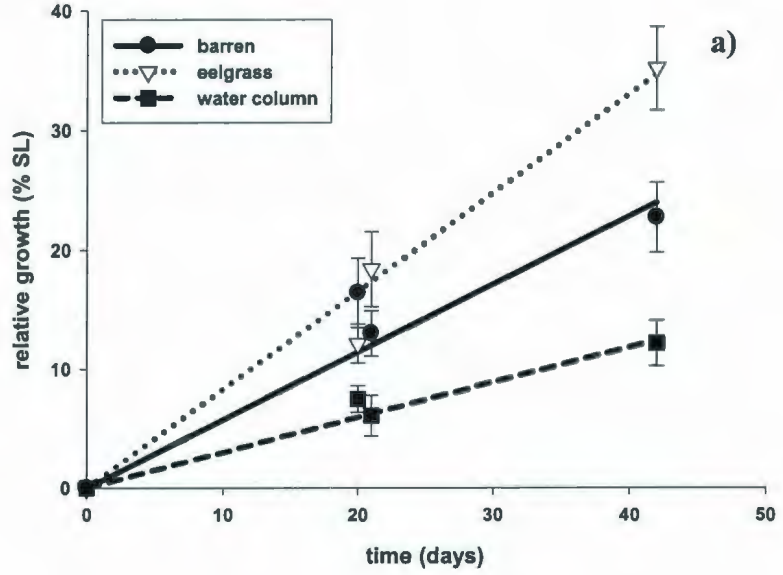


Figure 8. **(a)** Mean (± SE) relative growth (% standard length in mm) and **(b)** mean (± SE) relative growth (% volume in ml) of Atlantic cod, *G. morhua*, enclosed in barren, eelgrass and water column habitats from June 11 – July 24, 2003 at five sites in Newman Sound, Newfoundland. The y-axis represents relative growth in mm SL (%), while the x-axis represents time (days). Regressions for growth in each habitat are illustrated by the lines on each figure.



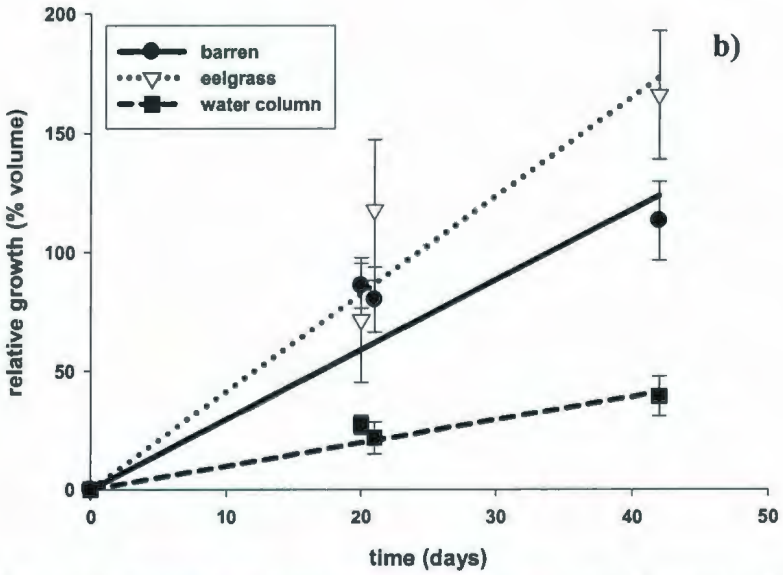


Figure 9. **(a)** Mean (± SE) relative growth (% standard length in mm) and **(b)** mean (± SE) relative growth (% volume in ml) of white hake, *U. tenuis*, enclosed in barren, eelgrass and water column habitats from July 29 – September 9, 2003 at five sites in Newman Sound, Newfoundland. The y-axis represents relative growth in mm SL (%), while the x-axis represents time (days). Regressions for growth in each habitat are illustrated by the lines on each figure.

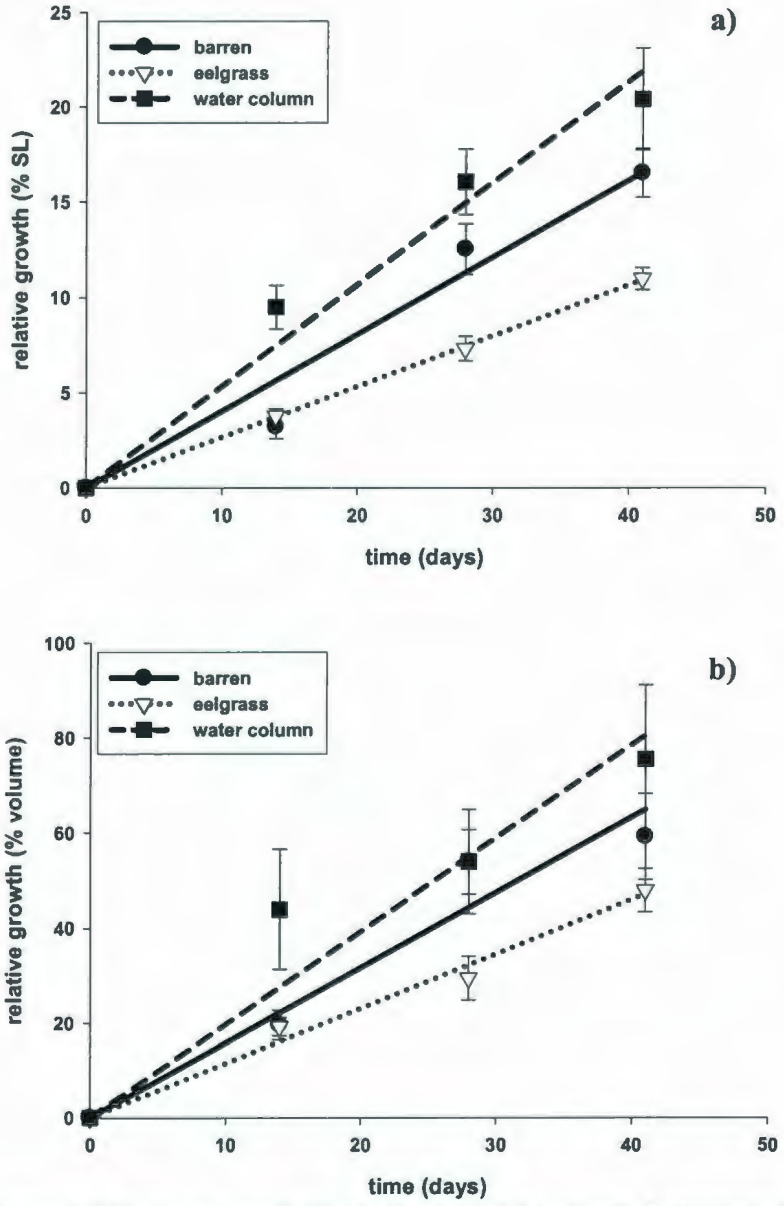
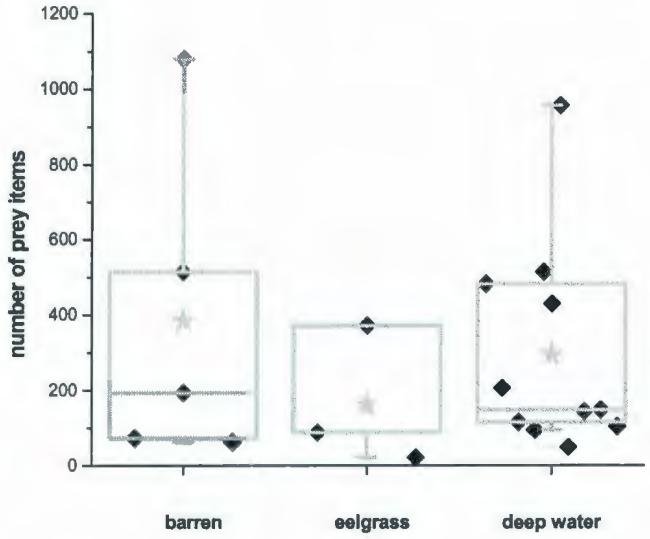


Figure 10. **(a)** Mean (± SE) relative growth (% standard length in mm) and **(b)** mean (± SE) relative growth (% volume in ml) of Greenland cod, *G. ogac*, enclosed in barren, eelgrass and water column habitats from September 9 – October 20, 2003 at five sites in Newman Sound, Newfoundland. The y-axis represents relative growth in mm SL (%), while the x-axis represents time (days). Regressions for growth in each habitat are illustrated by the lines on each figure.

a)



b)

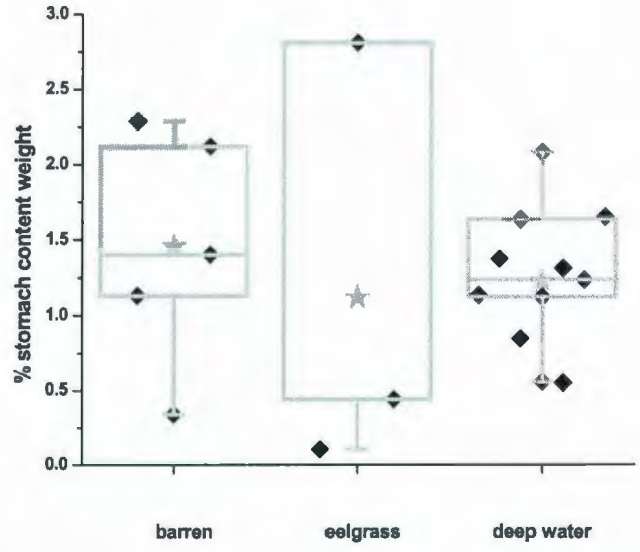


Figure 11. Box plots of **(a)** number of prey items and **(b)** percent stomach content weight of 19 Atlantic cod that successfully over wintered in enclosures in three habitats (four from barren (4 meters deep), three from eelgrass (4 meters deep), and 11 from deep water (8 meters deep) in Newman Sound, Newfoundland from 2002-2003. Stomach contents were analyzed from fish collected at the conclusion of the growth experiment on May 28, 2003. The box is bound by the upper and lower quartiles (75 % and 25 %) with the median (solid gray line) in the middle. The whiskers extend to the high and low values. The black diamonds are data points while the gray stars are the means.

