Benthic community structure within Eelgrass (*Zostera marina*) beds in southern Nova Scotia

Honours Thesis
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Abstract:
Seagrass beds are productive coastal habitats that provide numerous ecosystem services. Declines in seagrass beds worldwide will have profound influences on the trophic structure and overall functioning of coastal ecosystems. My objective was to relate benthic community structure to seagrass bed characteristics and to understand the potential effects of fragmentation on trophic structure. Core samples were taken from Port L'Hebert (PH) and Port Joli (PJ) from bare (no seagrass, >5m from bed edge), edge (within seagrass, <1m from edge), and interior (>10m from any seagrass-mud interface). Macroinvertebrate (>500 um) abundance, functional group abundance, community structure, seagrass leaf length and shoot density, and sediment grain size and organic matter were quantified in each core. Total macroinvertebrate abundance was highest in PH's edge habitat. Predator and detritivore abundances did not differ among sites or habitats. Grazer abundance was significantly higher in the interior and edge than in bare at both sites. Suspension feeder abundance was significantly higher in the bare and edge habitats than interior habitats at both PH and PJ. Species richness was significantly higher in edge and interior than in bare habitats, and higher in PJ than PH. Average leaf length and shoot density was greater in interior habitats than edge habitats at both PH and PJ. Sediment particle size was overall larger in PJ and PH. Organic content was significantly different between PH edge and PH interior and bare. Ordinations showed that community structure differed among habitat types at PJ. This study provides insight of how seagrass loss will influence trophic structure of seagrass beds, and offers basic information for restoration and conservation projects.

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1. Introduction

The following report presents an exploratory study of macroinvertebrate community structure within eelgrass (*Zostera marina)* beds on the South Shore of- Nova Scotia. The study is aimed at understanding the role of eelgrass density in influencing the distribution and abundances of macroinvertebrates within tidal flats of this area. A greater understanding of the macrophyte-invertebrate relationship in coastal seagrass beds can be used to develop appropriate conservation and best management practices for these highly productive and commercially-important ecosystems.

Seagrasses – a group of marine-adapted angiosperms in family Zosteraceae – are a unique macrophyte in the marine environment. They grow almost exclusively in soft sediments in the mid- to low-tidal zone of near-shore waters (Beer & Koch 1996). These species take about half of their nutrient requirements from the sediment through a system of root-like rhizome, and the other half through leaf tissues; this is in contrast to macroalgae, which lacks a root system and absorbs all nutrients directly from the water column through the thallus (Chambers *et al.* 1999; McRoy, Barsdate & Nebert 1972). Seagrasses also have some of the highest light requirements among flowering plants (Taylor *et al.* 1995). In optimal sediment and light conditions, eelgrass can grow very rapidly, up to 1300g dry weight/m^2year (Watanabe *et al.* 2005). Seagrass meadows are among the most diverse and highly productive coastal ecosystems in the world (Bostrom & Bonsdorff 2000), supporting several commercially important vertebrate and invertebrate species, and producing massive quantities of organic carbon (Orth *et al.* 2006).

Species within Zosteraceae significantly influence physical, chemical and biological oceanographic qualities within their environment; for this they can be considered keystone species. Zosteraceae can be regarded as autogenic ecosystem engineers, as they provide living space for other species through their own physical structure (Berkenbusch & Rowden 2007). They alter water flow, hydrodynamic forces, nutrient cycles, sedimentation, and the overall structure of their coastal homes

(Atrill *et al.* 2000). The slowing of water flow increases the settlement of fine sediments within beds, and the rhizome system stabilizes sediment (Bologna & Heck 2002). The stabilized sediment provides ideal habitats for many tube-building worms and other infaunal species (Orth *et al.* 1984). Many marine invertebrates have planktonic larva which have settling patterns similar to sediment grains of comparable size; seagrass beds influence the settlement location of planktonic larvae like mussels (Bologna & Heck 2000). The complex structure of the seagrass bed provides a sheltered habitat preferred by isopods (Bostrom & Matilla 1998).

Autogenic ecosystems like seagrass beds have been shown to have higher secondary production, or consumer species, than unvegetated landscapes (Peterson *et al.* unpublished). The energy transfer between trophic levels in seagrass ecosystems is four to five times higher than the 10:1 transfer ratio found in terrestrial ecosystems (Peterson *et al*. unpublished). Most of the productivity of northern seagrass beds comes from macroinvertebrates due to low fish diversity (in comparison to tropical or subtropical beds where more secondary production is based on fish populations). Therefore, the study of macroinvertebrate communities in Nova Scotia is critical to understanding the trophic exchanges made within seagrass ecosystems.

Several hypotheses have been developed to explain why seagrass meadows are so productive. Attrill *et al.* (2000) suggest that the structural complexity of a seagrass bed provides a multitude of distinct niches which animals can inhabit. The high leaf surface area and the network of rhizomes in the sediment creates habitat that is infinitely more complex than bare sediment. Stoner (1980) proposes that the number of individuals and number of species of seagrass-associated fauna in a bed is dependent solely upon seagrass biomass. Attrill *et al.* (2000) support the idea that plant biomass has a profound effect on species composition, but warn that it cannot be used as a univariate measure of complexity. In contrast, Irlandi (1996) shows that productivity of a seagrass habitat is dependent upon patch size, but shows no correlation between productivity and shoot density or blade length. Bell and Westoby (1986)

found that the abundance of decapods was more closely related to leaf height and density than patch area or sediment type. These conflicting theories suggest that perhaps there is a probable connection between biomass, structural complexity and shoot density that should be explored further.

The benefits of highly diverse and productive Zosteraceae beds extend beyond the physical limits of the ecosystem. Many small and juvenile fishes feed within seagrass beds and take advantage of its protective nature. Small fishes have been observed feeding in low-density patches of seagrass because such areas host many prey items while offering protection from larger fishes (Bostrom *et al*., 2006b). Animals that utilize eelgrass in Nova Scotia at some point in their life cycle include eels, shellfish, salmon, trout, and various types of seabirds (Edsel 1989; Beck et al. 2001; Heck et al. 2003). In addition to commercial benefits, highly productive eelgrass beds act as a carbon sink, which is important in an age where humans are facing the effects of high atmospheric carbon. Finally, a dense eelgrass bed has intrinsic value as a living ecosystem and can be appreciated in its own right by biologists and laypeople alike.

The unique qualities of seagrasses currently put them in a position of despair. Over the past three decades, the marked decrease in seagrass worldwide has far surpassed the recorded increases (Orth 2006). Declines in seagrass abundance have been noted in European Mediterranean (Marbà et al. 2005), Japan (Environment Agency of Japan 2000), Chesapeake Bay (Orth and Moore 1983), and Australia (Walker et al. 2006, Bulthuis 1983). It is hypothesized that seagrass decreases in temperate regions are multi-dimensional, being caused by a combination of eutrophication (Hauxwell *et al.* 2001), sediment re-suspension and deposition (Frederiksen *et al.* 2004), sea level rise (Glenmarc *et al.* 1997), extreme weather (Reusch *et al.* 2005, Birch & Birch 1984), coastal development (Orth *et al.* 2006), thermal pollution (Zeimen & Wood 1975), and dredging (Gordon *et al.* 1994).

Because seagrasses require high light levels, they are exceedingly vulnerable in areas of high eutrophication, sediment re-suspension and turbidity. Eutrophication will cause blooms of

phytoplankton and formation of algal mats which either cloud the water column or cover plants and the sea bottom, reducing light availability for seagrasses (Chambers *et al.* 1999). Sediment re-suspension also increases turbidity, causing reduced photosynthetic output by seagrasses and other macrophytes (Short & Burdock 1995). With the loss of seagrass comes the loss of crucial nursery habitats, protection from coastal erosion, sediment and nutrient supply for neighbouring ecosystems, and overall biodiversity on tidal flats (Orth *et al.* 2006).

Due to climate change and its various effects seagrasses face a number of challenges. These marine plants generally have poor mechanisms for dealing with inorganic carbon in HCO_3^-, which is currently the dominant form of inorganic carbon in the ocean (Beer & Koch 1996). As the global climate changes, ocean pH decreases, and dissolved CO_2 increases, seagrass may no longer find inorganic carbon as a limiting nutrient. Higher dissolved CO_2 and lower pH may be conducive to seagrass growth; however climate change, ocean freshening, sea level rise, and development of coastlines by humans pose chemical and physical challenges that could be quite severe (Orth 2006). Increased storm frequency and severity that is likely to be caused by climate change will cause further declines in seagrass beds. As sea level rises, seagrasses will be forced to migrate shoreward in order to maintain their required light levels for growth. Human structures such as breakwaters and wharves may prevent the successful migration of seagrasses, causing their eventual demise (Orth 2006). In addition to physically blocking their migration, human structures may also alter currents and sedimentation patterns such that the surrounding area will no longer be suitable for these soft-sediment dwelling plants (Fonseca *et al.* 2000). Furthermore, with increasing human populations and tendency for coastal development, these pressures will only become more widespread.

The loss of high-value ecosystem services of seagrass beds have global implications, such as reduced carbon storage due to loss of primary and secondary production (Duarte & Chiscano 1999), reduced carbon sequestration in sediments due to lack of sediment stability (Duarte *et al.* 2005),

inability of seagrass beds to filter water entering the ocean (Hemminga & Duarte 2000), decreased biodiversity due to habitat loss (Hemminga & Duarte 2000), reduced nutrient transport to the deep sea exacerbating currently declining fish stocks (Suchanek *et al.* 1985), altered trophic interactions and food webs (Duarte 2002), and increased coastal erosion due to the loss of sediment-stabilizing rhizomes (Duarte 2002). Because seagrasses exist worldwide in sheltered coastal environments and are often the first marine ecosystems to be effected by human activity, they are an ideal species to study in terms of large-scale trends (Orth *et al.* 2007). For these reasons, both the Australian and American governments have recognized their respective species of seagrass as 'ecological sentinels' for use in determining pollution effects and ecological health (Bricker *et al.* 2003, Orth *et al.* 2007).

