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Potential effect of eelgrass (*Zostera marina*) loss on nearshore Newfoundland fish communities, due to invasive green crab (*Carcinus maenas*)

Effet potentiel de la disparition de la zostère marine (*Zostera marina*) sur les communautés de poissons de la côte de Terre-Neuve à la suite de l'invasion par le crabe vert (*Carcinus maenas*)

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ABSTRACT

Green crab (*Carcinus maenas*) is an invasive species in Newfoundland that may impact eelgrass habitats. High densities of green crab were first observed in Placentia Bay during 2007, in shallow water habitats used by juvenile fish of many species. This report synthesizes the results of several research projects conducted on eelgrass habitat in Newfoundland that have investigated the effects of loss of eelgrass on fish communities in coastal waters. Eelgrass habitat in Newfoundland has been shown to be preferred habitat for demersal juvenile Atlantic and Greenland cod, and various life-stages of several other fish species. In several studies during 1995-2009 we monitored fish densities, and conducted *in-situ* habitat manipulation experiments to identify possible changes in nearshore fish communities when eelgrass habitat is lost. Experimental removal of eelgrass resulted in an 80% decline in fish abundance and biomass. Eelgrass loss also altered the relative abundance of species resulting in declines in abundance of most species, including Atlantic and Greenland cod, white hake, and sticklebacks. In contrast, abundance increased for three species: rainbow smelt, shorthorn sculpin, and winter flounder. This research demonstrated the magnitude of effect of eelgrass habitat loss on fish communities, which is an important consideration when evaluating the potential impact of invasion and potential spread of green crab along the Newfoundland coast.

RÉSUMÉ

Le crabe vert (*Carcinus maenas*) est une espèce envahissante qui peut avoir un effet sur les habitats de zostère marine de Terre-Neuve. C'est en 2007 que l'on a observé pour la première fois de fortes densités de crabes verts dans des habitats peu profonds de la baie de Plaisance utilisés par des juvéniles de nombreuses espèces. Le présent rapport résume les résultats de plusieurs projets de recherche portant sur l'habitat de zostère marine et sur les effets que peut avoir la disparition de ceux-ci sur les communautés de poissons des eaux côtières de Terre-Neuve. À Terre-Neuve, l'habitat de zostère marine est un habitat de prédilection pour la morue franche et l'ogac, aux stades de juvéniles démersaux, et pour plusieurs autres espèces de poissons, à différents stades de développement. Dans plusieurs études menées de 1995 à 2009, on a assuré un suivi des densités de poissons et effectué des expériences de manipulation de l'habitat *in-situ* pour tenter de découvrir quels changements pouvaient survenir au sein des communautés de poissons côtières à la suite de la disparition de l'habitat de zostère marine. Or, le retrait expérimental de la zostère marine a entraîné un déclin de 80 % de l'abondance et de la biomasse des poissons. La disparition de la zostère marine a également entraîné une modification de l'abondance relative des espèces, à savoir des déclinés de l'abondance de la plupart des espèces, y compris la morue franche et l'ogac, la merluche blanche et les épinoches. En revanche, l'abondance de trois espèces s'est accrue : éperlan, chaboisseau à épines courtes et plie rouge. Ces travaux de recherche ont démontré l'ampleur de l'effet de la disparition de l'habitat de zostère marine sur les communautés de poissons, ce qui constitue une considération importante dans l'évaluation de l'effet que peuvent avoir l'envahissement et la propagation potentielle du crabe vert sur les côtes de Terre-Neuve.

INTRODUCTION

Life history attributes of the European green crab (*Carcinus maenas*) make it a model invader species (Klassen and Locke 2007). It has been ranked among the top 100 most invasive species in the world (Lowe et al. 2000), capable of impacting native species and their habitats, and ultimately affecting whole aquatic ecosystems. In addition to its aggressive behaviour, it is a generalist feeder and tolerant to a wide range of environmental conditions. Prey includes shallow water taxa, some of which are commercially valuable shellfish species. It “outcompetes” many native species including other decapods and “higher” taxonomic forms such as shorebirds for available resources. Green crab will uproot aquatic plants while burrowing in sediments (Short and Wyllie-Echeverria 1996; Floyd and Williams 2004), and tear and cut eelgrass plants at the sheath (Davis et al. 1998), which destroys the plant and affects important habitats (Dewitt 2009). Crooks (2002) described green crab as an “ecosystem engineer”. Therefore, green crab is capable of impacting the coastal environment at many trophic levels - as a predator, competitor, and through seabed habitat modification.

Eelgrass, *Zostera marina* L., is the dominant seagrass in the North Atlantic (Huges et al. 2002) and is the only seagrass in coastal waters off Newfoundland. Eelgrass is an Ecologically Significant Species (ESS) in Canada (DFO 2009). Eelgrass was considered an ESS by Fisheries and Oceans Canada because it creates habitat used preferentially by other species, it physically supports other biota, and it is often abundant enough and sufficiently widely distributed to influence the overall ecology of that habitat. Although it is widely distributed around the island of Newfoundland it is restricted to shallow water within protected bays and inlets and grows primarily in soft bottom substrates near freshwater inflow. The complex spatial structure provided by patches of eelgrass creates habitat that is used preferentially by many species including juveniles of several fishes and invertebrates. Eelgrass meadows rank among the most productive ecosystems on the planet (DFO 2009). Loss of eelgrass and other seagrasses worldwide is largely associated with anthropogenic stressors (Duarte and Chiscano 1999; Orth et al. 2006), including the spread of invasive species such as green crab (Garbary 2004).