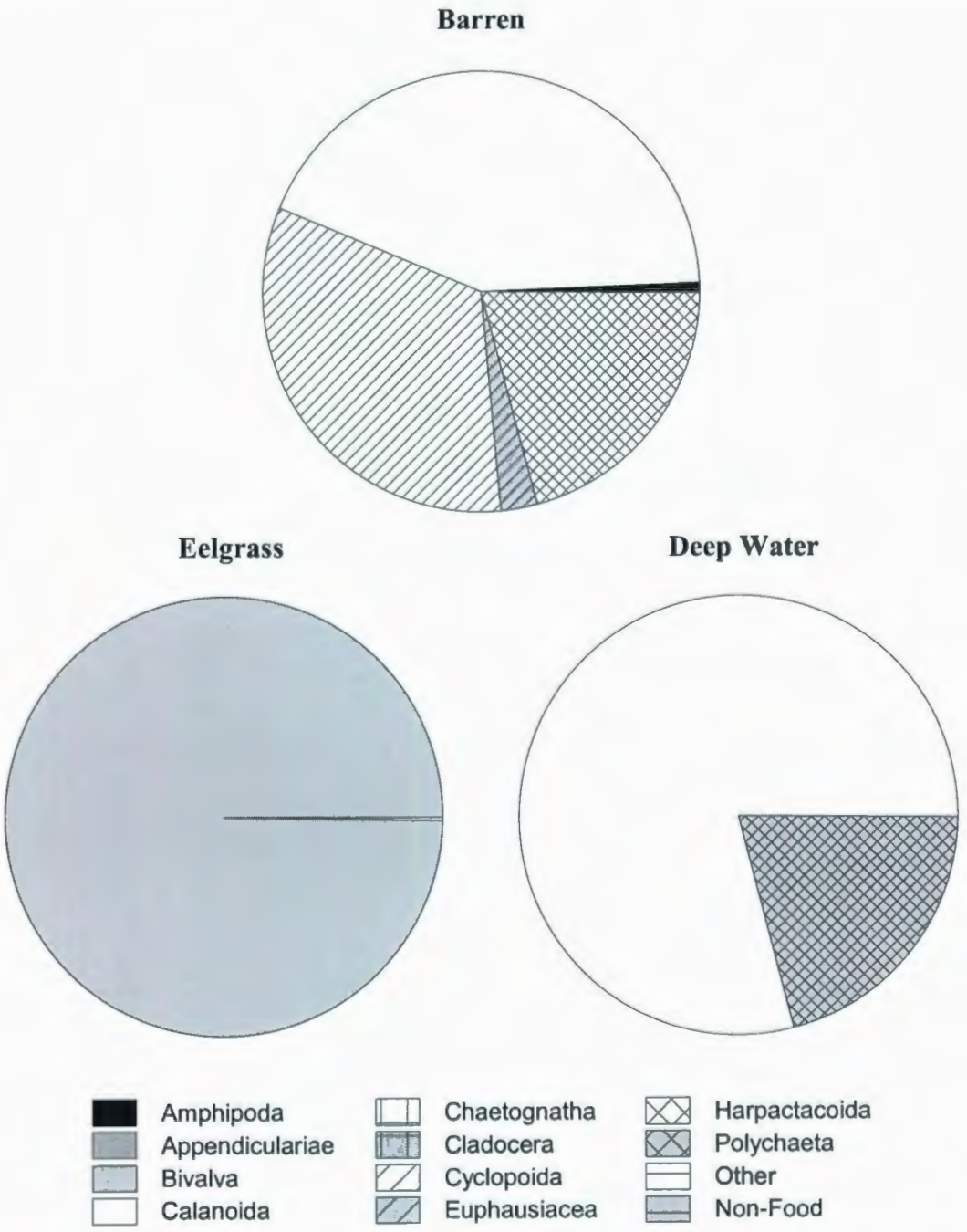
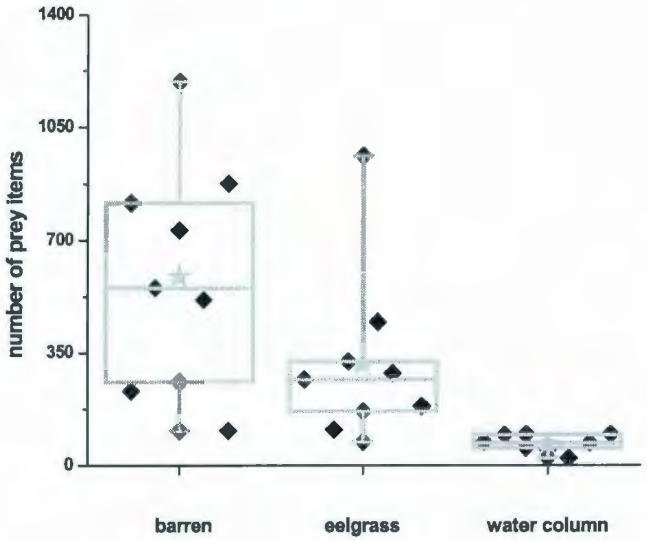


Figure 12. Proportional frequency (by number) of prey items of 19 Atlantic cod that successfully over wintered in enclosures in three habitats (four from barren, three from eelgrass, and 11 from deep water) in Newman Sound, Newfoundland from 2002-2003. Stomachs were sampled only at the conclusion of the growth experiment on May 28, 2003.

a)



b)

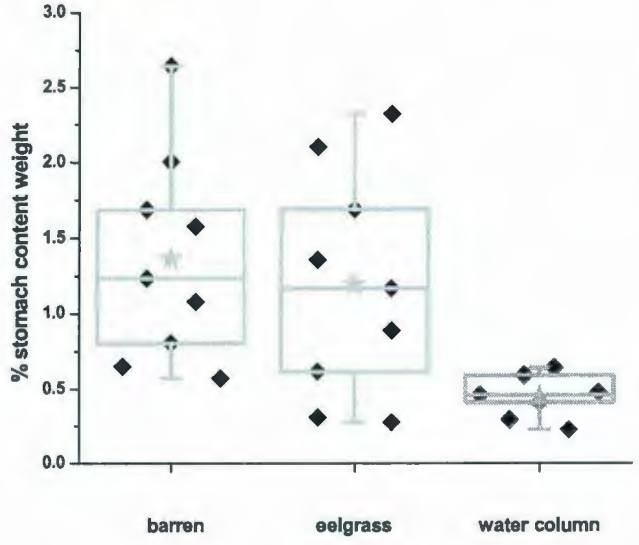


Figure 13. Box plots of **(a)** number of prey items and **(b)** % stomach content weight of 25 age 1+ Atlantic cod that were enclosed in three habitats (9 from barren, 9 from eelgrass, 7 from the water column) in Newman Sound, Newfoundland during the spring of 2003. Stomachs were sampled at the conclusion of the growth experiment on July 24, 2003. The box is bound by the upper and lower quartiles (75 % and 25 %) with the median (solid gray line) in the middle. The whiskers extend to the high and low values. The black diamonds are data points while the gray stars are the means.