Effects of eelgrass loss in Nova Scotia are more specific than global seagrass declines. However, due to the limited study of eelgrass in this area, prediction about the fate of seagrass is challenging. Seymour *et al.* (2002) showed that a decline in eelgrass near Antigonish resulted in a massive decline in the population of Canada Geese (*Branta canadensis*) and common goldeneye (*Bucephala clangula*). Eelgrass rhizome biomass declined 95% in 1998-2000, resulting in 50% population declines in both avian species and a massive reduction in use of main foraging grounds. Studies in New Brunswick have shown that eelgrass declines are associated with eutrophication events in coastal bays and estuaries (Milewski 2004).

The goal of this research is to quantify the relationship between eelgrass beds in Nova Scotia and macroinvertebrates that live within them in consideration of conflicting paradigms of macroinvertebrate distribution (Stoner 1980, Attrill *et al.* 2000, Irlandi 1996, Bell & Westoby 1986). In light of global climate change this information will be valuable for understanding trophic linkages and foodwebs in seagrass beds and how these linkages might change under changing conditions. The primary objective of this research is to compare eelgrass bed characteristics with macroinvertebrate abundance, density, species composition and biomass. This was accomplished by taking physical

samples from *Z. marina* beds in Port L'Hebert and Port Joli, Nova Scotia, from the exterior of the bed (bare sediment), the edge of the bed (within 1m of the bed's edge) and the interior of the bed (>1m from the edge). These samples were analyzed for plant and animal biomass, species diversity and abundances. It was hypothesized that the highest abundance, diversity and biomass of macroinvertebrates would be found in the interior of the seagrass bed, while samples from bare sediment would have the lowest. The secondary objective of this research is to provide baseline information about eelgrass densities and dynamics in Nova Scotia, as such information is currently minimal. Additionally, information regarding the structural dynamics of eelgrass beds will be useful in implementing conservation measures most effectively.

The outcomes of this research will be of interest to organizations wishing to preserve eelgrass beds in light of the global decline of seagrass. Should the stated hypotheses be confirmed by research findings, this information could be used to create a system of identification of communities with maximum productivity and biodiversity, which would be of great importance to conservationists. The area-specific information could be used by local conservation groups like the Port Joli Basin Conservation Society or the Ecology Action Centre's Coastal Action Committee. However, the contribution to general seagrass ecology could be used by national or global groups such as the Nature Conservancy of Canada and the World Wildlife Fund. Conservation projects require a solid understanding of the ecosystem in question, yet there is a serious lack on information regarding eelgrass on the South Shore Nova Scotia. Such is the motivation for the following research.

This paper will first delve into finer details of seagrass-macroinvertebrate relationships in the Literature Review (Chapter 2). Following the literature review will be an explanation of sample collection and storage, seagrass size and biomass analysis, and a review of macroinvertebrate identification. These methods can be found in chapter 3. Chapter 4 presents the results of my analyses

and chapter 5 speculates on the significance of these findings and extrapolate their consequences for future study of seagrass bed dynamics.

2. Literature Review

2.1 Seagrasses: General Biology and Ecosystem Services

Seagrasses are a highly unique group of angiosperms which have adapted to life in marine environments with soft substrates (Beer & Koch 1996). Seagrass beds are highly productive, ecologically diverse ecosystems that exist from artic regions down to subantarctic regions. Orth & Heck (2007) emphasize that seagrass beds are providers of important ecosystems services such as carbon capture and storage, sediment stabilization, habitat complexity, nutrient cycling, and biodiversity support. It has been shown that seagrass beds perform significant carbon capture and storage is facilitated by rapid growth rates, up to 1.3 kg dry weight/m^2year (Watanabe *et al.* 2005). Carbon burial in vegetated sediments is a significant carbon sink (Duarte, Middelburg & Caraco 2005).

In addition to productivity, seagrasses have structural complexity that adds much to the ecosystem. Sediments are stabilized through the network of rhizomes which provides diverse habitats for benthos while preventing coastal erosion (Bologna & Heck 2002). Established beds provide 3-dimensional structure and multiple niches, whereas unvegetated sediment would have very little structure or specific niches. Not only does the above-ground portion of seagrass plants provide shelter for animals, but the leaves also damper wave action, causing changes in sedimentation. Because seagrass beds are efficient sediment traps, they collect fine particulate organic matter and its associated nutrients, phosphorus and nitrogen (Erftemeijerb & Middelburg 1995). Thus, the presence of a bed provides structural complexity and nutrient capacity necessary for a diverse ecosystem (Attril *et al.* 2000).

Biotic and abotic factors affect the productivity of seagrass beds. In a biotic sense, their highly diverse and productive nature is not solely caused by the seagrass, but by other primary producers like epiphytic algae and phytoplankton which benefit from the safety and stability of these habitats. These areas also have high secondary production, largely caused by the presence of benthic invertebrates

(Larkum, Orth & Duarte 2006). The secondary production, measured by dry biomass, of macroinvertebrates can be up to 200g/m2 per year (Fredette *et al.* 1994). This secondary production is quite substantial and adds to the ecosystem services and general stability provided by seagrass beds.

Secondary production (the rate of increase in somatic tissue of macroinvertebrates) is often used as a measure of habitat value. This value is often the comparative productivity between two or more habitats. Secondary production is measured for habitat restoration purposes by comparing the habitat being restored to a habitat that is deemed to have a higher value, or higher secondary production. This allows for the identification of how much value has been lost and what is an acceptable level of restoration. Habitat value is also used in conservation efforts to establish how much secondary production can be protected by the implementation of conservation measures. Habitats that support more secondary production offer a diversity of ecosystem goods and services, and are preferentially protected and restore by conservation and restoration law (Fonseca *et al.* 2000).

Secondary production is a good measure of the ecological value of a habitat. It is a good proxy of value because biological production scales with ecosystem services. Usually value is determined by the amount of primary production; this means that marshes and seagrass beds are highly valued because of their high plant abundances. However, other highly productive habitats, such as oyster beds, do not have high primary production but they do have high ecosystem functions and secondary production. In light of this, scientists often use secondary production as a representative of habitat value because it accounts for services not only from food production in plants, but from other services like structural provision and habitat connectivity. Because it is a better proxy of ecosystem services, secondary production is often used in conservation and restoration projects as a determinant of how much of a specific habitat is required to produce a certain standard of ecosystem services (Peterson *et al.* unpublished).

Restoration or mitigation of seagrasses damaged by human endeavours has typically been completed by calculating a replacement ratio (how much seagrass habitat is needed to replace that which was destroyed) and creating a new seagrass bed nearby. Replacement ratios vary in size and scale, and have sometimes been quite high due to the low success rate of mitigation projects. Fixed compensation ratios are often unrepresentative of the true value lost from seagrass damages. For example, if an injured bed is restored within a year, and all ecosystem functions are back to a pre-injury state in two years, the overall loss of ecosystem services is quite low. However, if that same ecosystem has receives no reparative treatment for six years and it takes an addition two year to reach pre-injury production, the losses are far greater (Fonseca *et al.* 2000). As we increase our understanding of seagrass services and compensatory restoration, the replacement ratios may change to be smaller in area but greater in functionality and biodiversity.

2.2 Seagrass Beds as Landscapes

Bostrom *et al.* (2006a) proposed that looking at beds through large-scale patterns and processes rather than fine-scale interactions can paint a picture of an ecosystem that are more useful in model-building and extrapolation. He suggests that landscape ecology looks at the consequences of ecosystem heterogeneity on dynamic biological and oceanographic processes. Forman (1995) defines a landscape as being a heterogeneous area composed of a set of interacting ecosystems that are repeated in similar form throughout. Because seagrass beds are often heterogeneous in density and plant species, and occupy vast areas of the intertidal zone, they can be considered a marine landscape.

The spatial heterogeneity of a landscape is highly influential upon the species composition of the ecosystem. Heterogeneity is a measure of structural complexity, showing the degree to which a vegetated and inhabited ecosystem differs from a homogeneous habitat (like a bare sediment bottom). Seagrasses add heterogeneity to an otherwise homogeneous sediment bottom; this especially true of *Zostera marina* (Orth 1984). Several studies attribute changes in seagrass-macroinvertebrate dynamics

to spatial heterogeneity rather than to seasonal growth patterns, extinction, or immigration (*e.g.*: Kaldy & Dunton 2000, Attrill *et al.* 2000). The spatial heterogeneity of seagrasses cannot be ignored in studies seeking to understand large-scale patterns and changes within beds.

Consequently, landscape ecology must be understood in order to contend with habitat loss and conservation. However, landscape-scale projects have rarely been undertaken due to the recent realization of their importance and the logistical difficulties associated with accurately sampling areas as large as 100x100km (Bostrom *et al*. 2006a). This type of study is especially important when considering widespread stressors, as their affects create far-reaching problems. These stressors are further discussed in the following section.

2.3 Threats to Seagrass Beds

Orth *et al.* (2006) state that multiple stressors affect the health of seagrass beds, including eutrophication, algal blooms, sediment runoff, physical disturbance, invasive species, commercial fishing practices, aquaculture, and global warming. These external pressures affect the health and growth of seagrass beds.

Eutrophication is the addition of extra nutrients to an aquatic environment, and persists largely in coastal areas with high human development. The primary suspect of eutrophication is nitrogen, as it is abundant in fertilizers and other runoff (Duarte 2002), and it the limiting nutrient in most ecosystems (Deegan *et al.* 2002). The excess nitrogen stimulates the growth of opportunistic algae like phytoplankton, filamentous macroalgae and epiphitic algae. This rapid growth of algae, also termed an 'algal bloom', can increase turbidity, which reduces the light available to seagrass, in turn causing slowed growth or mortality. The growth of planktonic algae is generally measured by observing the amount of chlorophyll a in the water column – elevated chla indicates a degree of turbidity and light attenuation (Kaldy & Dunton 2000). Severe eutrophication can cause anoxia, which results in high-sulphide environments (Hauxwell *et al.* 2003). The most predominant cause of decline by

eutrophication is the attenuation of light.