Lazzari et al. (2003) suggested the shallow water fish community is broadly similar from the Virginia to the Canadian Maritime provinces (38-45 degrees of latitude). They compared habitat studies using seining and trawling methods in Virginia (Orth and Heck 1980), New Jersey (Szedlmayer and Able 1996), New York (Briggs and O'Connor 1971), Connecticut (Warfel and Merrimen 1944), Rhode Island (Percy and Richards 1962), Massachusetts (Heck et al. 1989), Maine (Ayvazian et al. 1992; Lazzari et al. 1999) and Atlantic Canada (Tyler 1971; MacDonald et al. 1984; Black and Miller 1991). As expected, the Maine fish fauna was similar to Massachusetts and intermediate in composition compared with Canadian Maritime provinces to the north or more southern locations within their study area. The fish community in Maine shallow waters consisted primarily of cold temperate species, with few of the more southerly distributed species that commonly add to the faunal richness of New Jersey and Virginia estuaries. Newfoundland studies were not included in the synoptic review by Lazzari et al. (2003). Similar beach seining surveys in Newfoundland (e.g., Gotceitas et al. 1997, Gregory et al. 1997, Methven et al. 2003) have indicated that the fish community in coastal Newfoundland, not surprisingly, contains more arctic or sub-arctic species than the areas further south reported in Lazzari et al. (2003). However, taken as a whole, these studies demonstrate that eelgrass is a significant fish nursery habitat wherever it occurs, despite latitudinal changes in the species assemblage.

The wide temperature tolerance range of eelgrass, from freezing to 35 °C (Hidalgo et al. 2005), is beyond the range of most individual fish species. Therefore the fish community composition of an eelgrass meadow in Newfoundland will be different from that of warmer coastal waters further south. The depth distribution of eelgrass is controlled by the penetration of light for photosynthesis (DFO 2009), which is geographically variable and based on ambient conditions. In Newfoundland, eelgrass occurs at greater depths than in the coastal waters of New England because the clear water in the former area permits light penetration to greater depth. Our observations suggest that Newfoundland represents the northern extent of eelgrass habitat. Although it occurs sporadically in Labrador, the habitat benefits related to species abundance and biomass appear to be limited to areas south of the Strait of Belle Isle. In Newfoundland, eelgrass is a preferred habitat (compared to less complex habitat types) for juveniles of several gadids, including Atlantic cod, Greenland cod, and white hake (Gotceitas 1997). Few gadids are sampled in eelgrass beds south of Nova Scotia, such as the Gulf of Maine (Lazzari et al. 1999). The Newfoundland fish community is influenced by the cold Labrador Current and warm Gulf Stream, creating important differences in the fish community compared to more southerly locations.

Green crab has invaded the south coast of Newfoundland, and high densities exist at some locations (McKenzie and Perry 2008). A review of the functional significance of eelgrass in the region is merited. The objective of our synoptic study was to evaluate the probable effects of eelgrass loss on the nearshore Newfoundland fish community, specifically given the seabed disrupting behaviour of green crab. We evaluate the findings of several published studies (Gregory et al. 1997; Laurel et al. 2003a, 2003b; Burt 2005; Copeman et al. 2007; Warren et al. 2010) which are based on long term monitoring and ecological research conducted in Newman Sound, Newfoundland 1995-2009. The important role of eelgrass habitat on the biomass and distribution of fish is considered in the context of the likely deleterious effects of green crab on eelgrass beds in the Newfoundland coastal environment.

METHODS

Newman Sound is a moderately sized inlet (ca. 45 km²) in Bonavista Bay located adjacent to Terra Nova National Park. Water temperature varies from 18 °C in August to -1.5 °C in late-December (Laurel et al. 2003b). The nearshore substrate ranges in particle size from mud to bedrock with eelgrass being a dominant vegetative component in many of the more sheltered areas (Laurel et al. 2003b).

Twelve sites were regularly sampled for juvenile fish in Newman Sound, from July until November each year, 1995-2009. Eight sites were dominated by eelgrass growing in mud and silt; four sites were "non-eelgrass", consisting of unvegetated mud and sand. The eelgrass sites included: Big Brook-BB, Buckley's Cove-BC, Dockside-DS, Hefferen's Cove-HC, Minchin's Cove-MC, Mistaken Cove-MI, South Broad Cove-SB, and White Rock-WR (Fig. 1). The non-eelgrass sites included Canning's Cove-CC, Little South Broad Cove-LSB, Mount Stamford-MS, and New Bridge Cove-NB (Fig.1).

We collected fish using a 25 m demersal seine net with 19 mm stretched mesh. The net was deployed from a small boat at a distance of 55 m from the shore and then retrieved by two individuals standing 16 m apart on the shore pulling the seine towards them. The seine was pulled along the bottom and sampled 880 m² of habitat from the substrate to 2 m upward into the water column. The maximum water depth sampled was approximately 8 m. Fish caught in the seine were transferred to holding containers filled with seawater, then identified and

counted. All fish were measured except when catches were high, and then a subsample of most species was measured to reduce handling stress on the fish. All fish were returned alive to the original site of capture. Seining was done every two weeks for each site usually beginning in July and ending in November. To standardize sampling among sites seining was conducted during a 4 hour period, 2 hours before and after a low tide, during daylight while avoiding periods near dusk and dawn.

Juvenile forms were the predominant life history stage captured in the nearshore (Gregory et al. 1997). Common fish species encountered during our surveys included: Greenland cod (*Gadus ogac*), Atlantic cod (*Gadus morhua*), cunner (*Tautoglabrus adspersus*), three-spine stickleback (*Gasterosteus aculeatus*), white hake (*Urophycis tenuis*), winter flounder (*Pseudopleuronectes americanus*), short-horned sculpin (*Myoxocephalus scorpius*), rock gunnel (*Pholis gunnellus*), arctic (*Stichaeus punctatus*) and radiated shanny (*Ulvaria subbifurcata*), smelt (*Osmerus mordax*), lumpfish (*Cyclopterus lumpus*), brook trout (*Salvelinus fontinalis*), sandlance (*Ammodytes americanus*), skate (*Raja* sp.), sea raven (*Hemitripterus americanus*), and yellowtail flounder (*Limanda ferruginea*).