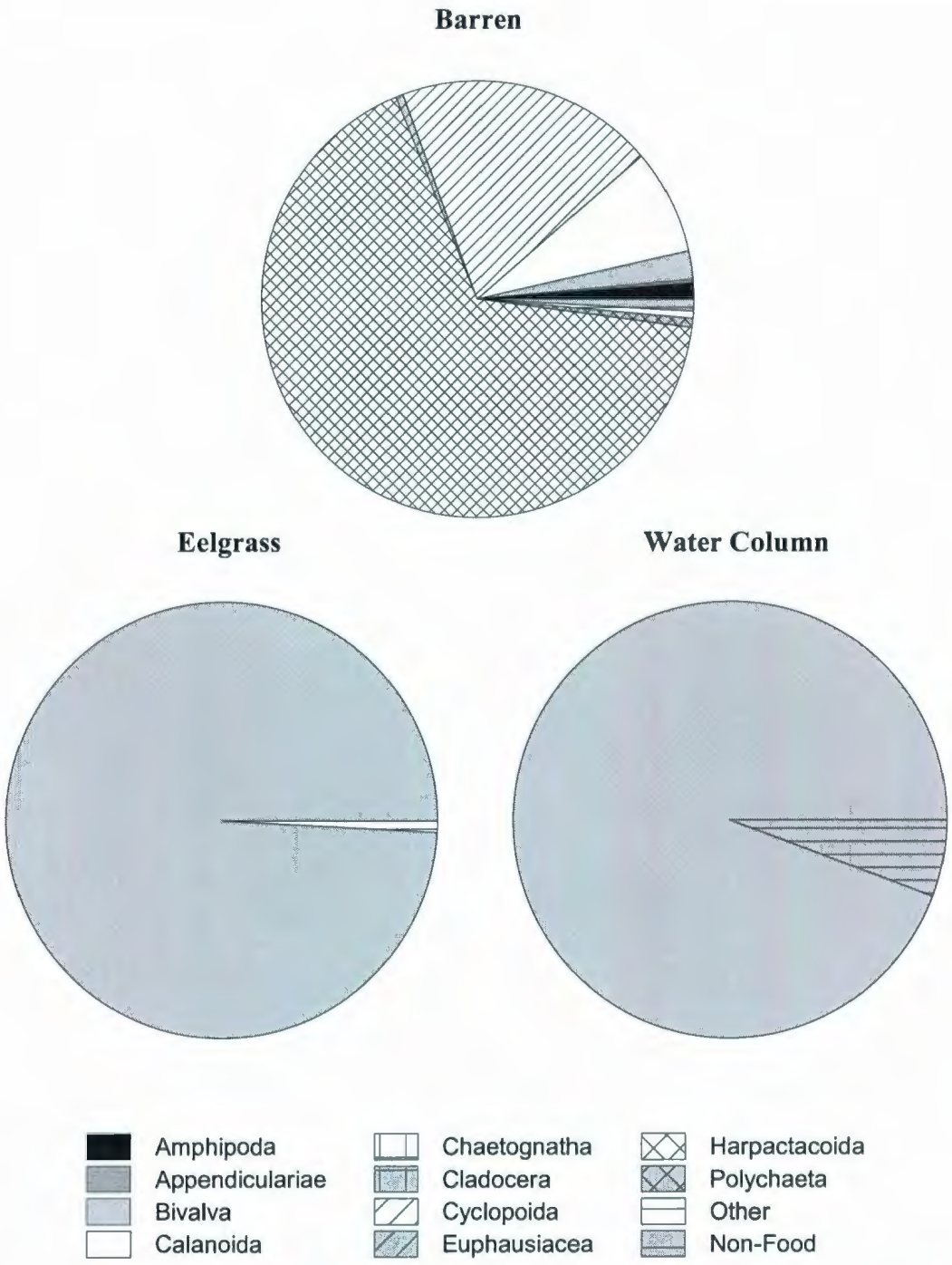
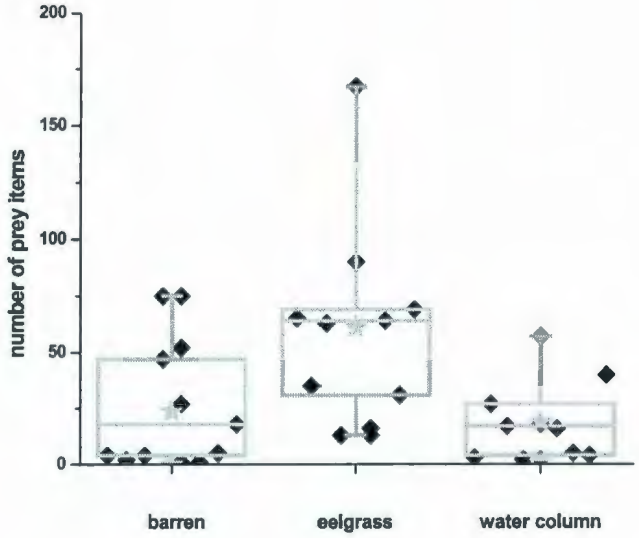


Figure 14. Proportional frequency (by number) of prey items of 25 age 1+ Atlantic cod that were enclosed in three discrete habitats (9 from barren, 9 from eelgrass, 7 from the water column) in Newman Sound, Newfoundland during the spring of 2003. Stomachs were sampled at the conclusion of the growth experiment on July 24, 2003.

a)



b)

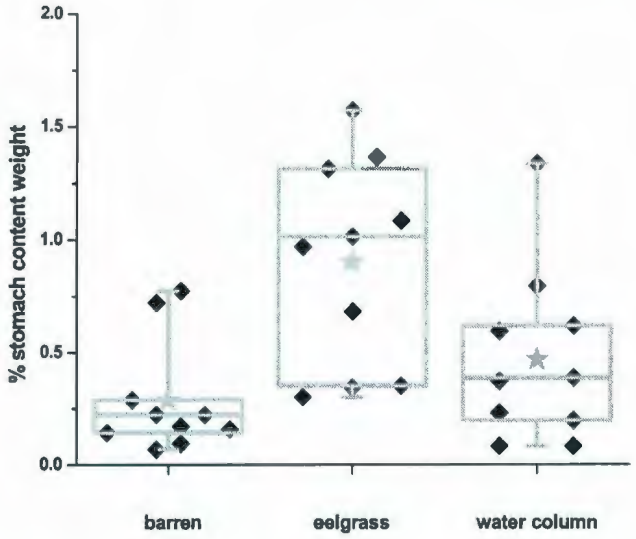


Figure 15. Box plots of **(a)** number of prey items and **(b)** % stomach content weight of 30 age 0+ white hake that were enclosed in three discrete habitats (10 from barren, 10 from eelgrass, 10 from the water column) in Newman Sound, Newfoundland during the summer of 2003. Stomachs were sampled at the conclusion of the growth experiment on September 9, 2003. The box is bound by the upper and lower quartiles (75 % and 25 %) with the median (solid gray line) in the middle. The whiskers extend to the high and low values. The black diamonds are data points while the gray stars are the means.

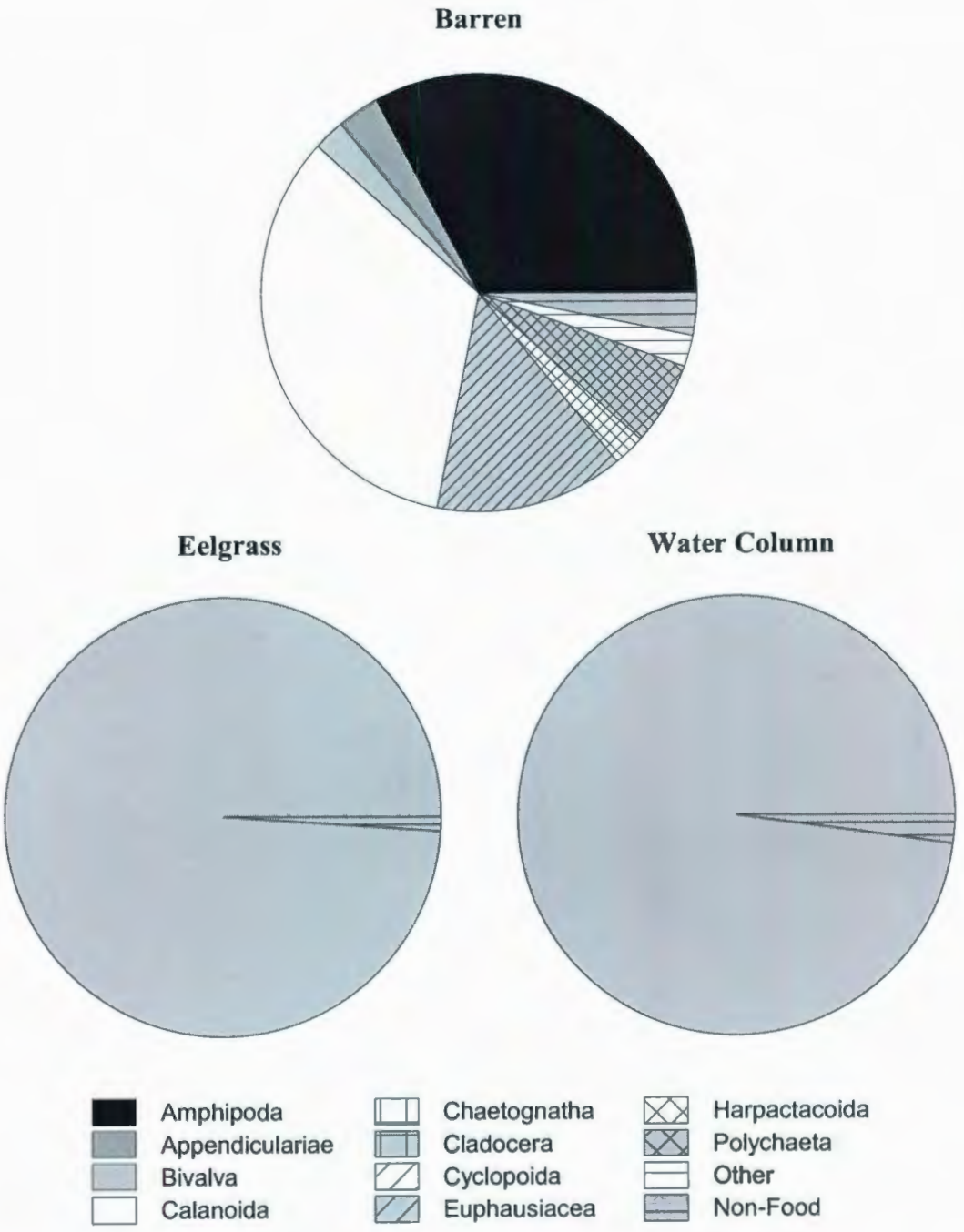
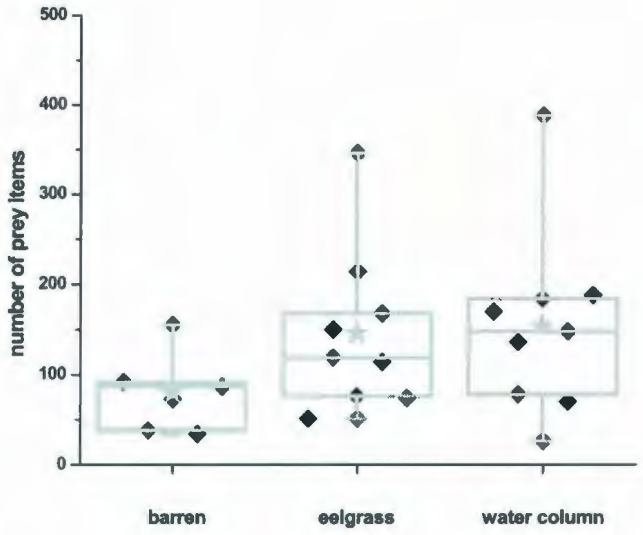