Estuaries are most susceptible to nitrogen loading due to human interference. These ecosystems are often subject to human development because of their sheltered nature and access to the ocean (ex: Halifax Harbour, Chesapeake Bay). Because nutrient loading is generally increased in such areas, and estuarine ecosystems are typically limited by nitrogen, accelerated eutrophication of these areas creates and imbalance in some of the most productive marine ecosystems on the planet (Deegan 2002). Nitrogen loading in Chesapeake Bay in the 1990's has caused the main primary producer in the bay to change from Eelgrass to macroalgae. This resulted in the decrease of eelgrass biomass, shoot density, as well as a reduction in the abundance of fish and decapods in the area (Deegan 2002).

Similar to nutrient loading, sediment runoff contributes greatly to light attenuation within coastal communities. An increase in total suspended solids and chromophoric dissolved organic matter (CDOM) prevents lights from reaching the plants that rely on it. As external sedimentation is introduced into an ecosystem, total suspended solids and CDOM measurements tend to increase, causing less light to penetrate the water's surface. Hauxwell *et al.* (2003) show that low light availability negatively effects seagrass recruitment, and also causes enhanced mortality of existing seagrass communities. These effects are direct, but reversible – if light availability returns to higher level, recruitment increases and the bed may recover from damages (Zimmerman *et al.* 1995). One of the major causes of sediment runoff is urban development– municipal wastewater systems often cause cloudy storm water to flow directly from city streets to a nearby water body, rather than being filtered by natural riparian buffers first. The suspended solids that water carries, like sand, yard waste, and debris, flow directly into waterbodies, causing increased turbidity and light attenuation.

Although chemical and spatial disruption can seriously harm seagrass beds, physical disturbance can be most damaging of all. The physical breaking and/or destruction of a seagrass bed can be very severe, sometimes rendering the ecosystem incapable of repair. Anthropogenic causes of

physical disturbance are boat scarring, dredging, and fishing anchoring; natural causes are storms, floods, cyclones, ice, grazing, all of which result in breaking of plants and fragmentation of the landscape (Duarte 2002). Coastal development, particularly ports and docks, changes sedimentation patterns that can cause partial or complete burial of seagrass beds, which encroaches on their ability to grow and reproduce (Duarte 2002).

Seagrass beds are highly affected by invasive species around the world. The tropical algal species *Caulerpa taxifolia* was introduced to the French Mediterranean in the early 1980s, and has spread all the way to the coast of Spain (Duarte 2002). Well known to Nova Scotia is the European green crab (*Carcinus maenas*), present in many seagrass beds around the province. These crabs have been known to cut the blades of seagrasses, effectively killing the plant (Davis, *et al*. 1998). Encrusting tunicates are another invasive species issue in New England and Atlantic Canada, because they tend to encrust on seagrass shoot and leaves, causing physical damage or light attenuation (Carman & Grunden 2010).

Commercial fishing and aquaculture practices put serious pressure on the health and success of seagrass beds. Such practices can cause physical damage by trawling or boat scarring, and biological damage by removing top predators and upsetting the ecological balance (Orth *et al.* 2006). In 2006, Marbà *et al.* showed that the rapid expansion of fish farming and other aquaculture practices causes increased deposition of organic matter and nutrients, which can upset the nutrient balance in an ecosystem and cause changes in the relationships between trophic levels. The results of aquaculture and commercial fishing can be highly damaging to the health of seagrass beds even after the aquaculture operations have shut down.

Threats posed on seagrass beds can lead to fragmentation, which is one of the largest pressures on biodiversity within a bed (Frost 1999). Fragmentation causes habitat loss and a change in habitat use. As fragmentation occurs, not only is habitat lost, but the ratio of edge to interior habitat changes (Bell

et al. 2001). Species that have fidelity to one area within the bed will be affected most by fragmentation as the edge to interior ratio goes up and the amounts of each habitat available changes (Bell *et al.* 2001). Edge habitats are typically higher in species interaction (pollination, predation, competition) than interior habitats. As fragmentation increases, edge habitat increases, level of interaction increases, causes further shifts in biotic composition of habitat (Bell *et al.* 2010). Due to their productivity and ecological services, some areas of seagrass ecology have been studied heavily; however others have not (Bostrom, Jackson & Semenstad 2006). Fragmentation is common in both terrestrial and marine ecosystems, but has been understudied in marine environments. Robbins & Bell (1994) suggest that seagrass beds are the perfect candidate for study of fragmentation in marine landscapes because they exist in vast areas, are intertidal and easily accessible, and have obvious issues with fragmentation.

2.4 Foci of Fragmentation Study

It is known that fragmentation and patchiness of habitat affects the macrofaunal community within a bed, but which factor is most important in affecting macrofauna composition and abundance? There is some controversy in the answer to this question. One major theory is that habitat complexity most greatly affects the makeup of invertebrate species within a bed (Attrill *et al.* 2001). Orth & Van Monfrans (1982) show differences in macrofauna between vegetated and non-vegetated areas, but not between vegetated areas of differing density. Bell *et al.* (2001) infer that faunal abundance is related to the size of the seagrass patch, and that abundance increases as patch size decreases. Bologna & Heck (2002) argue that macroinvertebrate dynamics are more closely related to the location within the bed (centre, edge or bare patch), and Bowden (2001) discusses the importance of subdivisions within a bed, or the distance from the edge of the bed.

As mentioned above, there is controversy over which focus of study is most representative of the true factors effecting seagrass habitat composition. One outstanding theory is that habitat complexity weighs heavily on the type and abundance of species inhabiting a certain seagrass bed. That

being said, there are further subdivisions of this theory into types of complexity. Heck & Orth (1980) show that shoot density can have effects on predation; by providing protection from predators, seagrass beds can effect predator-prey relationship dynamics. Attrill *et al.* (2000) argue that this is too simplistic a view, and more factors must be taken into consideration. These additional factors of complexity are shoot length (Attrill *et al.* 2000, Tolan *et al* 1997), root-rhizome mat (Orth 1984), canopy cover (Heck and Orth 1980), and plant biomass (Healey & Hovel 2004). These issues will be discussed in the following section.

Leaf length was assumed to be one of the main factors influencing macroinvertebrate composition of beds in classical seagrass studies (*e.g.*: Orth 1980). This opinion has since changed in light of more recent studies. Attrill *et al*. (2000) show that seagrass beds increase the complexity of the surrounding bare sea bottom; however the increase in complexity is not only in a vertical dimension. Therefore, solely measuring leaf length as a measure of complexity is insufficient to understanding the true effects of complexity on habitat functions. Additionally, Tolan *et al.* (1997) showed that shoot length, shoot density and the number of leaves per shoot correlated with complexity, indicating that simply looking at one factor would be inconclusive. However, as the variables in Tolan's study were chosen arbitrarily, and the physical structure of seagrass beds is highly variable, the use of one or few seagrass characteristics is too simplistic, and the integration of many variables is required (Attrill *et al.* 2000).

Shoot density was not originally thought to have an effect on macroinvertebrate composition; Orth & van Montfrans (1982) found there was no difference in faunal abundance between differing densities, and that the only notable difference is between vegetated and non-vegetated areas. This finding was quickly refuted by Lewis (1984), who found that the relationships between associated macroinvertebrates and seagrass biomass, shoot density, and surface area are not easily distinguishable and must be studied holistically. In support of this idea, Healey & Hovel (2004) indicated that shoot

biomass and shoot density both influence faunal abundance, diversity and survival.

The canopy of the seagrass bed has been known to have a huge influence on the makeup of the associated community. Like other features of seagrass beds, there are numerous theories regarding the ways that canopy cover effects macrofaunal composition. The canopy of beds slow wave action, and because the water is moving more slowly, smaller particles have a chance to settle out of the water column. The sediment particle size within a habitat affects the species that can inhabit it; therefore the establishment of seagrass directly affects the macrofauna in an area (Orth 1984). Additionally, the canopy of a seagrass bed can act directly as habitat for species of amphipods and bivalves, and provide protection for fish and epibenthos. Heck & Orth (1980) suggested that plants with more foliose leaves, and therefore greater surface area per unit weight, should provide more protection than plants with simpler leaves and lower surface area per weight. The study also shows that predation upon amphipods that use leaf habitat for protection decreases non-linearly with increased blade density, and also gives strong evidence that shoot density regulates the structure of communities of macroinvertebrates larger than .5 mm.

The root-rhizome network of seagrass beds effects the ways that associated macrofauna use that habitat. The rhizome mat prevents predation by epibenthic fish and crabs by creating a physical boundary between predatory species and benthic macroinvertebrates (Orth 1984). The same study also indicated that macroinvertebrates greater than .5 mm use habitat for protection, and that more of such invertebrates are found in vegetated areas than non-vegetated areas. The mat also prevents predatory gastropods from burrowing, as they are generally large and cannot navigate through the network of rhizomes. Additionally, the root-rhizome system can even the playing field between hard-bodied and soft-bodied burrowers, whereas bare sediment leaves hard-bodied burrowers at a distinct disadvantage (Orth & Heck 1984).

Biomass is generally studied in conjunction with other seagrass properties. Many studies have

shown that biomass, alongside many other individual measures, cannot be studies in singularity, but must be examined in conjunction with shoot length, shoot density, etc. Attempting to use biomass as a sole indicator of macroinvertebrate dynamics is inadequate due to a host of biotic and abiotic factors that play a role in habitat composition (Heck & Orth 1980). Attrill *et* al. (2000) claim that the use of biomass of seagrass as a complexity measure in an *a posteriori* inference resulting from a strong relationship between biomass and invertebrate community parameters, rather than from an *a priori* investigation of the structural environment. In the same study, Attrill found no relationship between plant biomass and diversity of macroinvertebrates; however Mills & Burkenbusch 2009 did. This disparity may indicate that the relative effect of biomass on macrofaunal assemblages varies between sites, and must therefore always be taken into consideration. Many recent studies have emphasized the importance of holistic studies, and a shift towards studying seagrass beds as landscapes rather than splitting them into small-scale, finite microhabitats (*e.g.*: Hovel 2003, Bostrom *et al*. 2006b).