We conducted aerial photography surveys of the beach seining sites during several years to determine approximate rates of vegetative habitat change at our sites. The data analyses protocol and methods are described in Warren et al. (2010). Aerial surveys were conducted in 1998, 1999, 2000, 2001, 2002 and 2006. We used data from 2000 to 2006 herein, due to superior quality of the imagery. Photos were taken during monthly low tide periods as close to mid-day as possible to increase the extent at which eelgrass habitat was visible. A Pentax FX10 analog camera was used, with 28-80 mm zoom lens (set to 50 mm) fitted with polarizing and haze filters to reduce glare from the water surface. Bright orange markers (0.5 x 0.5 m) were placed 25 m apart onshore and one marker was placed 50 m offshore (90 degrees to one of the shore markers, relative to the other shore marker) at sampling sites to provide a measure of scale and correct for camera angle distortion. A box counting method was used to determine eelgrass percentage cover (Scheuring and Riedi 1994).

The experimental habitat manipulations and data analyses presented herein are described in Laurel et al. (2003b). In brief, approximately 500 m² of eelgrass was removed at each of two eelgrass sites (Buckley's Cove-BC and Dockside-DS), hereafter referred to as "removal" sites. At each of two non-eelgrass sites (Canning's Cove-CC and Mount Stamford-MS), hereafter referred to as "enhancement" sites, 80 m² of artificial eelgrass was added. The remaining six unmanipulated 'eelgrass' and two 'non-eelgrass' sites were used as controls for the relevant removals and enhancements, respectively. In removal sites, the entire eelgrass canopy was removed from a 500 m² area by scuba divers in 1999, and any eelgrass regrowth was also removed during 2000. Following 2000, eelgrass was allowed to regrow in the removal areas.

In enhancement sites, artificial eelgrass was placed on the seabed in 1999 and again in 2000; it was removed in November during both years, permanently so in 2000. Artificial eelgrass consisted of green, plastic ribbon (W= 0.8 cm H= 75.0 cm) attached to galvanized wire fencing and fixed by stakes to the seabed. Artificial eelgrass blade densities fell within the range of eelgrass patches naturally occurring in Newman Sound (i.e., 600 blades m⁻²). The artificial eelgrass patches were divided into a series of 10 smaller patches to loosely represent fragmentation common in natural eelgrass meadows. Two replicates of five patch sizes (0.3, 1.1, 5.5, 11, and 22 m²) were deployed at each of the two enhancement sites.

Data handling methods are described in Laurel et al. (2003a). Individual fish length data were transformed to biomass using species-specific length-weight regression equations derived by

Burt (2005) from existing data (Methven unpub. data). Biomass data was analyzed using randomized intervention analysis (RIA; Carpenter et al. 1989) to statistically test the significance of changes in fish biomass following habitat manipulation (i.e., eelgrass removal or eelgrass enhancement). RIA (Carpenter et al. 1989) is most commonly used to detect changes in manipulated ecosystems relative to undisturbed reference systems and is based on a before-after-control-impact (BACI) design model in which experimental and control sites are compared against each other both before and after experimental manipulation (Stewart-Oaten et al. 1986).

In our studies, relative differences between control and experimental sites were measured in the pre-habitat manipulation years (\bar{E}_{pre} ; 1995-1998) and again during the post-habitat-manipulation years (\bar{E}_{post} ; 1999-2000) by Laurel et al. (2003b) and Burt (2005) and beyond (i.e., 2002-2006) by Warren et al. (2010). The means of differences both before (\bar{E}_{pre}) and after the experimental manipulation (\bar{E}_{post}) were used to generate a test statistic (\bar{E}_{diff}) from the equation [E (PRE) – E (POST)]. The test statistic was then compared against 5000 random permutations of possible [E (PRE) – E (POST)] data using the data from all possible control-experimental site comparisons. The error distribution was self-derived from the randomization and therefore data did not have to meet the assumption of normality (Edgington 1980; Carpenter et al. 1989). An RIA was generated for each species and for each experimental and control-site comparison. Removal sites ($n=2$) were compared with naturally vegetated sites ($n=6$) and enhancement sites ($n=2$) were compared with naturally unvegetated sites ($n=2$). Catch data were log-transformed ($y = \text{Log}_{10}(x + 1)$) prior to analysis to control for high within-site catch variability within and among years; as a result differences can be interpreted as "order of magnitude effects".

RESULTS

In the studies spanning 15 years (1995-2009), conducted in Newman Sound Newfoundland, finfish biomass was variable both spatially (among sites) and temporally (within seasons and among years). This variability was consistent with the positive role of eelgrass on most shallow water marine fish species, primarily juvenile stages. Declines in biomass were observed for most species immediately following experimental eelgrass removal in 1999 and 2000 and for several years subsequently during its recovery (Fig. 2). In contrast, experimental eelgrass habitat enhancement in 1999 and 2000 generally resulted in increases in fish density and biomass. Natural expansion of eelgrass in several sites during a six year period (2001-06), also resulted in significant increases in density of species examined.