Figure 16. Proportional frequency of prey items of 30 age 0+ white hake that were enclosed in three discrete habitats (10 from barren, 10 from eelgrass, 10 from the water column) in Newman Sound, Newfoundland during the summer of 2003. Stomachs were sampled at the conclusion of the growth experiment on September 9, 2003.

a)



b)

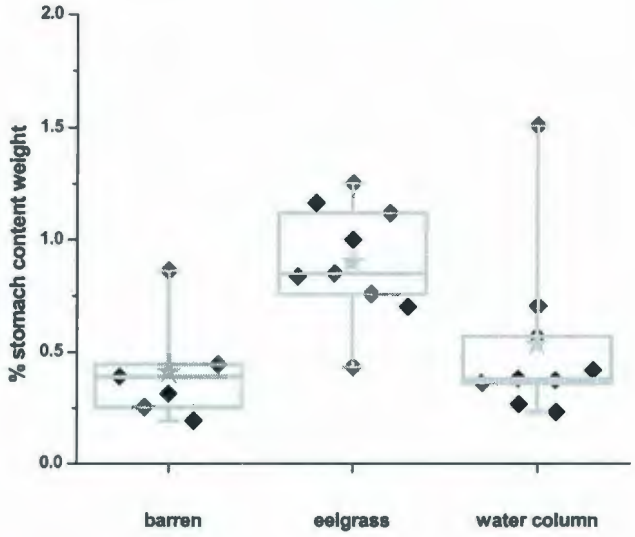


Figure 17. Box plots of **(a)** number of prey items and **(b)** % stomach content weight of 24 age 0+ Greenland cod enclosed in three discrete habitats (6 from barren, 9 from eelgrass, and 9 from the water column) in Newman Sound, Newfoundland in the fall of 2003. Stomachs were sampled at the conclusion of the growth experiment on October 20, 2003. The box is bound by the upper and lower quartiles (75 % and 25 %) with the median (middle horizontal gray line). The whiskers extend to the high and low values. The black diamonds are data points while the gray stars are the means.

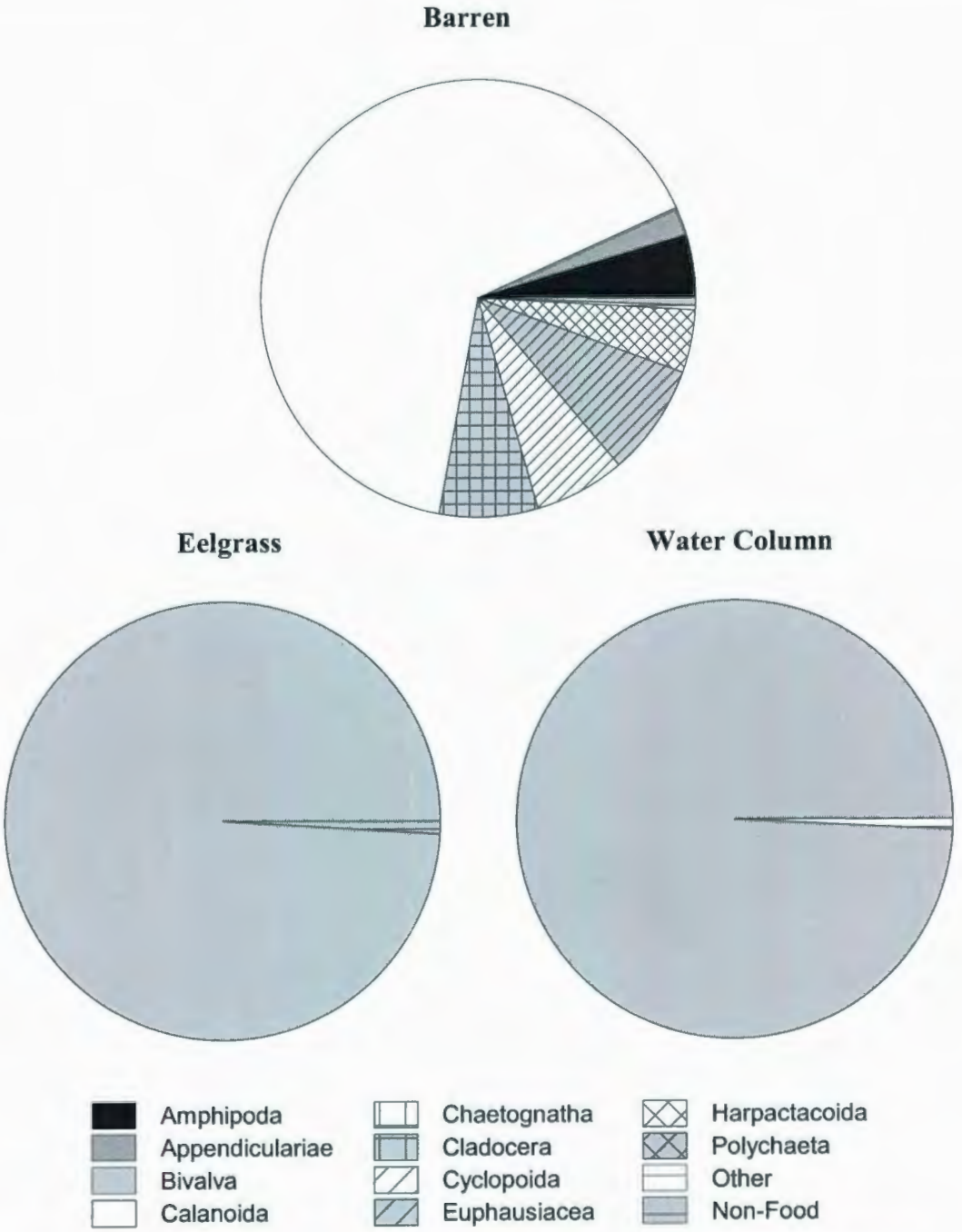


Figure 18. Proportional frequency (by number) of prey items of 24 age 0+ Greenland cod enclosed in three discrete habitats (6 from barren, 9 from eelgrass, 9 from pelagic) in Newman Sound, Newfoundland in the fall of 2003. Stomachs were sampled at the conclusion of the growth experiment on October 29, 2003.

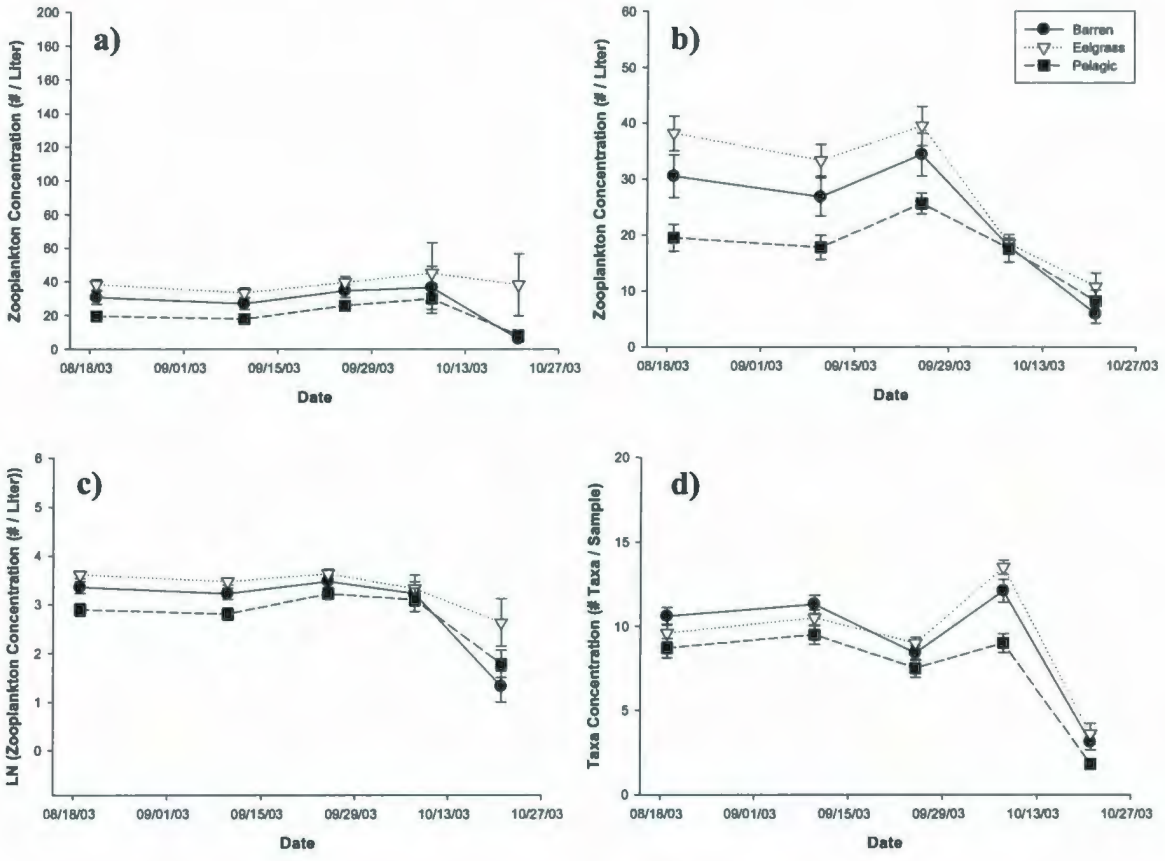


Figure 19. **(a)** Mean (± SE) zooplankton concentration (#/L), **(b)** mean (± SE) zooplankton concentration with outliers removed, **(c)** mean (± SE) natural log transformed zooplankton concentration and **(d)** mean (± SE) number of taxa per sample among barren, eelgrass and pelagic (i.e., water column) habitats at five sites in Newman Sound, Newfoundland from August 18, 2003 to October 21, 2003. Error bars represent the standard error. The 6 samples collected at Stairs Cove on October 8, 2006 and the two eelgrass samples from Mistaken Cove on October 21, 2003 were substantially large outliers and were removed from figure **(a)** for presentation purposes, but remain in **(b)** and required natural log transformation to standardize the variances for statistical analysis. Their magnitude is described in the text of the results.