2.5 Rationale

In light of previous research, and the apparent entanglement of above- and below-ground biomass, shoot density, shoot length, macrofaunal abundance and composition, and sediment characteristics, the current trend is to evaluate all of these elements simultaneously. The intent of this project is to understand the macrofaunal assemblages within different habitat types on a landscape scale, and test the following prevailing seagrass-macroinvertebrate paradigms: (i) higher faunal density and diversity exists within seagrass beds compared to unvegetated areas, (ii) faunal community structure differs between seagrass beds compared to unvegetated areas, (iii) macrofaunal abundance is positively correlated with plant density and biomass, (iv) interior of seagrass beds have higher biomass, shoot density, and leaf length than edge habitats, (v) macrofaunal density is highest at bed edges in temperate ecosystems, and (vi) macrofaunal parameters are related to sediment properties.

Because the study sites of this project have minimal patchiness and fragmentation, the data they

will provide will be highly useful in understanding the beginnings of habitat degradation, and in establishing a habitat value for a near-pristine seagrass habitat. There has been noted degradation in other areas of Nova Scotia, so by studying these relatively complete and healthy Eelgrass beds, it will be possible to determine whether restoration attempts have been successful in restoring beds to their pre-damaged state. Additionally, because seagrass data from this location is limited to severely damaged beds, this new information will fill in gaps in existing knowledge. It will allow for more complete models to be built so that more accurate extrapolation into seagrass decline can be made.

The geographic location of these sites is also ideal, as similar studies have largely been conducted in tropical zones (*e.g.*: Connolly 1997) and in the North-East Atlantic (Frost *et al.* 1999) zones, but very little is known about seagrasses in the West Atlantic, specifically in the Maritime- New England area. This data will contribute to the body of knowledge regarding seagrass in Atlantic Canada, and to that of seagrasses worldwide.

3 Methods

3.1 Sample Collection

Samples were taken in Port Joli (47.20, 64.90) and Port L'Herbert (43.80 64.92) in August 2009. These sites included contiguous *Zostera marina* beds with a few creeks running through them. The beds at both sites occurred on an elevated tidal platform. The mean temperature and salinity at Port Joli are 17.5 °C and 29.3 ppm respectively. Port L'Hebert had a mean temperature of 19.6 °C and average salinity of 20.1 ppm. The average depth at low tide for both sites is about 156m (Canadian Hydrographic Service 2010), although during spring low tides, sites were often exposed.
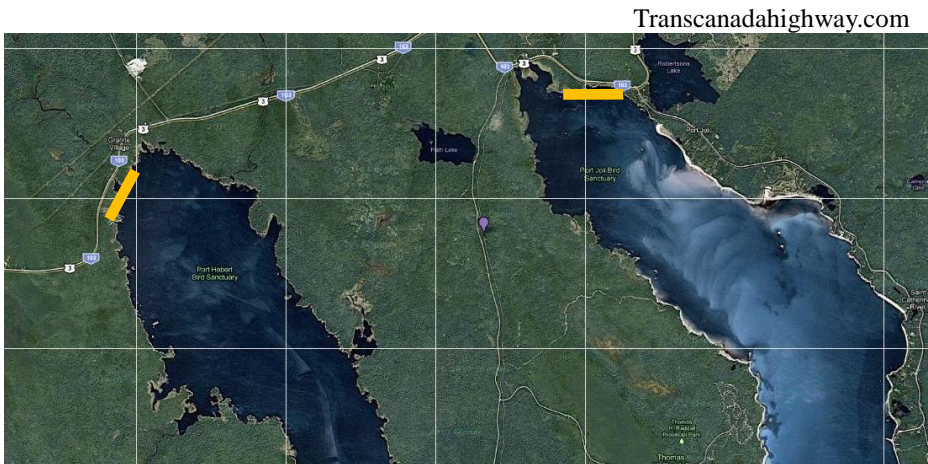
These sites were divided into three habitat types: interior, edge, and bare. The 'interior' samples were taken more than 1m from any bare areas. The 'edge' habitat was defined as any area of the seagrass bed within 1m of the outside bare area. The 'bare' samples were taken from unvegetated areas outside the seagrass bed. Ten samples from each habitat type at each site were taken, for a total of 60 samples. Samples were taken haphazardly, ensuring that samples were >10 m apart.

Samples were collected using a 10 cm diameter core to a depth of 12 cm (area 78.54cm^2). The above-ground biomass (including seagrass leaves and shoots) within this 10cm diameter was evaluated for shoot density prior to removal by counting the number of shoots within the area. The above ground biomass within the 10cm diameter was cut off and placed in a plastic sample bag before the core sample was taken to ensure no above-ground biomass was lost during core sample collection and to facilitate complete sample collection. This sample portion was placed in a bag with a label. The below-ground sample portion (sediment, rhizomes, and associated benthic invertebrates) was then collected using the 10cm core and placed in a bag with a label.

Sediment cores were collected alongside the biotic samples using a syringe. The syringe was pushed 5cm into the sediment, and 60mL of sediment was collected per sample. This sediment was

placed in a bag with a label.

All biotic samples were refrigerated at 4°C until analysis, while all sediment samples were frozen

at -18°C until processing.

Transcanadahighway.com

maps.google.com

Figure 1: a) A map of Nova Scotia with an orange circle indicating the location of study sites within Nova Scotia. b) A close-up map of the two study sites. The orange lines show the specific location of study sites within Port Joli (right) and Port L'Hebert (left).

3.2 Sample Processing

All biotic samples were sieved with 500μm mesh to remove sediment and to separate animals

from plant material. At this point, plant biomass was refrigerated until further processing, and

macrofauna was stored in 10% formalin for 14 days then transferred to ethanol for storage until

processing.

The above ground plant matter was analysed in several ways. First, the leaves were separated and their length and width in mm were recorded. The samples were then dried at 60°C for 48 hours, and their dry mass was recorded using a Metler AE163 balance. The below-ground biomass, including roots and rhizomes, were also dried and weighed.

Preserved macrofaunal samples were identified to species when possible and counted under a dissecting microscope. Macroinvertebrate species keys by Gosner (1978), Appy (1980), Pollock (1998), Abbott (1974), and Weiss (1995). Some samples were only identified to genus due to damage rendering some specimens unidentifiable. Oligochaetes were identified only to family level due to limited equipment, expertise, and time.

Sediment samples were analyzed for organic content and particle size. Organic content was determined by drying sediment samples at 60°C for 48 hours, then ashing the sediment at 500°C for 7 hours. Organic content was calculated as (dry mass − ashed mass) / dry mass x 100%. All masses were taken using a Mettler AE163 balance.

Although 60 biotic samples were analyzed, and 60 sediment samples were processed for organic content, in the interest of time only 12 sediment samples (2 samples from each habitat type from each site) were processed for particle size. Whole sediment samples were dried at 60°C for 24 hours and the total dry mass was measured (g). Each sample was then mechanically stirred for 15 minutes with 250mL deionized water and 10mL hexametaphosphate (6.2g/L) using an IsoTemp magnetic stirrer. The mixture was left to disaggregate 24 hours, stirred for an additional 15 minutes, then poured through a 64μm seive to separate silt (particles < 64 μm) from sand (particles 64 μm − 2000 μm). The separated silt and sand fractions were dried at 60°C for 7 days. The silt fraction of each sample was calculated as (dry mass of silt) / (total dry mass) x100%.

3.3 Statistical analysis

This data was used to determine whether invertebrate communities and ecological indicators of those communities differ with habitat type and site. This was done using two-way fixed factor ANOVAs, where the independent variables are habitat and site, and the dependent variables were total macroinvertebrate abundance, total species richness, predator abundance, detritivores abundance, square-rooted filter feeder abundance, and square-root grazer abundance. Sediment grain size fraction, and organic content of sediment were also tested using ANOVAs with site and habitat as independent variables. Similar ANOVAs were completed for above- and below-ground plant biomass, shoot density, and leaf length; however these tests did not include data from Bare habitats, as these samples did not contain plant matter. Outliers, data points that fall outside further than 1.5 times the distance of the Q1-Q3 interquartile range from the third quantile, were removed from macroinvertebrate data as well as above-ground biomass and organic content data. Significant results of ANOVA tests indicate a significant difference between sites, among habitats, or as a result of the interaction of site and habitat. If such a significance was found, Tukeys test was used to determine the where specific differences lay between habitats and invertebrate communities. This test performs pairwise comparisons of all means of each treatment. ANOVA and Tukeys statistical tests were run on Minitab15 as provided by Dalhousie University.

A multidimensional scaling test (MDS) was performed to determine if invertebrate community structure differed among habitats. MDS creates matrices of dissimilarity based on species abundance data for each habitat type. These matrices were then used to calculate 'distances' between samples, and these distances were plotted onto a graph. Two samples that are close together have more similar community structures than two points that are further apart (McGarigal *et al*. 2000). The relationship among invertebrate parameters and environmental data was examined using multiple regression analyses with one dependent and several independent variables to test which factor accounted for the

majority of the variation in the data. ANOSIM (analysis of similarity) tests were also run. ANOSIM uses the same matrices as MDS to computes a test statistic reflecting the observed differences among replicates between sites, contrasted with differences among replicates within sites. In that way, the results of ANOSIM are comparable to that of a one-way ANOVA. The tests statistic is formulated between 0 and 1, where R=1 if all replicates within sites are more similar to each other than to replicates among sites. The statistic is recomputed using permutations of the sample label to see if there is an effect on the arbitrary reassignment of sample labels, testing H_0 that there is no difference among sites. The global R-value shows the overall difference between and among sites. The following R-values are pairwise comparisons.