Enhancements resulted in significant declines in the fish biomass in removal sites compared to control sites (Fig. 2); fish biomass declined by 80% when eelgrass was removed. Although some species of fish tended to increase in biomass following eelgrass removal, the only significant changes were observed when species biomass decreased. Eelgrass began to re-colonize removal sites in 2001, approximately one year after the experiment was concluded. However, some sites showed significantly lower fish biomass for several years following manipulation. In 1999 and 2000, fish biomass increased in enhancement sites (Fig. 2). After the removal of eelgrass in late autumn in 2000, there were no longer significant differences between enhancement sites and control. The reversion back to pre-manipulation biomass levels suggested it was the enhancement itself which resulted in the increase in fish biomass at these sites.

During the 15 yr study, eelgrass naturally expanded into three formerly non-eelgrass sites over a period of several years, 2002-06 (Fig. 3). Increased density of age 0 juvenile Atlantic and Greenland cod was correlated with this observed increase in eelgrass habitat (Fig. 4).

There was high variability among individual species in response to enhancement and removal of eelgrass. The gadids (Atlantic cod, Greenland cod and white hake), cunner and sticklebacks, all responded negatively to eelgrass removal (Fig. 5), declining as a group by up to 80% in density and biomass. Temporal sensitivity to habitat manipulation was species-specific, likely a consequence of differences in settlement timing and seasonal residency in eelgrass areas along the coast. For example, white hake, stickleback and rock gunnel all responded to habitat changes in July-September, whereas Atlantic cod and Greenland cod responded most strongly to habitat changes later in the season (September-October). Cunner and rock gunnel were captured less frequently by mid-October, at the same time large adult sculpin in spawning condition were captured in increasing numbers at our sites (Fig. 6).

DISCUSSION

The Newfoundland studies summarized here suggest that the loss of eelgrass habitat will have a substantive deleterious effect on productivity. These studies were not designed specifically to investigate the rate of eelgrass loss due to the presence of green crab. However, the available evidence from other areas within the range of green crab describing the burrowing behaviour, indicate that green crab behaviour can negatively affect eelgrass. Recent expansion of the range of green crab in coastal waters in southern Newfoundland (mainly Placentia Bay), make the recent invasion of green crab in Newfoundland a significant cause for concern. It seems apparent from other investigations in Placentia Bay (Cynthia McKenzie DFO - St. John's, personal communication) and elsewhere in Atlantic Canada (Garbary and Miller 2006; Klassen and Lock 2007) and further south (e.g., Davis 1998), that reduction in eelgrass due to green crab can be reasonably expected in the Newfoundland coastal zone, if green crab continue to spread along the coast unabated and in numbers.

The results we have described in this study lead us to suggest that loss of eelgrass due to seabed modification by invasive green crab will negatively influence productivity of the immediate areas in which the plant currently grows. Other long term studies addressing the effect of eelgrass on fish abundance or biomass have reported results similar to those we have described here. Hughes et al. (2002) considered fish community changes during an 11-year sampling period (1988-99), within which natural eelgrass beds disappeared along the coast of Massachusetts between 1996 and 1998. They report a ~50% reduction in the number of species sampled and a ~80% reduction in fish biomass after eelgrass disappeared. They concluded that the loss was a substantive decrease in the capacity of Waquoit and Buttermilk Bays to support a productive and diverse fish community. Species composition and the water temperatures were different in their study than in our study area. However, the fish community response to habitat change was similar - loss of eelgrass produced a substantial decline in fish biomass. Whitfield et al. (1989) identified that the organizing effects of eelgrass habitat on fish abundance and diversity apply throughout the plant's range.

Green crab foraging habits can significantly alter endemic benthic community structure and ecological interactions, such as support for higher trophic levels and fisheries production (Cohen et al. 1995; Grosholz and Ruiz 1995). Green crab burrowing and feeding activity has been shown to affect the top few centimeters of sediment down to as deep as 15 cm searching for prey (Short and Wyllie-Echeverria 1996; Davis and Short 1997; Davis et al. 1998; Garbary and Miller 2006; Dewitt 2009), causing changes in infaunal populations due to sediment bioturbation (Le Calvez 1987; Gee et al. 1985). Green crab also influence eelgrass by tearing or cutting the plant's sheath bundle while foraging (Davis et al. 1998; Garbary and Miller 2006); although they

are not directly attracted to eelgrass plants *per se* (Davis et al. 1998). Mesocosm experiments by Davis et al. (1998) found that as much as 39 % of transplanted eelgrass shoots were lost within one week when exposed to crab densities of 4 individuals $\cdot\text{m}^{-2}$, in Great Bay Estuary, New Hampshire. In their study, crab densities of 5.4 m^{-2} were found in the vicinity of an eelgrass transplant site, where crab activity was believed to have caused the loss of 0.5 ha of transplanted eelgrass within 4 months of transplanting.

Green crab densities have not been explicitly measured in Placentia Bay. However, removal efforts which collected approximately 350,000 green crab from an area less than 2 km^2 (i.e., 0.35 crab $\cdot\text{m}^{-2}$) had little apparent impact on the number of crab in the area (Cynthia McKenzie, DFO St. John's personal communication). Therefore, the density of green crab in this area may potentially be high enough to damage eelgrass meadow habitat.

Hughes et al. (2002) and our recent studies (Laurel et al. 2003; Burt 2005; Copeman et al. 2007; Warren et al. 2010; and this study) all found that fish species in general were positively related to eelgrass habitat complexity and there is a strong tendency for mean fish abundance and biomass to be highest in complex habitat, especially in aquatic vegetation. Furthermore, the functional role of eelgrass habitat to support a diverse and abundant fish assemblage appears to be impaired before the habitat is lost completely (Hughes et al. 2002). Thistle et al. (2010), working in our study area observed that intermediate area complexity due to eelgrass presence was most often more productive for juvenile gadid fishes than lower or higher complexity sites.