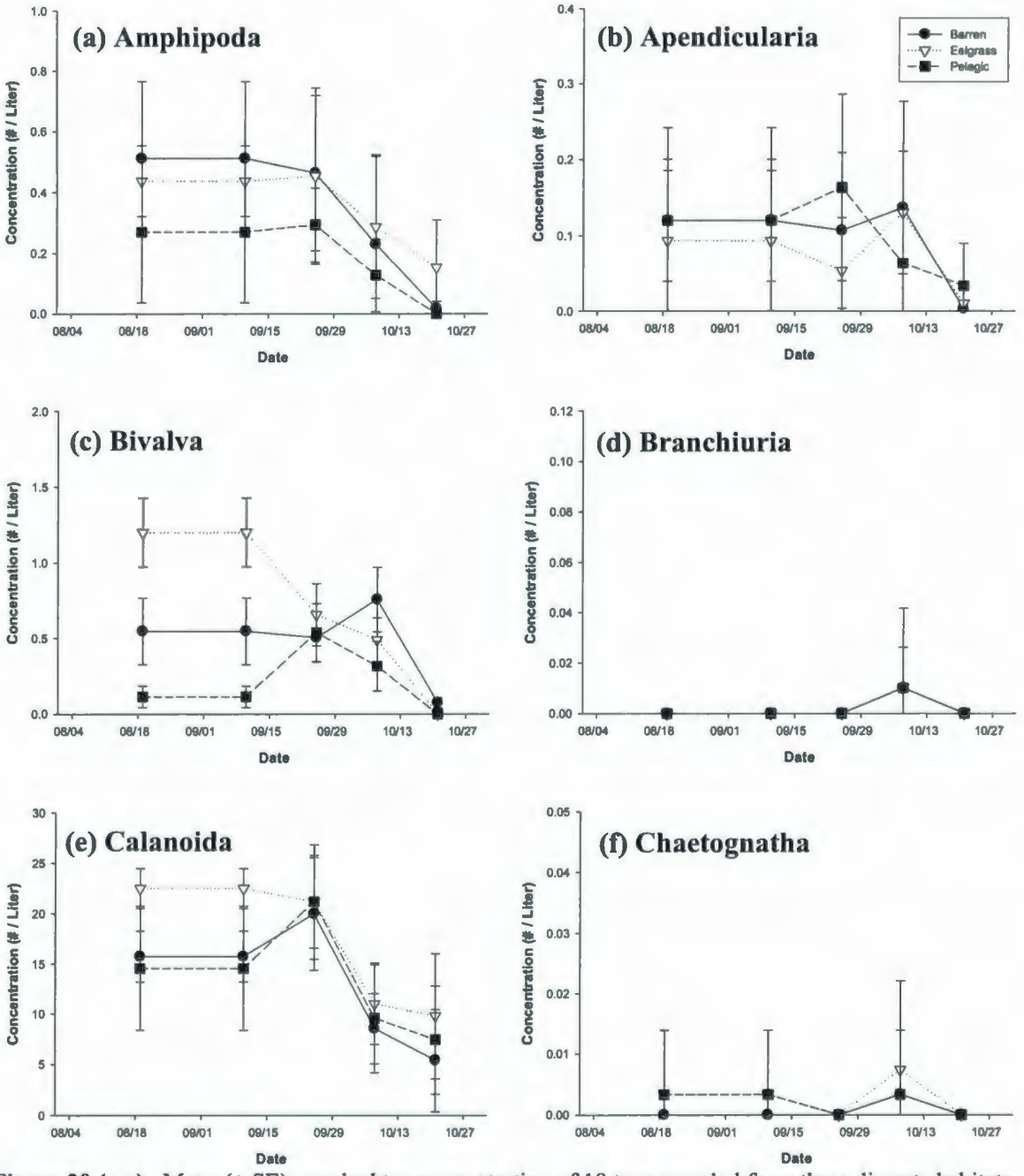
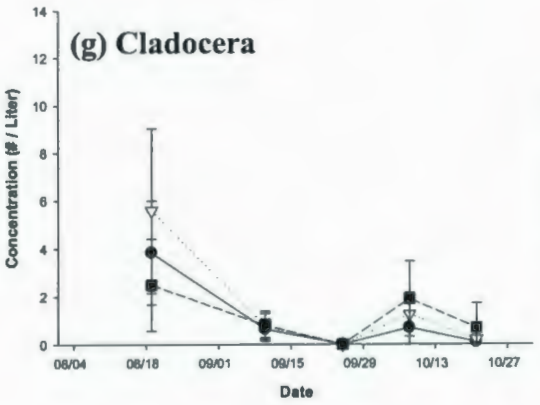
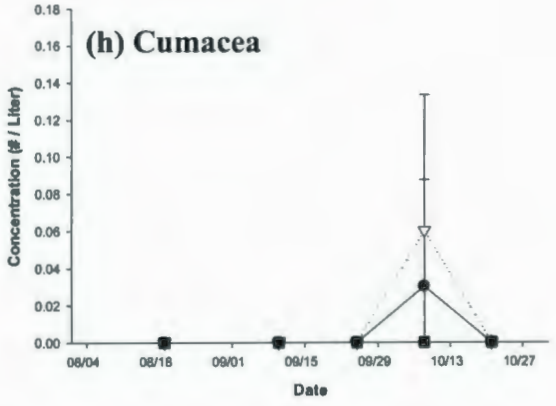
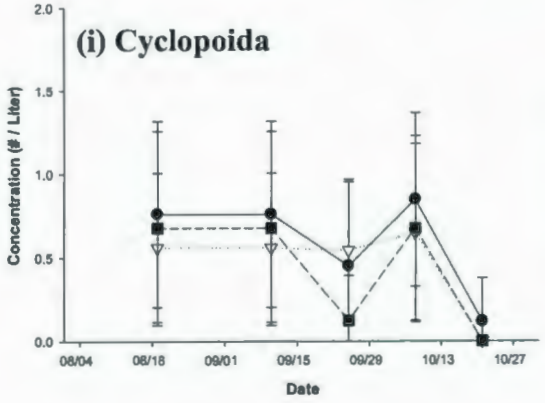
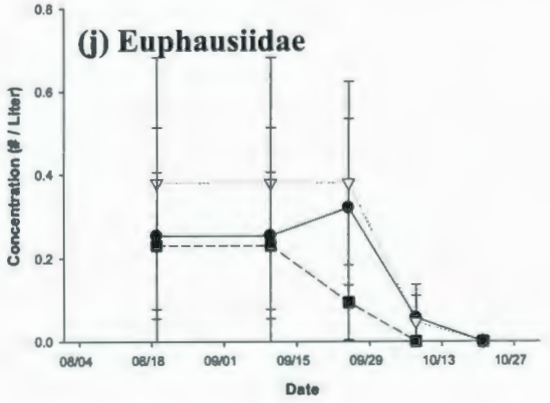


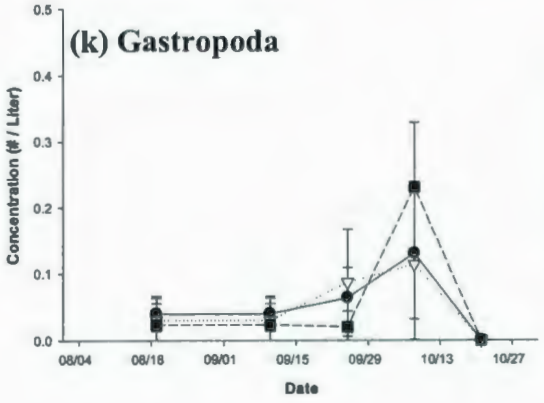
Figure 20 (a-r). Mean (± SE) zooplankton concentration of 18 taxa sampled from three discrete habitats (barren seafloor, eelgrass, and pelagic (i.e., water column) at five sites in Newman Sound, Newfoundland from August 18, 2003 – October 22, 2003. The x-axis values are the calendar date, while the y-axis values are zooplankton concentration (#·Liter^{-1}), and are at various scales in order to accommodate the high degree in variability between species. 30 liters of seawater was collected for each sample.

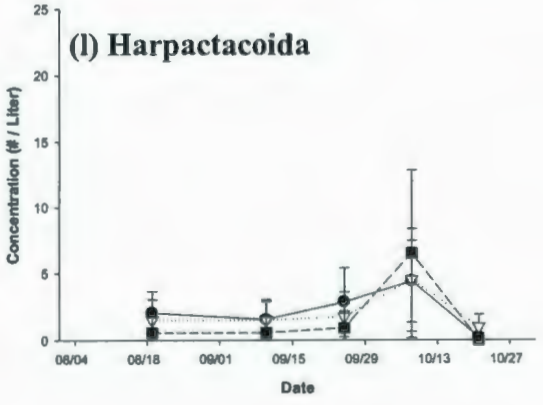

(g) Cladocera
Concentration (# / Liter)
Date
08/04
08/18
09/01
09/15
09/29
10/13
10/27