Ordination plots and ANOSIM were run on Primer6 provided by the Department of Fisheries and Oceans.

4. Results

Analysis of Variance (ANOVA) tests showed significant differences in the total macrofaunal abundances when site and habitat were compared simultaneously. The post-hoc Tukeys test found that at PJ Bare samples had significantly more individuals than Interior or Edge samples. The removal of outliers showed that edge habitats at PH had significantly more individuals than bare or interior areas (Table 3). Previous to this removal, Tukeys test showed no significant differences between habitats at PH (Table 1). State outliers removed in methods

Species richness was significantly higher in edge and interior habitats than in bare, and higher in PJ than PH (Table 1). Removal of outliers did not change the levels of significance in species richness among sites and habitats (Table 2). ANOVAs showed no significant differences in the abundances of predators or detritivores neither in different habitats nor at different sites (Table 1), despite the removal of outliers (Table 3). Tests did however show significantly more filter feeders in bare and edge habitats than in interior ones, at both sites. Port l'Hebert had a higher abundance of grazers than Port Joli possibly due to the existence of more filamentous algae at PH than PJ, and edge and interior habitat housed significantly more grazers than bare patches (Table 1). The removal of outliers did not show any changes in statistical significance in any functional group abundances (Table 3).

No significant differences in leaf length or width were seen when comparing site or habitat (Table 2), however a general trend towards longer leaves in interior habitats was seen (Figure 5). The shoot density was significantly higher in interior habitats than in edge (Table 2, Figure 5). There was no observed difference between above ground biomass between habitats or sites when all data was used in comparisons, but after the removal of high-value outliers Tukeys tests showed significantly more above-ground biomass in interior than edge habitats. There was also significantly more below ground biomass in interior habitats than edge habitats (Table 2, Figure 4). There were no outliers in the leaf

length or width, shoot density, or below ground biomass data.

The silt fraction and organic content of sediments in Port Joli was higher than that of Port l'Hebert. Additionally, the organic content of edge habitats was significantly higher than either interior or bare areas (Table 2). The removal of outliers changed the p-value of habitat comparisons from 0.001 to <0.0001, but did not change the p-value of site comparisons (Table 3, Figure 6). There were no outliers in the silt fraction data as the sample size was very low.

It was generally observed that *Gemma gemma,* a species of filter-feeding bivalve, occurred in very high frequencies (up to 575 individuals) in bare samples, but occurred in relatively low abundances in interior samples (0-50 individuals). It was also observed that predatory species existed in very low frequencies (on the order of 10 individuals per core) in comparison with other functional groups, and that detritivores in interior habitats occurred in very low abundances in Port Joli (Figure 3).

MDS plots indicate the dissimilarity between habitats at Port Joli and Port l'Hebert (Figure 7). The graphical representation of community structure in Port Joli (Figure 7, top) indicates that the samples in each habitat are less dissimilar to each other than they are to other habitats. Figure 6 (bottom) shows that samples in edge and interior areas at Port l'Hebert are less dissimilar to each other than they are to bare samples. ANOSIM results show that the community structures among habitats at PJ are more different from each other than the community structure among habitats at PH (global R PJ = 0.539, global R PH = 0.369). The structures at PH Bare and Edge habitats are far more similar to each other than they are to Interior habitats. ANOSIM results at PJ show that Bare and Interior habitats and Edge and Interior habitats have very different community structures, while Bare and Edge are less distinctly different from each other.

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Table 1: Results of general linear ANOVAs for abundances of total faunal abundance, abundance of faunal functional groups, and species richness in core samples. The values for grazer and filter feeder abundances were square root transformed. Bold p-values indicate significance. Post hoc comparisons were done using Tukeys test. Sample types are listed in order of increasing means. Sample types that share an underline do not differ significantly from one another. Sources of various: S=site, H=Habitat. The Tukeys test for total abundance was done by hand due to lack of power in Minitab statistical software.

Analysis	Degrees of freedom	Source of variation	MS	F	P	Post hoc comparisons
Total abundance of all fauna	1	S	20409	1.54	.220	
	2	H	12963	1.13	.330	
	2	S x H	49865	3.77	**.029**	PH: Bare Interior Edge PJ: Interior Edge Bare Bare: PH PJ Edge: PJ PH Interior: PJ PH
	53	Error	13227			
Species number	1	S	209.36	15.66	0.000	PH PJ
	2	H	3123.72	9.26	0.000	Bare Edge Interior
	2	S x H	0.82	0.06	0.940	
	52	Error	13.37			
Total predator abundance	1	S	9.60	0.67	0.418	
	1	H	22.02	1.53	0.226	
	2	S x H	13.71	0.95	0.393	
	53	Error	14.41			
Detritivore abundance	1	S	1414	0.50	0.485	
	2	H	1340	0.47	0.628	
	2	S x H	2475	0.87	0.426	
	53	Error	2855			
Total filter feeder abundance	1	S	9.17	0.71	0.402	
	2	H	191.02	14.89	**0.000**	
	2	S x H	71.16	5.55	**0.006**	PH: Interior Bare Edge PJ: Interior Edge Bare Bare: PH PJ Edge: PJ PH Interior: PJ PH
	53	Error	12.83			
Total grazer abundance	1	S	173.908	21.42	**0.000**	PJ PH
	2	H	78.703	9.70	**0.000**	Bare Edge Interior
	2	S x H	19.106	2.35	0.105	
	52	Error	8.118			

Table 2: Results of general linear ANOVAs for plant structure characteristics. Silt fraction was tested for equal variance using Bartlett's instead of Levene's due to low sample size. Post hoc comparisons that share an underline do not differ significantly. Sample types for post hoc comparisons are listed in order of increasing means. P-values in bold indicate significant results. S=site, H=habitat.

Analysis	DF	Source of variation	MS	F	P	Post hoc comparisons
Average leaf length	1	S	238.8	1.30	0.261	
	1	H	485.8	2.65	0.112	
	1	S x H	42.4	0.23	0.663	
	35	Error	183.3			
Average leaf width	1	S	0.0000029	0.00	0.957	
	1	H	0.0000006	0.00	0.980	
	1	S x H	0.0022925	2.32	0.137	
	35	Error	0.0009875			
Above ground biomass	1	S	0.299	0.30	0.590	
	1	H	3.091	3.06	0.089	
	1	S x H	0.028	0.03	0.869	
	35	Error	1.009			
Below ground biomass	1	S	3.908	2.61	0.115	
	1	H	17.5514	11.70	**0.002**	Edge Interior
	1	S x H	0.440	0.29	0.591	
	32	Error	1.397			
Shoot density	1	S	442.2	1.88	0.179	
	1	H	4473.2	19.04	**0.000**	Edge Interior
	1	S x H	126.0	0.54	0.469	
	36	Error	234.9			
Silt fraction	1	S	394.90	6.74	**0.041**	PH PJ
	2	H	27.60	0.47	0.646	
	2	S x H	216.58	3.70	0.090	
	6	Error	58.57			
Organic content	1	S	1192.11	6.52	**0.014**	PH PJ
	2	H	1440.5	7.87	**0.001**	Bare Interior Edge
	2	S x H	182.9	1.00	0.375	
	54	Error	183.0			

Table 3: Results of ANOVAs of macroinvertebrate, plant and sediment characteristics after the removal out outliers. The values for grazer and filter feeder abundances were square root transformed. Bold p-values indicate significance. Post hoc comparisons were done using Tukeys test. Sample types are listed in order of increasing means. Sample types that share an underline do not differ significantly from one another. Sources of various: S=site, H=Habitat.

Analysis	Degrees of Freedom	Source of variation	MS	F	P	Post Hoc Comparisons
Total abundance of all fauna	1	S	7529	0.73	0.395	
	2	H	12318	1.20	0.309	
	2	S x H	74763	7.30	**0.002**	PH: <u>Bare Interior</u> Edge PJ: <u>Interior Edge Bare</u> Bare: PH PJ Edge: PJ PH Interior: <u>PJ PH</u>
	52	Error	10246			
Species richness	1	S	216.67	16.09	0.00	PH PJ
	2	H	127.77	9.49	0.00	Bare <u>Edge Interior</u>
	2	S x H	1.30	0.10	0.908	
	52	Error	13.47			
Predators	1	S	1.43	0.13	0.718	
	2	H	13.01	1.19	0.311	
	2	S x H	25.68	2.36	0.105	
	52	Error	10.90			
Detritivores	1	S	5024	2.97	0.091	
	2	H	1347	0.80	0.457	
	2	S x H	3912	2.31	0.109	
	52	Error	1693			
Filter	1	S	5.35	0.42	0.517	
	2	H	178.58	14.22	**0.000**	
	2	S x H	79.50	6.33	**0.003**	PJ: Interior <u>Edge Bare</u> PH: Interior <u>Edge Bare</u> Bare: PH PJ Edge: <u>PJ PH</u> Interior: PJ PH
	51	Error	12.56			
Grazer	1	S	157.914	19.74	**0.000**	PJ PH
	2	H	84.799	10.60	**0.000**	Bare <u>Edge Interior</u>
	2	S x H	22.953	2.87	0.066	
	52	Error	8.002			
Above Ground Biomass	1	S	0.2459	0.33	0.567	
	1	H	6.0679	8.25	**0.007**	Edge Interior
	1	S x H	0.0159	0.02	0.884	
	33	Error	0.7359			
Organic Content	1	S	1083.9	6.48	**0.014**	PH PJ
	2	H	1661.7	9.93	**0.000**	<u>Bare Interior</u> Edge
	22	S x H	65.9	0.39	0.677	
	52	Error	167.4			

Table 4: BIOENV results for Port l'Hebert. Variables are environmental factors tested for their ability to explain the differences in community structure among habitat types. Variables explaining community structure are listed from highest to lowest correlation to faunal structure. Values approaching 1 are highly correlated.