All fish species do not benefit from the presence of eelgrass. The density and biomass of some species either do not respond to eelgrass enhancement or decrease when eelgrass coverage expands (Whitfield et al. 1989; Hughes et al. 2002; this study). For example, oyster toadfish (*Opanus tao*) and American eel (*Anguilla rostrata*) densities increase with the loss of eelgrass while striped bass (*Morone saxatilis*) and scup (*Stenotomus chrysops*) may not be affected by the loss of eelgrass (Hughes et al. 2002). In Newfoundland studies, shorthorn sculpin, winter flounder, and rainbow smelt were not adversely affected by eelgrass loss, but all other species common in the nearshore coastal zone were negatively impacted, some substantially so.

The disruptive effects of invasive green crab on seabed habitat have been observed repeatedly during its history of invasion in several areas around the world. These habitat disrupting behaviours include burrowing and foraging activity (Davis et al. 1998). If this behaviour affects eelgrass habitat elsewhere, similar habitat effects are expected here in coastal Newfoundland, particularly in areas where green crab densities are high. In Newfoundland, cooler water temperatures may influence green crab behaviour and biology, but there is no evidence to indicate such a change in other studies. Therefore, the effects of green crab on habitat are likely to differ only if their densities are somehow affected by low temperature.

Although the majority of fish that prefer eelgrass habitat in Newfoundland are also small-bodied (primarily juveniles; Gregory et al. 1997), several species are commercially important, including Atlantic cod and white hake. Furthermore, some Atlantic cod populations are at very low levels of abundance, several of these even being designated as "special concern", "threatened", or "endangered" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2010).

CONCLUSION

Eelgrass provides nursery habitat for several fish species in the more sheltered and protected habitats along Newfoundland's coast, most notably Atlantic cod. Eelgrass offers protection from predators, significantly reducing mortality rate. Green crab is well known to destroy eelgrass habitat by cutting plant blades and digging up subsurface rhizomes which anchor the plant to the seabed. The studies we describe here spanning 15 years, have collectively shown that a loss of eelgrass habitat will result in a disproportionate decrease in productivity and abundance of fish which utilize this habitat, compared to other available habitat types.

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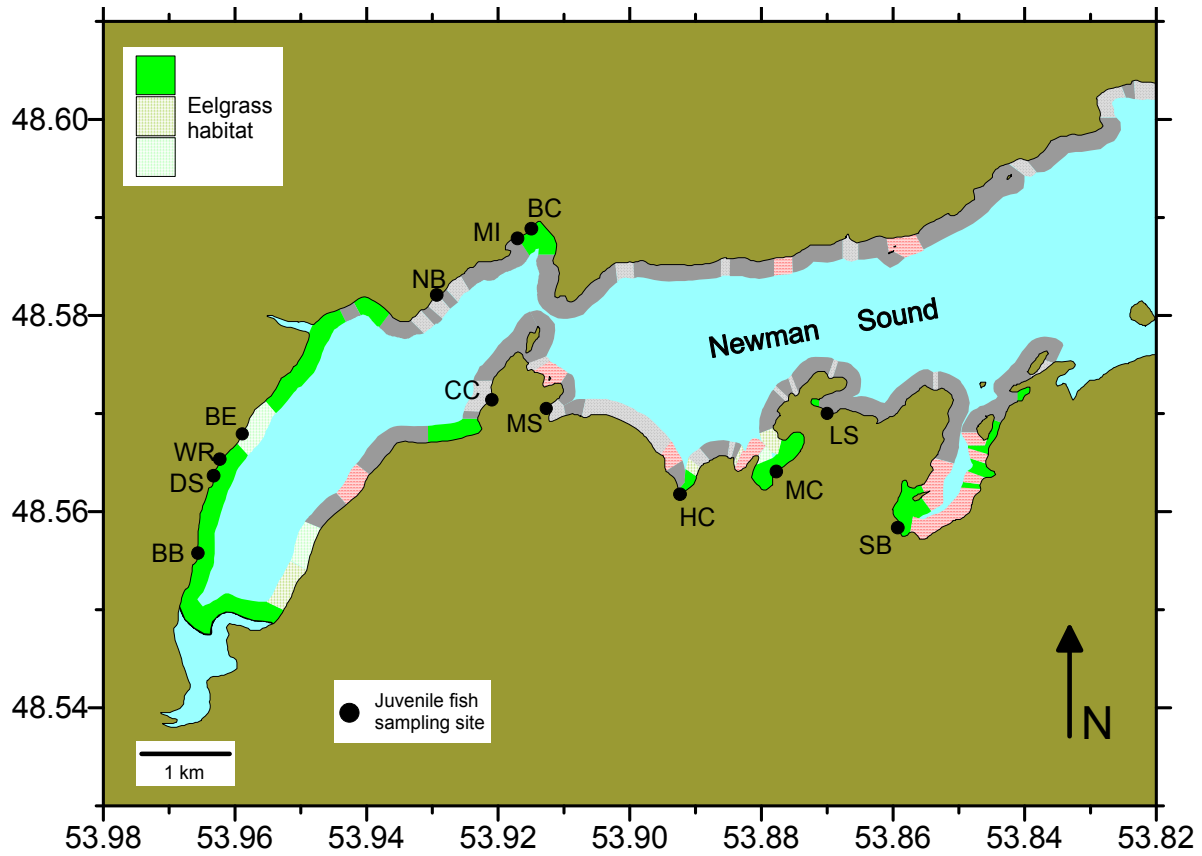


Figure 1. Map of Newman Sound showing sites sampled during 1995-2009, indicating eelgrass habitat types. Other habitats are non-eelgrass coarse bottom substrate types.