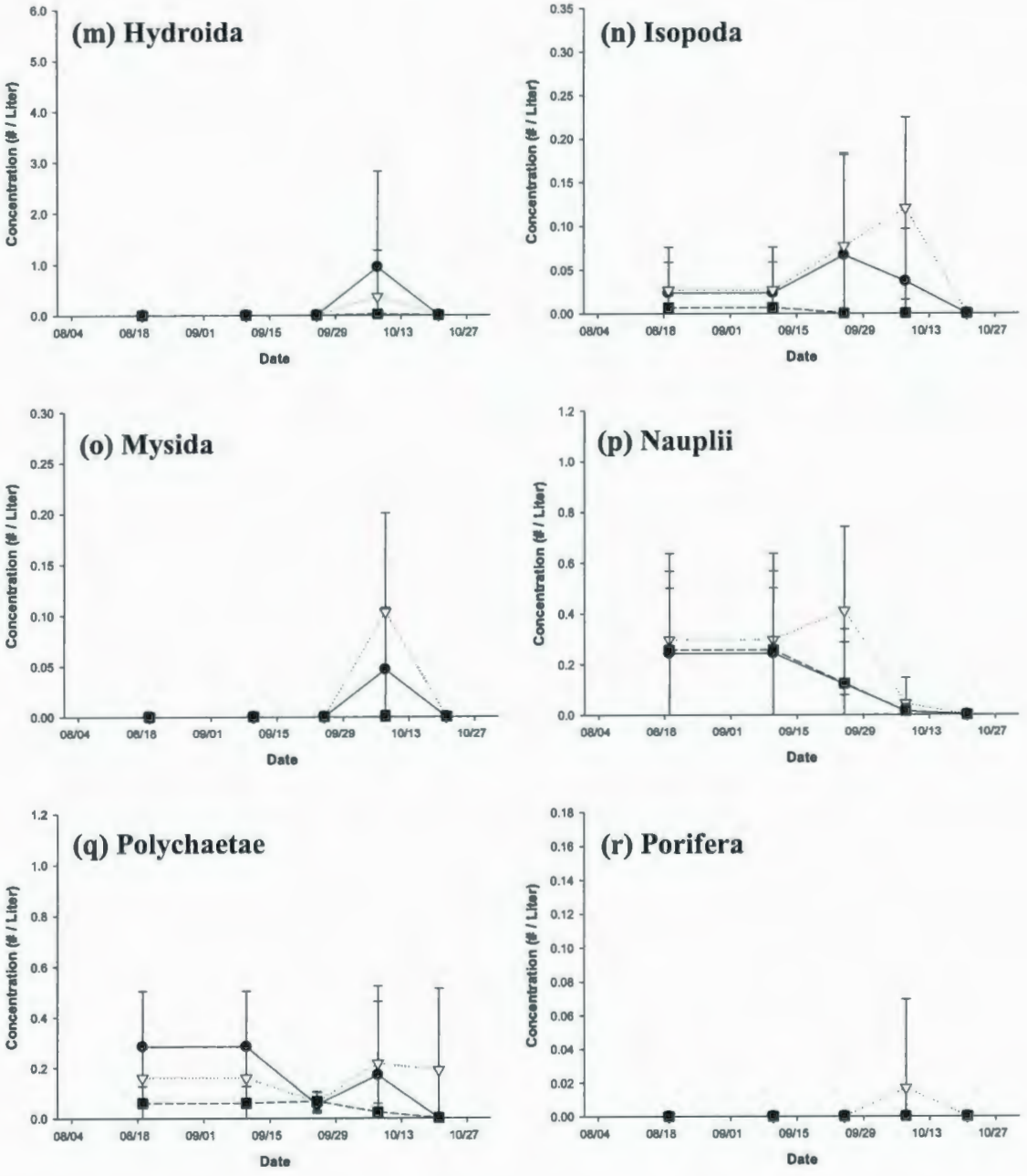

(h) Cumacea
Concentration (# / Liter)
Date
08/04
08/18
09/01
09/15
09/29
10/13
10/27


(i) Cyclopoida
Concentration (# / Liter)
Date
08/04
08/18
09/01
09/15
09/29
10/13
10/27

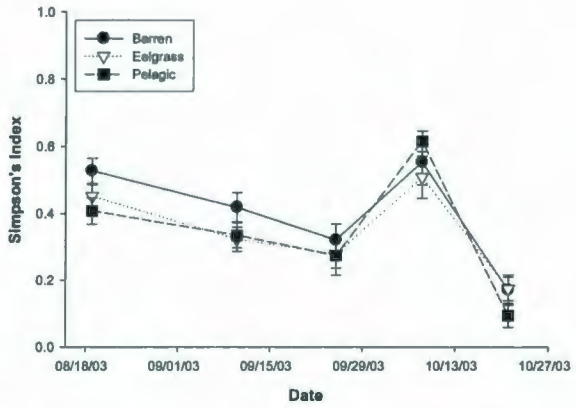

(j) Euphausiidae
Concentration (# / Liter)
Date
08/04
08/18
09/01
09/15
09/29
10/13
10/27


(k) Gastropoda
Concentration (# / Liter)
Date
08/04
08/18
09/01
09/15
09/29
10/13
10/27

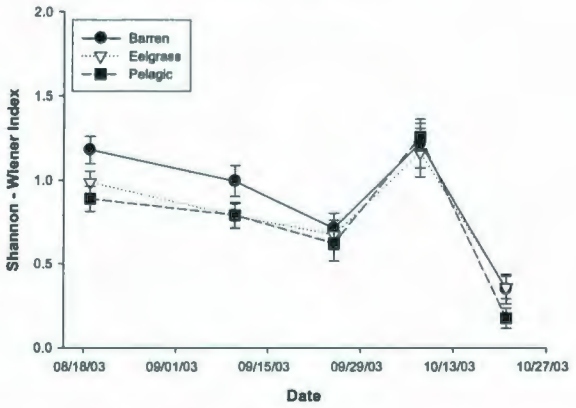

(l) Harpactacoida
Concentration (# / Liter)
Date
08/04
08/18
09/01
09/15
09/29
10/13
10/27


(m) Hydroida
(n) Isopoda
(o) Mysida
(p) Nauplii
(q) Polychaetae
(r) Porifera
Concentration (# / Liter)
Date
08/04
08/18
09/01
09/15
09/29
10/13
10/27

a) Simpson's Index



b) Shannon -Wiener Index



c) Berger - Parker Index

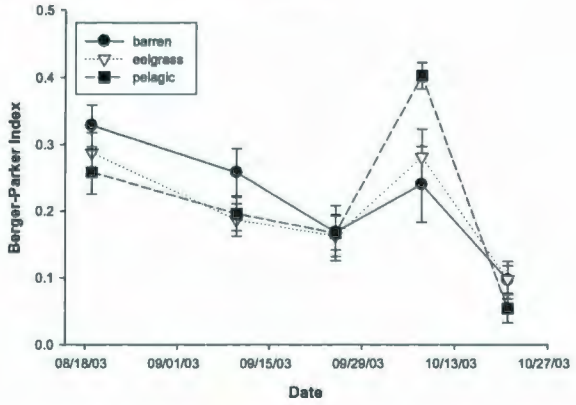


Figure 21. Three diversity indices relating the number and species of zooplankton to barren seafloor, eelgrass and pelagic (i.e., water column) habitats at five sites in Newman Sound, Newfoundland from August 18, 2003 to October 21, 2003. Simpson's Index **(a)**, measured on a scale of 0 (least diverse) to 1 (most diverse), is the probability that any two individuals chosen at random belongs to different species. The Shannon-Wiener Index **(b)** ranks the value of species as a function of their frequency in the community. Low scores, 0, indicate low diversity, while higher scores indicate greater diversity. The inverse of the Berger-Parker Index **(c)**, a measure of how common the most common species is in a sample, ranges from 0 (least diverse) to 1 (most diverse). Values represent index means ± standard error.

7.0 APPENDICES

Appendix I: Global Positioning System (GPS) coordinates of sites used for juvenile fish collection, growth experiments, and plankton sampling experiments in Newman Sound, Newfoundland from 2002 – 2003.

Location	Purpose	Habitat Type	Lattitude	Longitude
Mistaken Cove	Cage Exclusion Experiment	Barren	48°35.279' N	53°55.051' W
Stairs Cove	Fish Collection Site	Various	48°33.655' N	53°57.845' W
Piper's Cove	Fish Collection Site	Various	48°35.347' N	53°54.999' W
South Broad Cove	Reference seining site	Various	48°38.687' N	53°51.227' W
Minchin Cove	Reference seining site	Various	48°33.834' N	53°52.501' W
Hefferen's Cove	Reference seining site	Various	48°33.661' N	53°53.501' W
Mistaken Cove	Reference seining site	Various	48°35.347' N	53°54.999' W
Stairs Cove	Reference seining site	Various	48°33.655' N	53°57.845' W
South Broad Cove	Growth Experiment & Plankton Sampling	Barren	48°33.667' N	53°51.354' W
South Broad Cove	Growth Experiment & Plankton Sampling	Eelgrass	48°33.668' N	53°51.316' W
South Broad Cove	Growth Experiment & Plankton Sampling	Water Column	48°33.685' N	53°51.226' W
Minchin Cove	Growth Experiment & Plankton Sampling	Barren	48°33.924' N	53°52.535' W
Minchin Cove	Growth Experiment & Plankton Sampling	Eelgrass	48°33.938' N	53°52.519' W
Minchin Cove	Growth Experiment & Plankton Sampling	Water Column	48°33.982' N	53°52.597' W
Hefferen's Cove	Growth Experiment & Plankton Sampling	Barren	48°33.716' N	53°53.420' W
Hefferen's Cove	Growth Experiment & Plankton Sampling	Eelgrass	48°33.748' N	53°53.409' W
Hefferen's Cove	Growth Experiment & Plankton Sampling	Water Column	48°33.788' N	53°53.412' W
Mistaken Cove	Growth Experiment & Plankton Sampling	Barren	48°35.264' N	53°55.039' W
Mistaken Cove	Growth Experiment & Plankton Sampling	Eelgrass	48°35.284' N	53°55.025' W
Mistaken Cove	Growth Experiment & Plankton Sampling	Water Column	48°35.262' N	53°55.007' W
Stairs Cove	Growth Experiment & Plankton Sampling	Barren	48°33.656' N	53°57.745' W
Stairs Cove	Growth Experiment & Plankton Sampling	Eelgrass	48°35.661' N	53°57.759' W
Stairs Cove	Growth Experiment & Plankton Sampling	Water Column	48°35.651' N	53°57.730' W

Appendix II: Method used to estimate the effect of initial body size on overall specific growth rate (SGR) in terms of length and volume of juvenile Gadiformes used in five experiments from 2002-2003 in Newman Sound Newfoundland (Derivation by D.C. Schneider). The resulting equation allowed for multiple regressions to generate estimates of the β coefficients (i.e., the slope parameters) and associated confidence limits for each of the five growth experiments. The resulting test statistic and p values were free of part-whole (i.e., spurious) correlation (Pearson 1897).