Variables	Variables explaining structure	Correlation coefficient
1=Leaf length	2	0.149
2= Above ground biomass	2,3	0.046
3= Below ground biomass	2,4	0.033
4= Organic Content (%)	2,3,4	0.029
	4	0.015
	1,2	0.003
	3,4	-0.013
	1,2,3	-0.022
	1,4	-0.052
	1,2,3,4	-0.056

Table 5: BIOENV results for Port Joli. Variables are environmental factors tested for their ability to explain the differences in community structure among habitat types. Variables explaining community structure are listed from highest to lowest correlation to faunal structure. Correlation coefficient must fall between 0 and 1.

Variables	Variables explaining structure	Correlation coefficient
1=Leaf length	4	0.174
2= Above ground biomass	1,4	0.137
3= Below ground biomass	1,3,4	0.134
4= Organic Content (%)	1,3	0.102
	All	0.098
	1,2,4	0.098
	2,4	0.097
	3,4	0.85
	3	0.080
	2	0.078

Table 6: ANOSIM results for Port l'Hebert. The global R-value is the test statistic reflecting differences seen between all three habitat types. The pairwise R-values represent differences between the two habitats in question. An R-value of 1 indicates that all samples within a habitat are more similar to each other than they are to samples among habitats.

Global R-value: 0.369		Significance level of Global R: 0.1%
Pairwise Tests	R-statistic	R Significance level
Bare, Edge	0.222	0.1
Bare, Interior	0.672	0.5
Edge, Interior	0.242	0.1

Table 7: ANOSIM results for Port Joli. The global R-value is the test statistic reflecting differences seen between all three habitat types. The pairwise R-values represent differences between the two habitats in question. An R-value of 1 indicates that all samples within a habitat are more similar to each other than they are to samples among habitats.

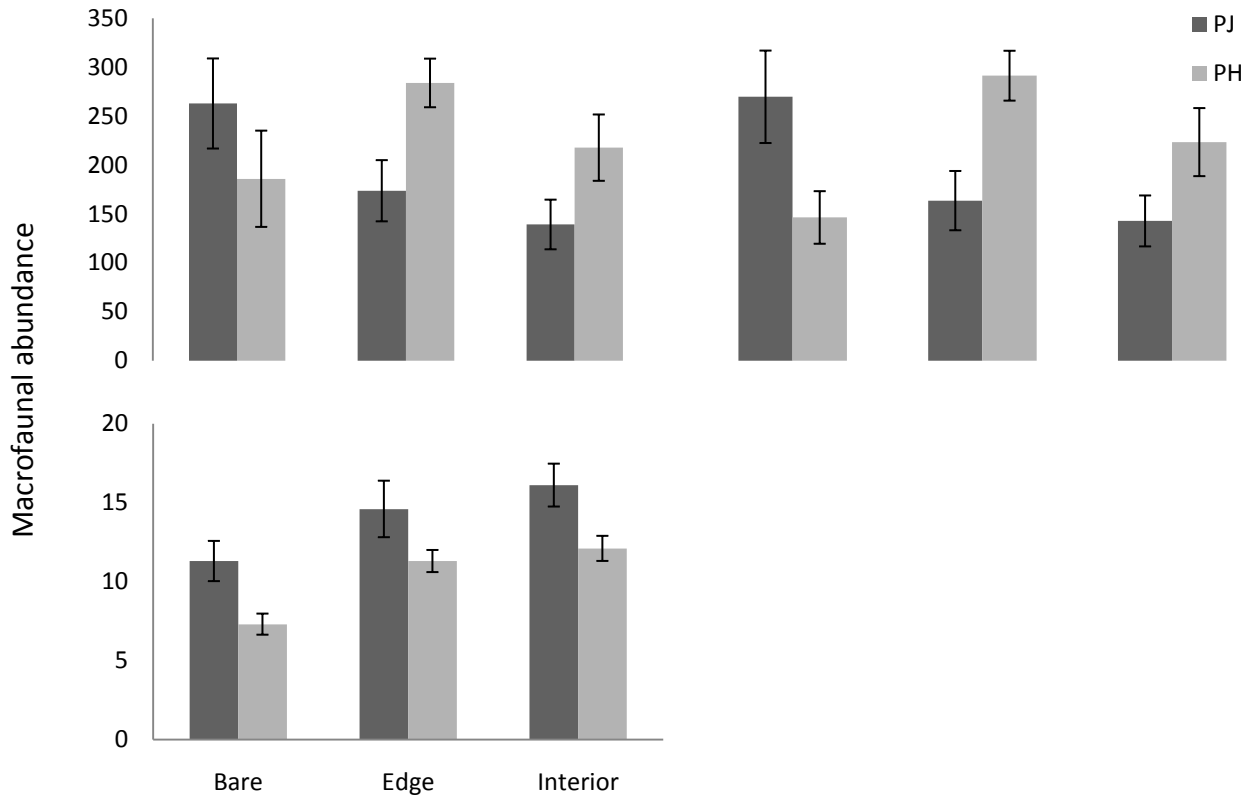| Global R-value: 0.539		Significance level of Global R: 0.1%
Pairwise Tests	R-statistic	R Significance level
Bare, Edge	0.311	0.1
Bare, Interior	0.791	0.1
Edge, Interior	0.635	0.1