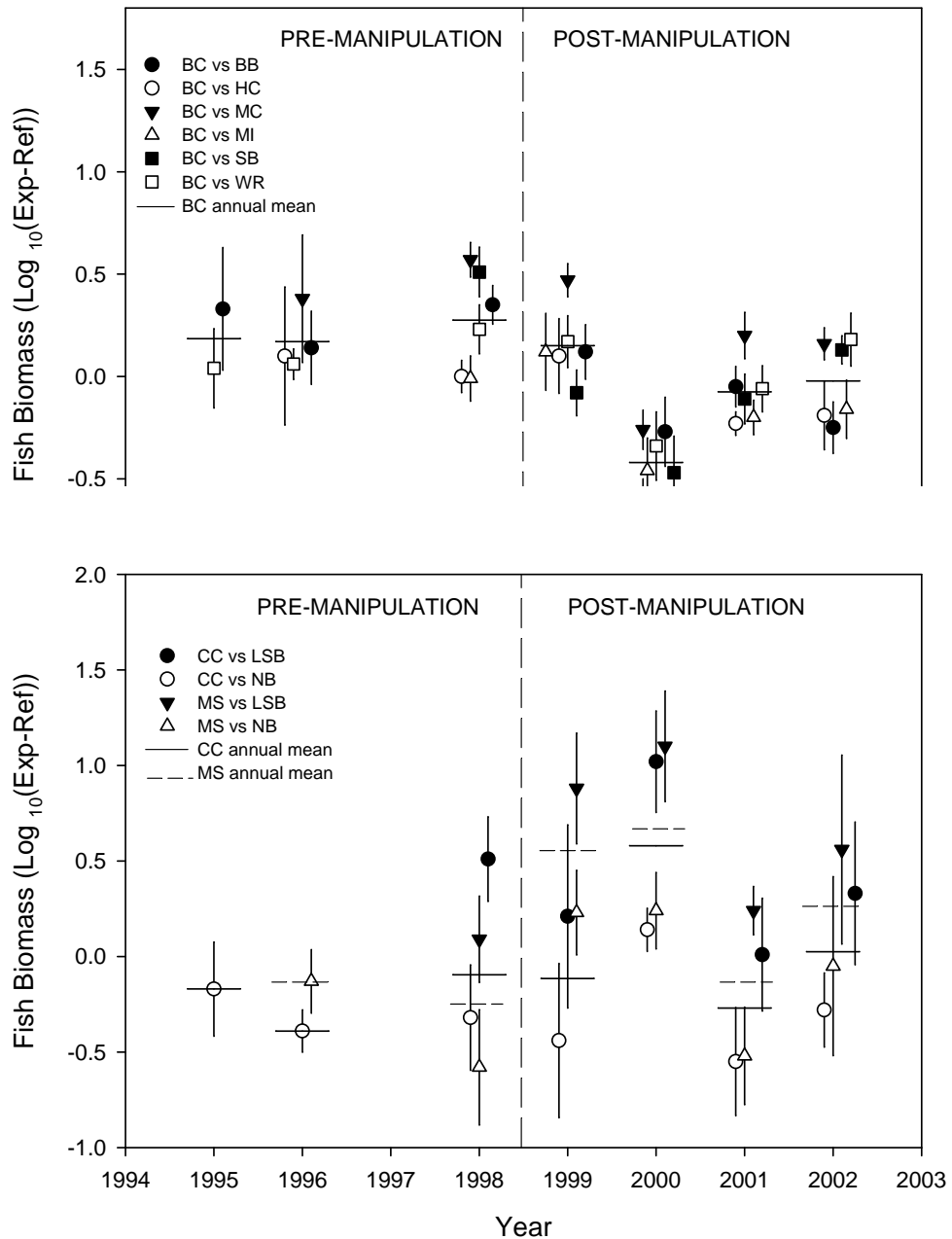


Figure 2. Relative differences of resident finfish biomass at an experimental removal site, BC, compared with 6 natural eelgrass control sites (top panel), and experimental enhancement site, CC, compared with three natural non-eelgrass reference sites during pre- and post- manipulation years (1999-2000) in Newman Sound Newfoundland. (Values represent the biomass (g) of annual mean bi-weekly seine catches \pm S.E.; points for each year are staggered for visual purposes; a y-axis value of zero indicates "no difference" in paired comparisons - figure adapted from Copeman et al. 2007).