The density – dependent equation used for the specific growth rate calculations in these experiments was,

$$SGR = \alpha + \beta\, SL_i \qquad (1)$$

where β was the strength of density-dependence. SGR is calculated from SL_i such that

$$SGR = (\ln SL_x - \ln SL_i)\,(t_x - t_i)^{-1} \qquad (2)$$

Consequently, there is a built in correlation between SGR and SL_i. This is illustrated by substituting (1) into (2), which shows that SL_i appears on both sides of the equation as follows:

$$(\ln SL_x - \ln SL_i)\,(tx - ti)^{-1} = \alpha + \beta\, SL_i \qquad (3)$$

This can inflate the estimate of r^2 and the F-ratio, depending on the variance in SL_i versus SL_x. The estimate of β (the slope of the regression) is however, correct. To evaluate statistical significance, equation (3) was rearranged to isolate SL_x. The term $(tx - ti)$ was first carried through on the left side of equation (3) to yield:

$$(\ln SL_x)\,(t_x - t_i)^{-1} - (\ln SL_i)\,(t_x - t_i)^{-1} = (\alpha + \beta\, SL_i) \qquad (4)$$

Then the term $(SL_i)\,(t_x - t_i)^{-1}$ was added to both sides of the equation to yield:

$$(\ln SL_x)\,(t_x - t_i)^{-1} = (\alpha + \beta\, SL_i) + SL_i\,(t_x - t_i)^{-1} \qquad (5)$$

Next the term $(t_x - t_i)$ was multiplied to both sides of equation (5) to yield:

$$(\ln SL_x)\,(t_x - t_i)^{-1}\,(t_x - t_i)^{1} = [(\alpha + \beta\, SL_i)\,(t_x - t_i)^{1}] + [SL_i\,(t_x - t_i)^{-1}\,(t_x - t_i)^{1}] \qquad (6)$$

The time terms on the left side of equation (6) canceled out, isolating $\ln SL_x$. The time term was carried through the right side of the equation to yield the following:

$$\ln SL_x = [(\alpha + \beta\, SL_i)\,(t_x - t_i)] + \ln SL_i \qquad (7)$$

$$= (\alpha)\,(t_x - t_i) + (\beta\, SL_i)\,(t_x - t_i) + \ln SL_i \qquad (8)$$

To estimate the density dependence free of part-whole correlation, ln SL_x was regressed against the three terms, $(t_x - t_i)$, $(t_x - t_i)\ SL_i$, and ln SL_i, from equation (8). The estimate of the slope parameter, the β coefficient, of the term $(t_x - t_i)\ SL_i$ was the slope of the SGR, and the associated statistic and p-value were not inflated by spurious correlation. The same regression was conducted with measurements of volumetric growth, by substituting the length terms with volume terms. The null hypothesis, that size dependent growth was not occurring, and alternate hypothesis, that size dependent growth was occurring, were as follows:

$$H_a: \beta = 0 \tag{9a}$$

$$H_o: \beta \neq 0 \tag{9b}$$

The slope parameter estimate, the β coefficient, was not considered significant if the 95% confidence interval included 0.

Appendix III: Results of fixed factor ANCOVA's (GLM) used to test for the effects of date, site, habitat and their interactions on the mean daily water temperature (°C) during three different experiments from June – October, 2003 in Newman Sound, Newfoundland. Date was considered a covariate in the model. The non-significant interaction terms with the covariate were removed from the models. **(a)** The age 1+ Atlantic cod experiment was conducted between June 11, 2003 and July 24, 2003. **(b)** The age 0+ white hake experiment was conducted between July 29, 2003 and September 9, 2003. **(c)** The age 0+ Greenland cod was conducted between September 9, 2003 and October 20, 2003.

a)

Source	DF	MS	F	P
Date	1	10.255	11.66	< 0.001
Site	4	1.529	1.43	0.223
Habitat	1	2.200	2.50	0.115
Site x Habitat	4	0.904	1.03	0.397
Error	406	0.880		
Total	416			

Term	Coef	SE Coef	T	P
Constant	-3643.00	1069.00	-3.41	< 0.001
Date	0.09655	0.02828	3.41	< 0.001

b)

Source	DF	MS	F	P
Date	1	11.339	4.92	0.027
Site	4	4.200	1.82	0.123
Habitat	1	4.934	2.14	0.144
Site x Habitat	4	1.338	0.58	0.677
Error	419	2.304		
Total	429			

Term	Coef	SE Coef	T	P
Constant	509.40	223.30	2.28	0.023
Date	-0.013086	0.00589	-2.22	0.027

c)

Source	DF	MS	F	P
Date	1	1046.670	877.43	< 0.001
Site	4	1.660	1.39	0.236
Habitat	1	1.430	1.20	0.274
Site x Habitat	4	1.170	0.98	0.416
Error	409	1.190		
Total	419			

Term	Coef	SE Coef	T	P
Constant	5221.5	166.6	31.34	< 0.001
Date	-0.13024	0.00439	-29.62	< 0.001

Appendix IV: One-way ANOVAs relating initial length (and volume in the 2003 experiments) to habitat type (i.e., barren, eelgrass and water column) for **(a)** the 2002 Greenland cod pilot, **(b)** the 2002-2003 Atlantic cod over winter, **(c & d)** the 2003 Atlantic cod, **(e & f)** the 2003 white hake, and **(g & h)** the Greenland cod growth experiments. No differences in the initial lengths and volumes among habitats were detected at the beginning of each of the five experiments.

(a)

Source	DF	SS	MS	F	P
Habitat	2	14.40	7.20	0.17	0.845
Error	57	2437.25	42.76		
Total	59				

(b)

Source	DF	SS	MS	F	P
Habitat	2	26.81	13.41	0.67	0.515
Error	52	1036.53	19.93		
Total	54				

(c)

Source	DF	SS	MS	F	P
Habitat	2	17.82	8.91	0.75	0.482
Error	27	320.10	11.86		
Total	29				

(d)

Source	DF	SS	MS	F	P
Habitat	2	0.87	0.43	0.69	0.511
Error	27	17.00	0.63		
Total	29				

(e)

Source	DF	SS	MS	F	P
Habitat	2	23.22	11.61	1.11	0.345
Error	27	282.90	10.48		
Total	29				

(f)

Source	DF	SS	MS	F	P
Habitat	2	3.01	1.51	2.12	0.139
Error	27	19.13	0.71		
Total	29				

(g)

Source	DF	SS	MS	F	P
Habitat	2	140.47	70.23	2.77	0.080
Error	27	683.40	25.31		
Total	29				

(h)

Source	DF	SS	MS	F	P
Habitat	2	4.52	2.26	1.75	0.193
Error	27	34.85	1.29		
Total	29				

Appendix V: Hierarchical ANOVAs for **(a)** the 2002 Greenland cod pilot experiment and **(b)** the Atlantic cod over winter growth experiment relating SGR_{Length} between two sites, among three habitats, two enclosures per habitat and five marked fish per enclosure.

a)

Source	DF	MS	F	P
Site	1	0.0001	0.04	0.836
Habitat	2	0.0104	2.02	0.138
Enclosure	1	0.0071	4.37	0.068
Mark(Enclosure)	8	0.0016	0.31	0.961
Error	94	0.0051		
Total	106			

b)

Source	DF	MS	F	P
Site	1	0.0063	8.68	0.026
Habitat	2	0.0022	3.06	0.121
Enclosure	1	0.0002	0.12	0.734
Mark(Enclosure)	8	0.0023	3.22	0.086
Error	6	0.0007		
Total	18			

Appendix VI: One-way ANOVAs relating over winter survival (2002-2003) of Atlantic cod in experimental field enclosures among **(a)** three habitats (barren, eelgrass and water column), and **(b)** two depths (4 meters and 8 meters).

a)

Source	DF	MS	F	P
Habitat	2	0.8667	4.39	0.017
Error	57	0.1974		
Total	59			

b)

Source	DF	MS	F	P
Depth	1	1.6333	8.35	0.005
Error	58	0.1957		
Total	59			

Appendix VII: Results of analyses of variance (ANOVA) for a growth experiment using enclosed age 1+ Atlantic cod that relate standard growth rates for **(a)** length (SGR_{Length}) and **(b)** volume (SGR_{Volume}) among three habitats, two enclosures per habitat, at five sites in Newman Sound, Newfoundland, from June 11 – July 24, 2003. Type III adjusted mean squares were used in the analyses.

a)

Source	DF	MS	F	P
Site	4	0.0046	0.12	0.974
Habitat	2	0.3450	9.18	< 0.001
Enclosure	1	0.0004	0.01	0.923
Site*Habitat	8	0.0062	0.16	0.995
Site*Enclosure	4	0.0061	0.16	0.956
Habitat*Enclosure	2	0.0041	0.11	0.896
Site*Habitat*Enclosure	8	0.0046	0.12	0.998
Error	45	0.0376		
Total	74			

b)