Figure 2: Graphical representation of the average distribution of total abundance of macrofauna across habitat types (top left) and total abundance of macrofauna with outliers removed (top right), and the total species richness (bottom left). Error bars represent the standard error within each habitat.
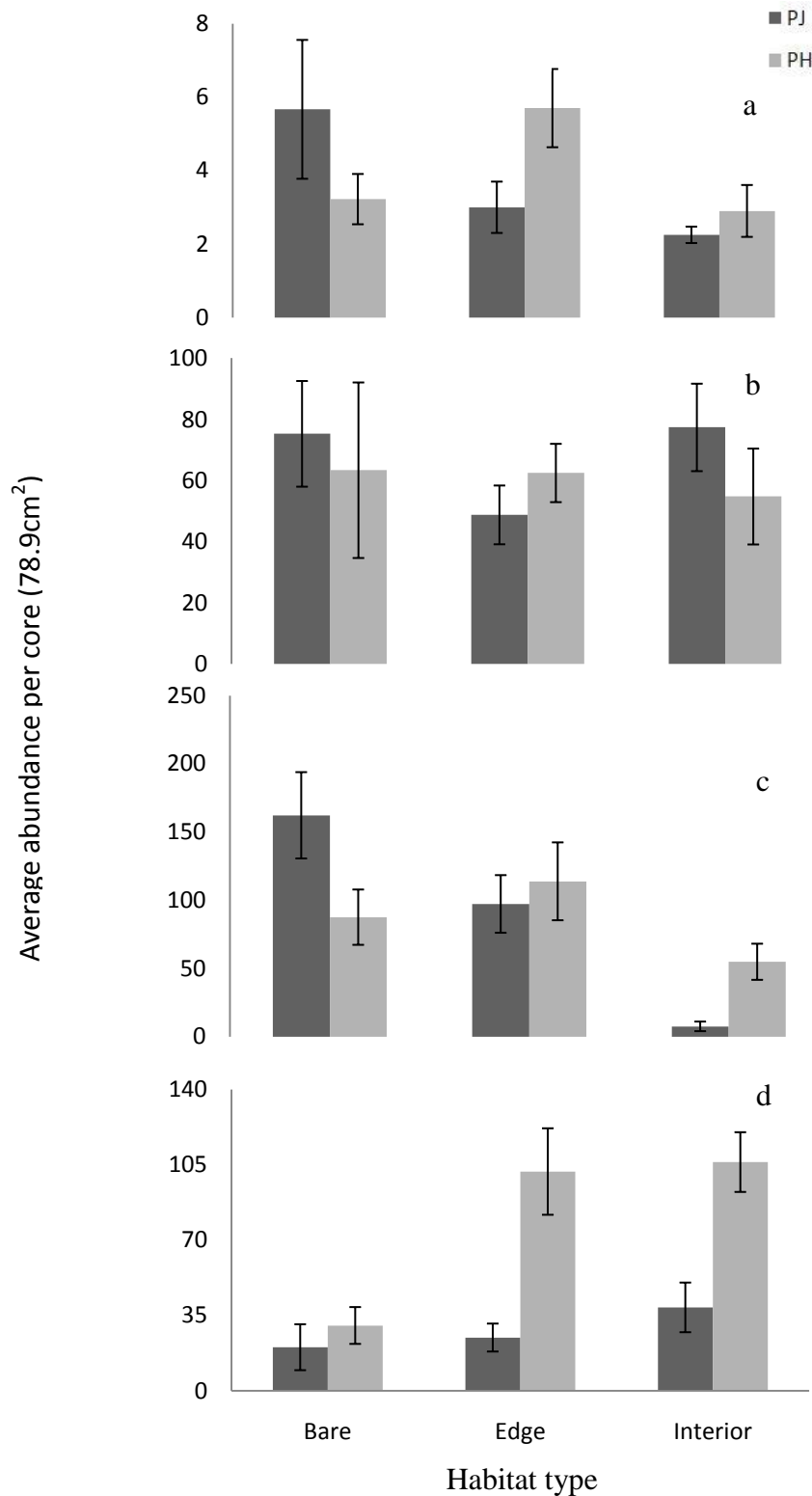
Figure 3: Graphical representation of the average abundance of predators (a), average abundance of detritivores (b), average abundance of filter feeders (c), and average abundance of grazers (d). Error bars represent the standard error within each habitat.
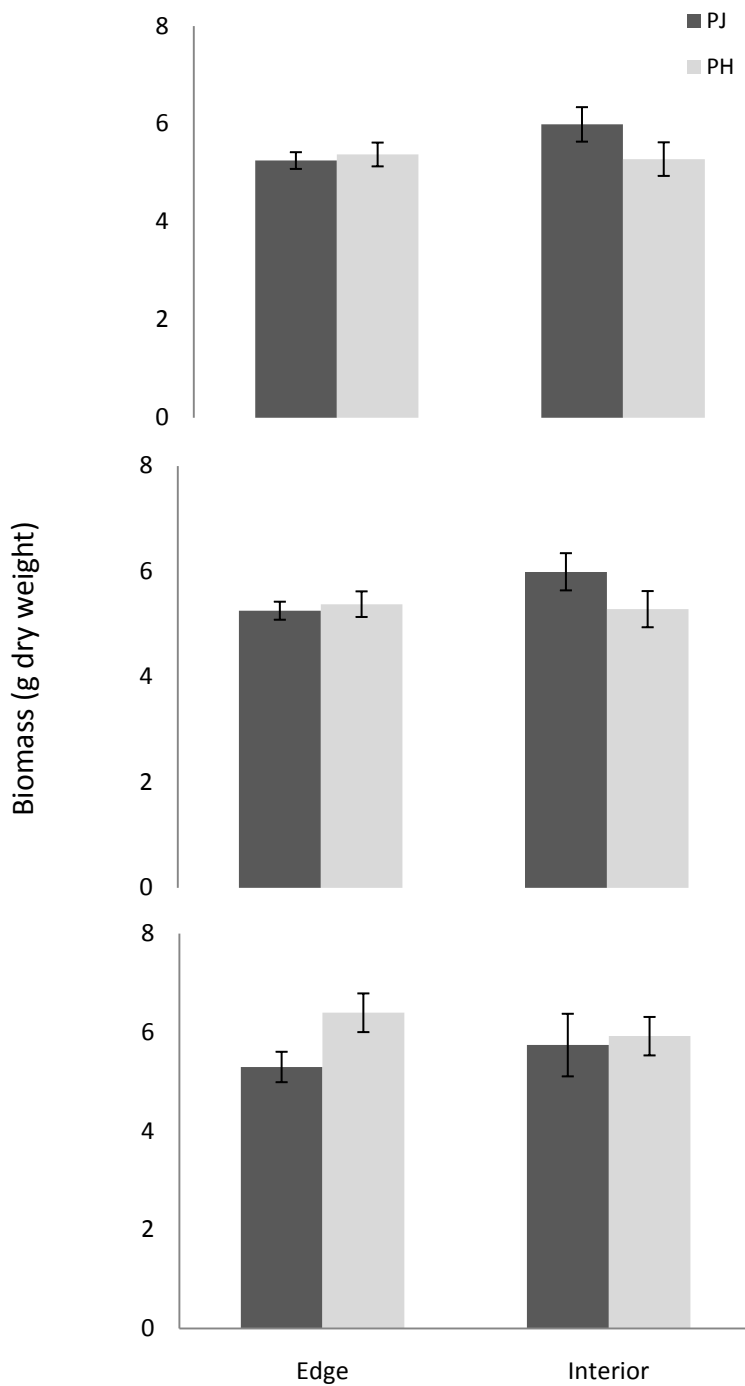
Figure 4: Graphical representation of the above ground seagrass biomass (top), above ground biomass after the removal of outliers (middle) and the below ground biomass (bottom) at edge and interior seagrass beds in Port l'Hebert (PH) and Port Joli (PJ). Error bars represent the standard error within each habitat.
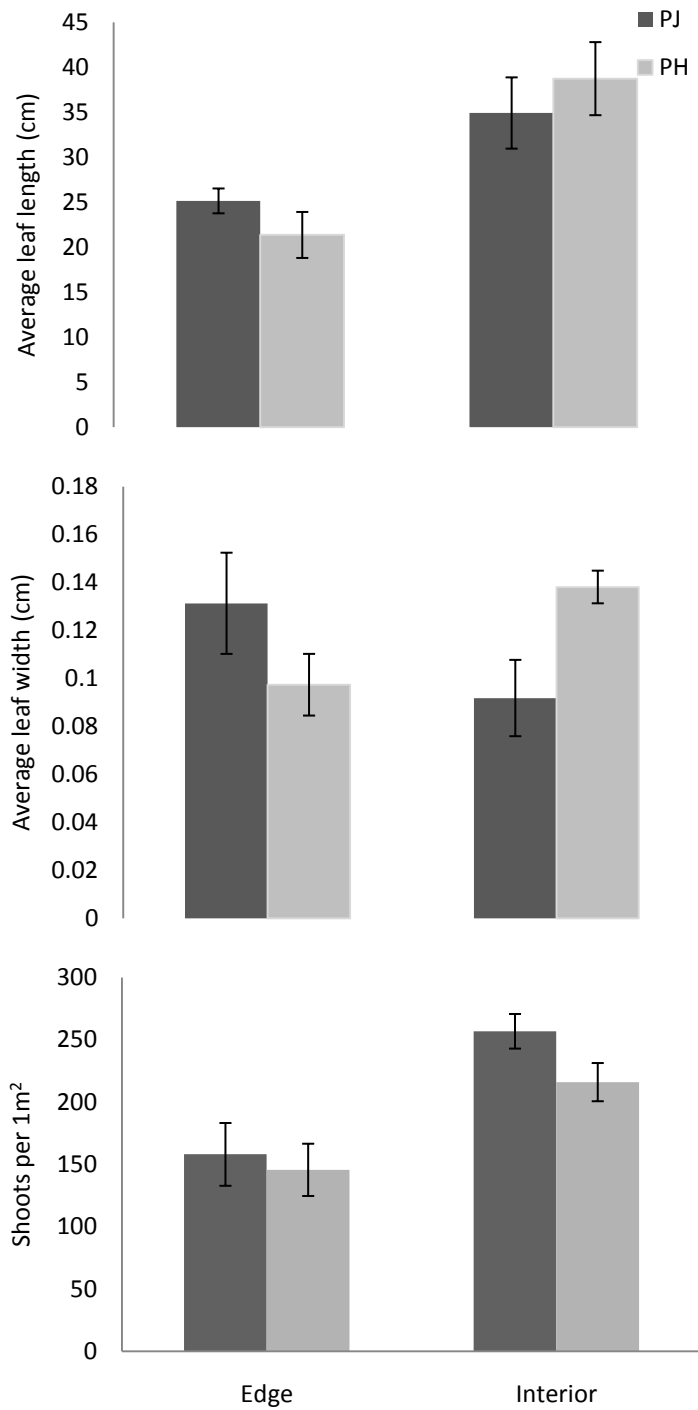
Figure 5: Average leaf length (top), leaf width (middle) and shoot density (bottom) at edge and interior seagrass beds in Port l'Hebert (PH) and Port Joli (PJ).
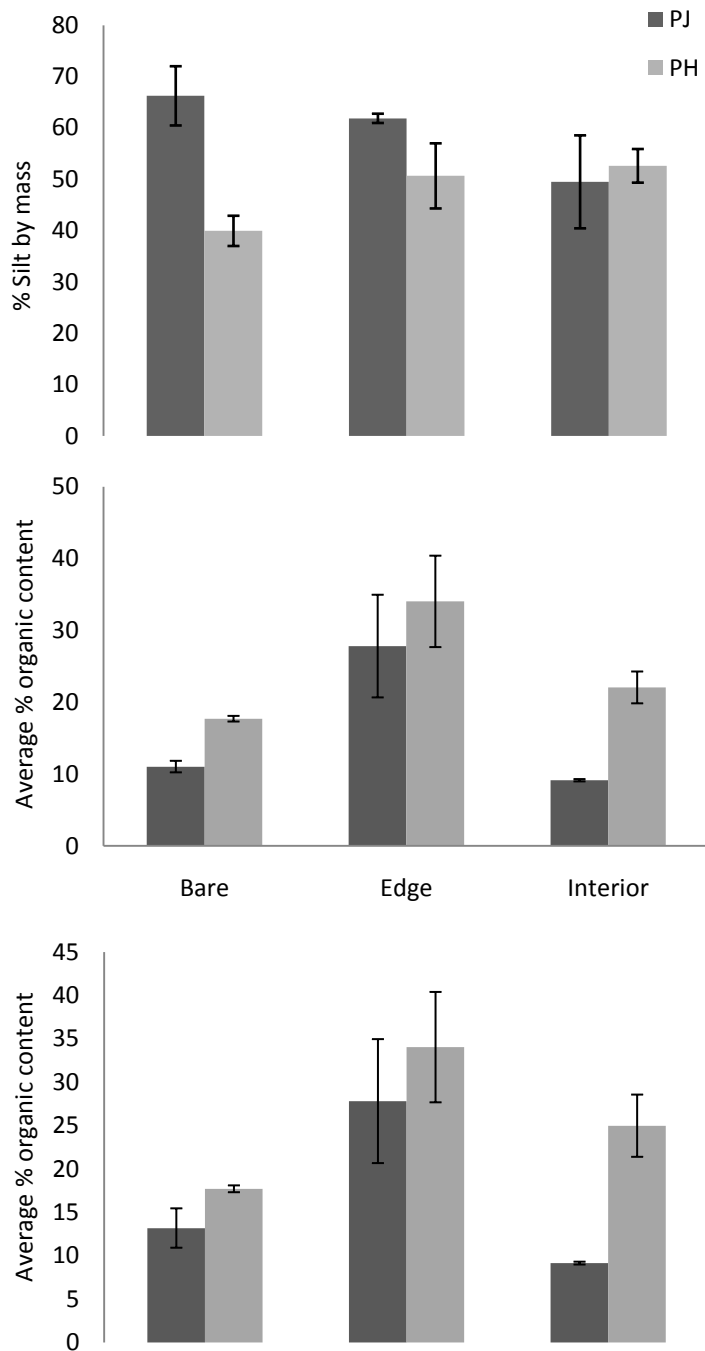
Figure 6: Graphical representation of the average silt (<65μm) fraction (top), average % organic content of all samples (middle), and % organic content with outliers removed (bottom) within bare, edge and interior habitats of seagrass beds in Port l'Hebert (PH) and Port Joli (PJ). Error bars represent the standard error within each habitat.
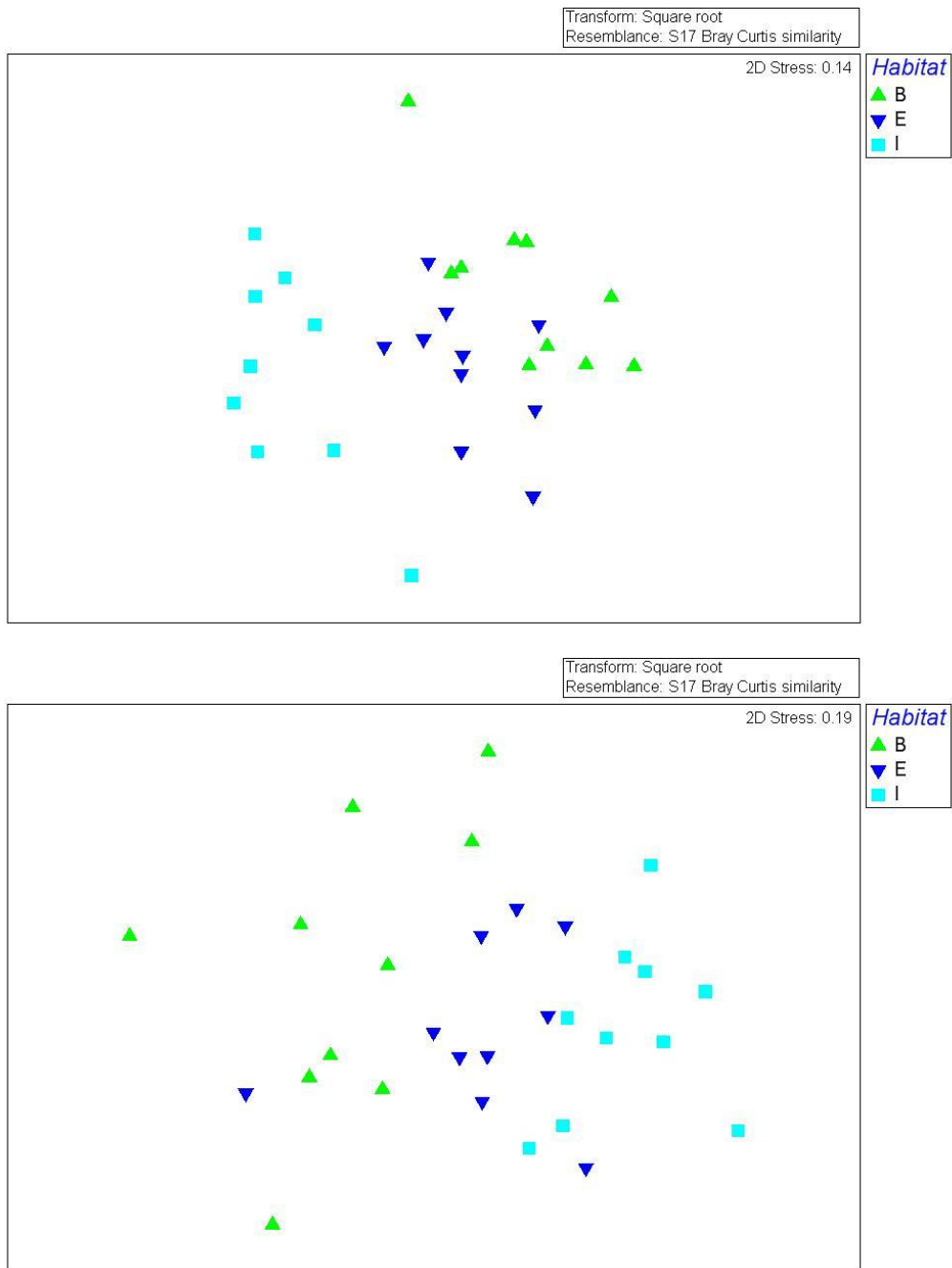
Figure 7: MDS ordination plot indicating dissimilarities between samples at Port Joli (top) and Port l'Hebert (bottom). The distance between two points is a relative representation of their dissimilarity; points close together are slightly dissimilar, points far away from each other are very dissimilar.