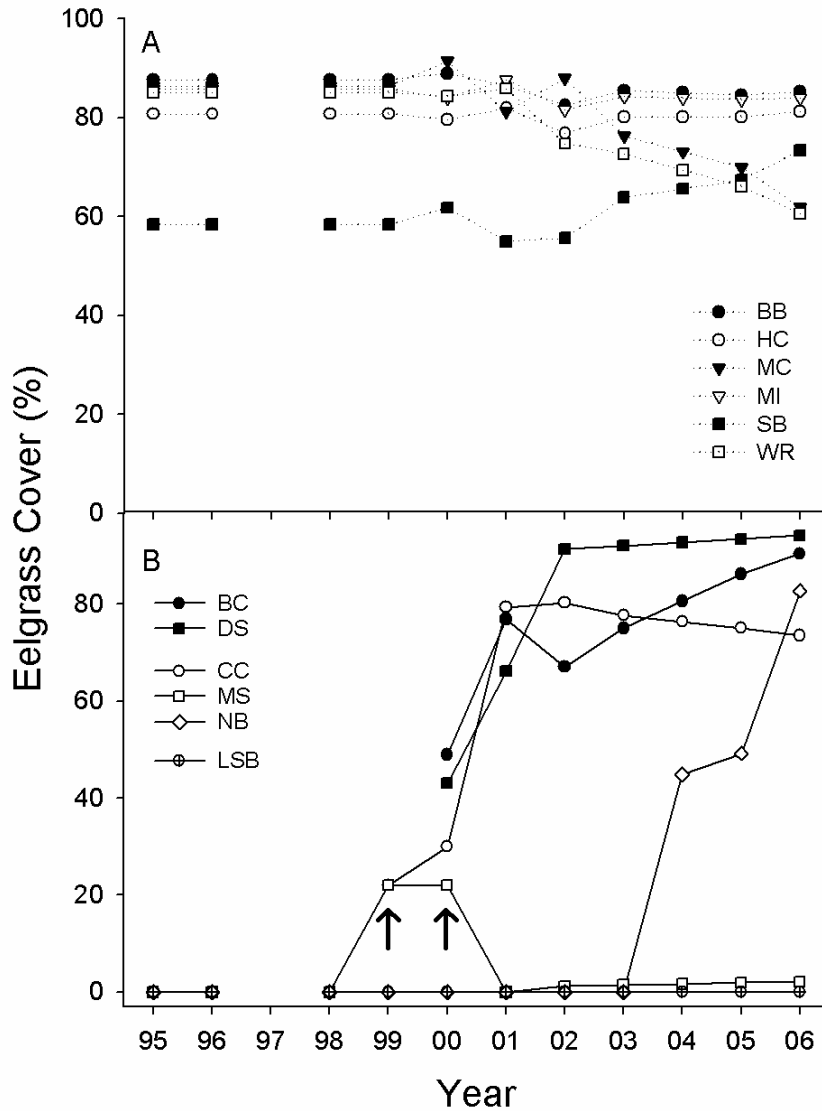


Figure 3. Annual percent eelgrass cover at A) natural eelgrass and B) removal-recovery (closed symbols), expansion (open symbols), and unvegetated sites (cross hatched symbol) over an 11 year period, (No data were available for 1997; 1995-96 and 1998-99 data were estimated from Sheppard (2002) and Gregory et al. (1997); 2000-02 and 2006 data were obtained from aerial photographs; 2003-05 data were interpolated between photograph years); all data were qualitatively supported by annual visual inspections or scuba transects. Arrows indicate Laurel et al. (2003b) manipulation years (removal and addition); data as reported by Warren et al. (2010).

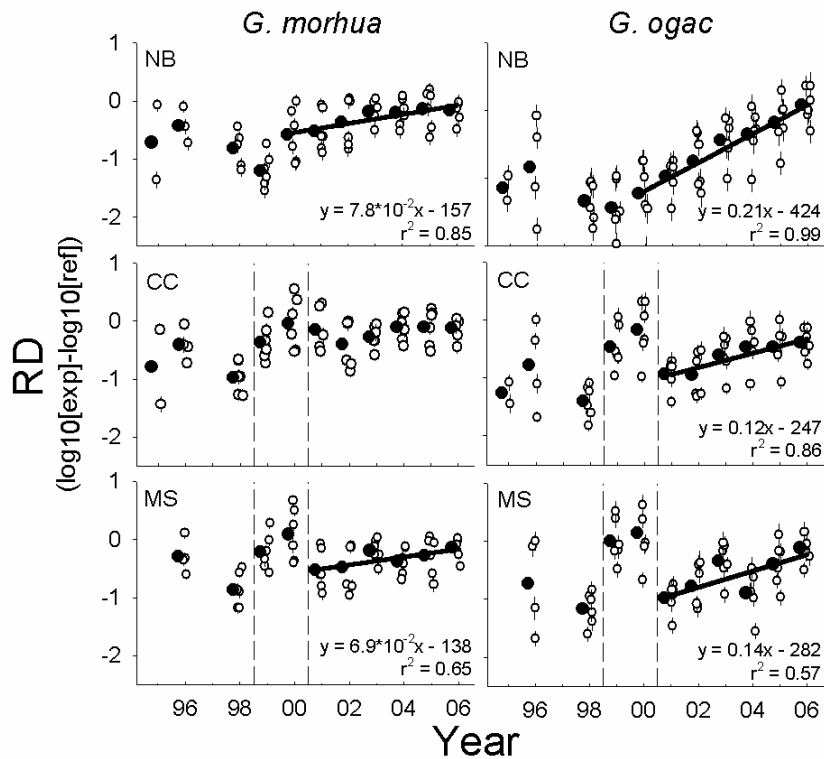


Figure 4. Relative differences (RD) of age-0 abundances at eelgrass expansion sites (NB, CC, MS) and natural eelgrass reference sites. The area enclosed by dashed lines indicates years of artificial eelgrass addition (CC and MS; Laurel et al. 2003b). Open circles represent differences between mean catches ($n=4-13$) \pm SE each year. Annual means are indicated by closed circles; RD=0.0 indicates "no difference" among paired comparisons. Points are jittered along the x-axis for visual purposes. Line fits represent significant trends in the abundance of juvenile cod at the experimental site vs reference sites during years of eelgrass expansion (2001-06); data as reported by Warren et al. (2010).