Source	DF	MS	F	P
Site	4	0.0358	0.06	0.992
Habitat	2	3.8799	6.64	0.003
Enclosure	1	0.2796	0.48	0.492
Site*Habitat	8	0.2269	0.39	0.921
Site*Enclosure	4	0.2588	0.44	0.777
Habitat*Enclosure	2	0.0626	0.11	0.898
Site*Habitat*Enclosure	8	0.1698	0.29	0.965
Error	45	0.5842		
Total	74			

Appendix VIII: Results of analyses of variance (ANOVA) for a growth experiment using enclosed age 0 white hake that relate standard growth rates for **(a)** length (SGR_{Length}) and **(b)** volume (SGR_{Volume}) among three habitats, two enclosures per habitat, at five sites in Newman Sound, Newfoundland, from July 29 – September 9, 2003. Type III adjusted mean squares were used in the analyses.

a)

Source	DF	MS	F	P
Site	4	0.031	0.26	0.901
Habitat	2	0.609	5.09	0.009
Enclosure	1	0.033	0.28	0.601
Site*Habitat	8	0.090	0.76	0.643
Site*Enclosure	4	0.025	0.21	0.930
Habitat*nclosure	2	0.001	0.01	0.989
Site*Habitat*Enclosure	8	0.025	0.21	0.988
Error	60	0.119		
Total	89			

b)

Source	DF	MS	F	P
Site	4	0.441	0.21	0.931
Habitat	2	12.167	5.82	0.005
Enclosure	1	2.063	0.99	0.324
Site*Habitat	8	1.304	0.62	0.754
Site*Enclosure	4	0.406	0.19	0.940
Habitat*Enclosure	2	0.927	0.44	0.644
Site*Habitat*Enclosure	8	0.440	0.21	0.988
Error	60	2.089		
Total	89			

Appendix IX: Results of analyses of variance (ANOVA) for a growth experiment using enclosed age 0 Greenland cod that relate standard growth rates for **(a)** length (SGR_{Length}) and **(b)** volume (SGR_{Volume}) among three habitats, two enclosures per habitat, at five sites in Newman Sound, Newfoundland, from September 9 – October 20, 2003. Type III adjusted mean squares were used in the analyses.

a)

Source	DF	MS	F	P
Site	4	0.0492	0.71	0.590
Habitat	2	0.4836	6.95	0.002
Enclosure	1	0.0008	0.01	0.729
Site*Habitat	8	0.0208	0.30	0.964
Site*Enclosure	4	0.0386	0.55	0.696
Habitat*Enclosure	2	0.0051	0.07	0.930
Site*Habitat*Enclosure	8	0.0496	0.71	0.678
Error	66	0.0696		
Total	95			

b)

Source	DF	MS	F	P
Site	4	1.0121	0.92	0.458
Habitat	2	2.7906	2.53	0.087
Enclosure	1	1.6874	1.53	0.220
Site*Habitat	8	0.6384	0.58	0.791
Site*Enclosure	4	1.2281	1.11	0.374
Habitat*Enclosure	2	0.1172	0.11	0.899
Site*Habitat*Enclosure	8	0.6221	0.56	0.804
Error	66	1.1022		
Total	95			

Appendix X: Total numbers of various prey items found in the stomachs of juvenile Gadiformes confined to 3 distinct habitat types in Newman Sound, Newfoundland in 2003.

Species	Sampling Date	Habitat	Amphipoda	Appendicullariae	Bivalva	Calanoida	Chaetognatha	Cladocera	Cyclopoida	Euphausiacea	Harpactacoida	Polychaeta	Other	Non-Food
Atlantic cod	May 23, 2003	barren	12	0	0	809	0	0	615	51	389	2	0	0
		eelgrass	8	0	0	236	0	0	93	23	64	0	5	1
		deep water	25	0	31	1520	0	0	778	171	666	1	0	3
Atlantic cod	July 24, 2003	barren	55	11	94	349	2	0	867	25	2994	31	23	39
		eelgrass	77	0	12	184	0	1	276	48	1670	15	25	20
		pelagic	23	0	0	66	0	1	67	1	104	1	0	16
white hake	September 9, 2003	barren	42	4	3	43	0	0	0	18	3	8	3	4
		eelgrass	118	0	0	145	6	0	16	110	54	14	0	5
		pelagic	27	2	41	5	0	0	5	45	3	9	0	3
Greenland cod	October 20, 2003	barren	15	7	0	213	0	24	22	27	15	0	1	2
		eelgrass	55	15	3	783	0	55	7	77	32	3	1	10
		pelagic	5	4	0	629	0	275	90	32	5	1	3	8

Appendix XI: ANOVA tables of total items in the stomachs of fish enclosed in three discrete habitats in Newman Sound, Newfoundland at the end of four experiments: **(a)** over wintered Atlantic cod, **(b)** spring Atlantic cod, **(c)** summer white hake, **(d)** and fall Greenland cod.

a)

Source	DF	MS	F	P
Habitat	2	47130	0.48	0.627
Error	16	98055		
Total	18			

b)

Source	DF	MS	F	P
Habitat	2	541354	7.56	0.003
Error	22	71567		
Total	24			

c)

Source	DF	MS	F	P
Habitat	2	5413	5.39	0.011
Error	27	1005		
Total	29			

d)

Source	DF	MS	F	P
Habitat	2	11238	1.45	0.256
Error	21	7732		
Total	23			

Appendix XII: ANOVA tables of stomach content weight as a percent of body weight of fish enclosed in three discrete habitats in Newman Sound, Newfoundland at the end of four experiments: winter Atlantic cod **(a)**, spring Atlantic cod **(b)**, summer white hake **(c)**, and fall Greenland cod **(d)**.

a)

Source	DF	MS	F	P
Habitat	2	0.1313	0.23	0.795
Error	16	0.5629		
Total	18			

b)

Source	DF	MS	F	P
Habitat	2	1.8118	4.81	0.018
Error	22	0.3765		
Total	24			

c)

Source	DF	MS	F	P
Habitat	2	0.9896	7.01	0.004
Error	27	0.1412		
Total	29			

d)

Source	DF	MS	F	P
Habitat	2	0.5157	5.28	0.014
Error	21	0.0977		
Total	23			

Appendix XIII: Results of fixed factor analyses of covariance (ANCOVA) relating **(a)** the natural log of zooplankton concentration (#/L), **(b)** taxa concentration (#/sample), **(c)** Simpson's Index values, **(d)** Berger-Parker Index values and **(e)** Shannon-Wiener Index values to date, site and habitat during the zooplankton sampling experiment conducted from August 18, 2003 – October 21, 2003 in Newman Sound, Newfoundland.

a)

Source	DF	MS	F	P
Date	1	18.46	29.08	< 0.001
Site	4	4.92	7.75	< 0.001
Habitat	2	4.42	6.96	0.001
Replicate	1	0.01	0.02	0.882
Site*Habitat	8	0.38	0.59	0.782
Site*Replicate	4	0.05	0.08	0.989
Habitat*Replicate	2	0.09	0.14	0.866
Site*Habitat*Replicate	8	0.04	0.06	1.000
Error	119	0.63		
Total	149			

Term	Coef	SE Coef	T	P
Constant	608.9	112.4	5.42	<0.001
Date	-0.0160	0.0030	-5.39	<0.001

b)

Source	DF	MS	F	P
Date	1	396.20	36.00	< 0.001
Site	4	1.89	0.17	0.952
Habitat	2	58.53	5.32	0.006
Replicate	1	0.43	0.04	0.844
Site*Habitat	8	3.74	0.34	0.949
Site*Replicate	4	8.89	0.81	0.522
Habitat*Replicate	2	4.93	0.45	0.640
Site*Habitat*Replicate	8	1.09	0.10	0.999
Error	119	11.01		
Total	149			

Term	Coef	SE Coef	T	P
Constant	2816	467.9	6.02	< 0.001
Date	-0.0741	0.0124	-6.00	< 0.001

Appendix XIII ***continued:***

c)

Source	DF	MS	F	P
Date	1	0.5587	15.02	< 0.001
Site	4	0.0240	0.64	0.632
Habitat	2	0.0445	1.20	0.306
Replicate	1	0.0000	0.00	0.995
Site*Habitat	8	0.0707	1.90	0.066
Site*Replicate	4	0.0041	0.11	0.979
Habitat*Replicate	2	0.0495	1.33	0.268
Site*Habitat*Replicate	8	0.0166	0.45	0.891
Error	119	0.0372		
Total	149			

Term	Coef	SE Coef	T	P
Constant	105.79	27.2	3.89	< 0.001
Date	-0.0028	0.0007	-3.88	< 0.001

d)

Source	DF	MS	F	P
Date	1	0.1621	6.09	0.015
Site	4	0.0332	1.25	0.295
Habitat	2	0.0341	1.28	0.282
Replicat	1	0.0001	0.00	0.950
Site*Habitat	8	0.0459	1.72	0.100
Site*Replicate	4	0.0036	0.13	0.970
Habitat*Replicate	2	0.0275	1.03	0.359
Site*Habitat*Replicate	8	0.0086	0.32	0.957
Error	119	0.0266		
Total	149			

Term	Coef	SE Coef	T	P
Constant	-56.02	23.01	-2.43	0.016
Date	0.0015	0.0006	2.47	0.015

e)

Source	DF	MS	F	P
Date	1	3.4594	20.47	< 0.001
Site	4	0.0839	0.50	0.738
Habitat	2	0.2679	1.59	0.209
Replicat	1	0.0065	0.04	0.845
Site*Habitat	8	0.2655	1.57	0.141
Site*Replicate	4	0.0355	0.21	0.932
Habitat*Replicate	2	0.1252	0.74	0.479
Site*Habitat*Replicate	8	0.0555	0.33	0.954
Error	119	0.1690		
Total	149			

Term	Coef	SE Coef	T	P
Constant	263.14	57.98	4.54	< 0.001
Date	-0.0069	0.0015	-4.52	< 0.001