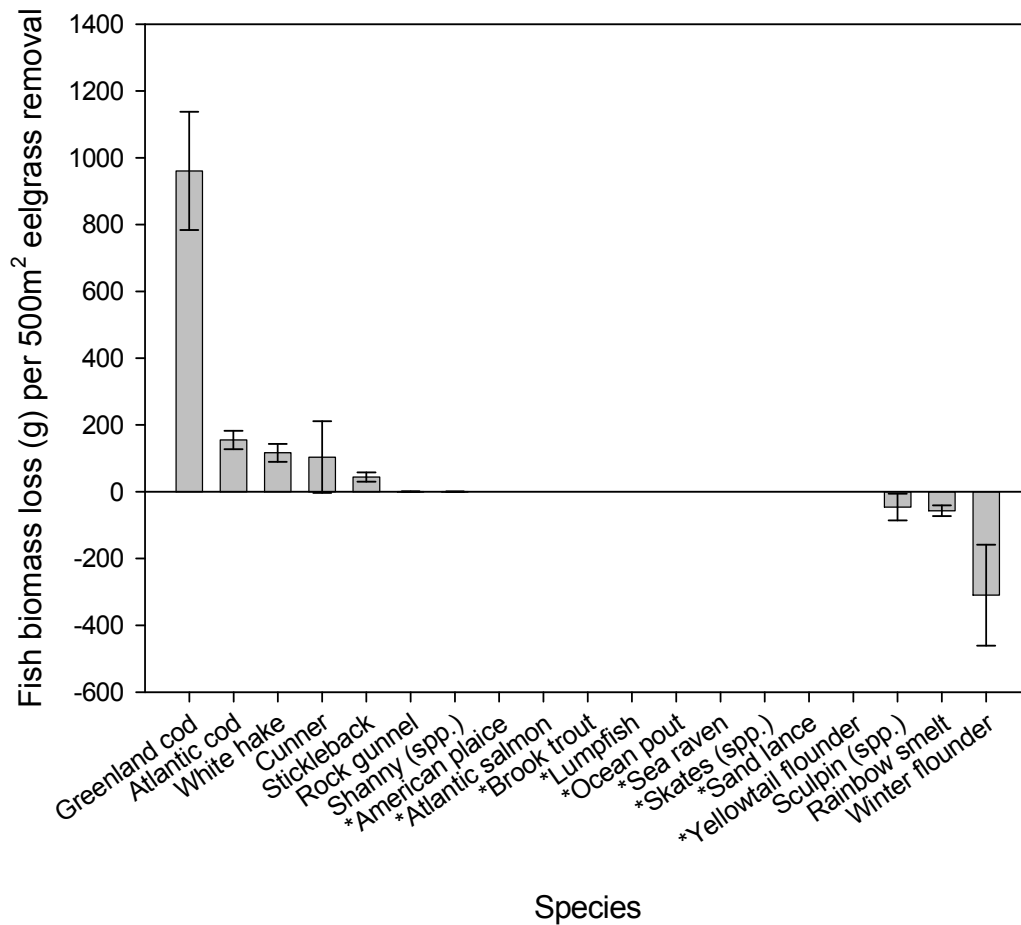


Figure 5. Species-specific change in fish biomass resulting from the removal of 500 m² of eelgrass at sites in Newman Sound Newfoundland, 1999 and 2000 using data presented by Laurel et al 2003b and Burt 2005) and seasonally integrated over the survey period July-November; figure adapted from Copeman et al 2007).

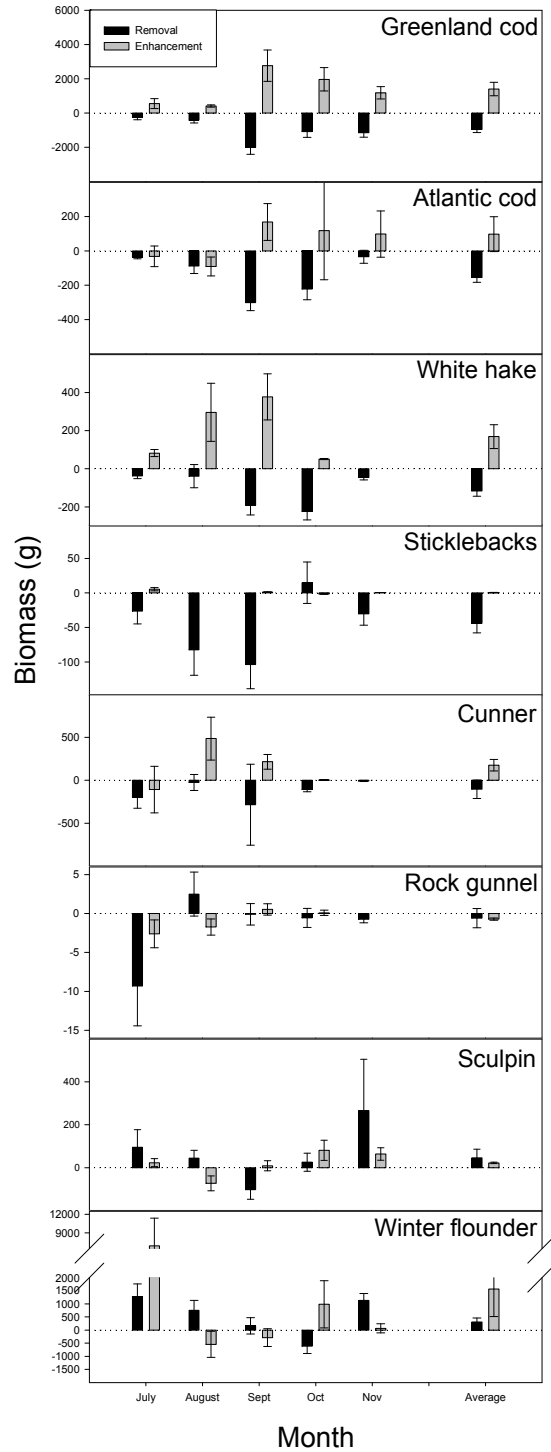


Figure 6. Seasonal change in relative biomass of common fish species in eelgrass removal sites and enhancement sites relative to corresponding control sites in Newman Sound Newfoundland, 1999-2000 (values are the pre- and post-intervention (enhancement or removal) monthly averaged relative differences among experimental and reference sites; positive and negative values indicate the relative increase or loss of biomass, respectively at an enhancement site compared to reference sites; figure adapted from Copeman et al. 2007).