5. Discussion

In this study, I examined the relationship between seagrass beds and the macrofauna that lives within them. The objective was to test current prevailing paradigms in seagrass dynamics. The specific aims were to compare plant parameters (ex: length, density) between edge areas and continuous interior beds, and to compare the macrofaunal density, abundance and community structure among bare, edge, and interior habitats. The discussion of the results has been broken down to reflect the original objective of testing prevailing paradigms in seagrass ecology.

5.1 Faunal density and community structure are different in vegetated vs. unvegetated areas

A study by Bologna and Heck (2002) exemplifies the theory that faunal density is highest at edge habitats. They found that the edge of a bed was often more productive and had more individuals and species than the interior of the bed. They speculate that increased edge space may act as a pathway for trophic exchange between bare and interior communities. This theory differs from my results, where the overall faunal density did not differ significantly between vegetated and unvegetated areas (Figure 1, Table 1). The density of some functional feeding groups and the overall species richness, however, did increase in interior habitats compared to bare and edge habitats (Figures 1&2, Table 1).

The main driver of the equal faunal abundances across habitat types was one species of bivalve, *Gemma gemma.* Very high abundances of the bivalve *Gemma gemma* were found in bare areas, and only slightly fewer were found in edge habitats. If *Gemma gemma* abundances were removed from the data, bare areas would have far lower overall macrofaunal abundance than edge or interior habitats. This species broods its larvae, so all dispersal is done in juvenile and adult forms by active and passive transport (Commito *et al.* 1995). It has been observed that *Gemma gemma* moves into areas of low *Gemma* density via passive bedload transport and suspended load transport (Commito *et al.* 1995). This means that when an area of the seagrass bed becomes fragmented and a bare area develops, *Gemma gemma* that settle and grow in that area become abundant due to the lack of competition with other

bivalves (Commito *et al.* 1995). This was commonly observed in my study.

Leeward edges of beds tend to have more species with planktonic larvae due to changes in hydrodynamic forces caused by the presence of seagrass (Bologna & Heck 2002). Because the larvae are planktonic they require moving water to remain in suspension. When moving water hits the leeward edge of the bed, it loses velocity and the capacity to suspend particles, and larvae drop out of the water column (Bologna & Heck 2002). This may explain the comparable level of immotile species like *Mytilus edulis* in edge samples, as well as small gastropods like *Cingula aculeus* and *Hydrobia minuta*. These observations are contrary to the prevailing paradigm that the overall faunal density of vegetated areas is higher than that of unvegetated space.

Port Joli and Port l'Hebert are both highly depositional areas because of the constricted water flow caused by the narrow mouth of the bays. It is likely that the presence of seagrass does very little to slow water because the current is already so slow. I think that the sedimentation patterns observed in other seagrass studies do not apply to my study sites for this reason.

In contrast to total faunal abundance, there are distinct differences in the number of species in different habitats. Vegetated areas (edge and interior) of the bed show significantly higher species richness than bare areas, but these two habitats to not differ from each other. This supports the paradigm that community structure and species diversity differs between bare and vegetated areas. Mechanisms of this change in species richness are likely the increased protection from predators, grazing material supplied by the plants, and general habitat complexity that provides multiple niches for species to fill (Attrill *et al.*2000)

Although ANOVA tests show no significant difference between predator abundance among the three habitats, Figure 2 indicates there is a trend towards fewer predators in interior habitats than edge or bare areas; it also appears that the predator abundances in bare and edge samples are more similar to each other than to interior areas. Lewis (1984) states that species use seagrass bed structures for

protection from predators. The 3D structure of seagrasses provides the ability to escape predations by hiding above ground among shoots, and below ground among roots. Therefore, predatory species hunt and survive best in bare areas that offer little to no protection (Lewis 1984).

As Lewis (1984) also states that species preferentially live in areas that accommodate their feeding strategies. Many more grazers were observed in edge and interior habitats than in bare ones. This is due to their reliance on live plant material which is found abundantly within the bed. Some grazer species were found in bare areas; it is my speculation that they would be feeding on damaged plant material that has not yet begun to decay, consuming benthic microalgae, are deposit feeders like *Nassarius spp.*, or that they are simply transient. These findings blur the line between vegetated and unvegetated areas, and suggest that edge habitats can be an intermediate habitat that can support fauna found on either bare or interior habitats.

The MDS plot for PJ indicated that the three habitat types supported significantly different community structures, while the plot for PH showed edge and interior sharing similar communities and bare having a different one. ANOSIM results indicated similar patterns, that the habitat types at PJ supported distinctly different community structures. The results from PJ support the hypothesis that the location within the bed determines the structure of a community (Bowden *et al.* 2001). The MDS and ANOSIM results for PH support an opposing theory, that the location within the bed has no effect on community structure, but rather the simple presence of seagrass does (Attrill *et al.* 2000).

5.2 Faunal abundance is positively correlated with plant density and biomass

This paradigm can be well described by a study by Webster, Rowden and Attrill in 1998. They found that the macrofaunal communities in this study were best explained by their above-ground plant characteristics. They do note, however, that further study needs to be applied to below ground plant material. These findings were supported by Attrill and others in 2000, who found that faunal abundance was positively correlated with the plant density and biomass, but also suggest that this correlation is

limited; increasing plant biomass (by increasing length and overall surface area) increases the space available to macroinvertebrates, but does not increase the number of possible niches. Therefore, increasing density and biomass can increase the number of individuals, but the ability to provide unique niches and increase the species richness of an area is limited.

In my study, plant density and below ground biomass were both significantly higher in interior areas than edge, and higher above ground biomass was found after the removal of outliers. The abundance of macroinvertebrates was not consistent among habitat types at PJ and PH; in PH edge habitats had the highest total abundance, while at PJ Bare and Edge areas were equally high (Table 1, Table 3). Despite this discrepancy, some correlation to plant characteristics can be seen in faunal functional groups.

Even after outliers were removed from statistical analysis, grazers were the only functional group to show a positive correlation with plant density and below ground biomass. It is logical that animals that feed on plant material would be more abundant where there are more plants; however, it is surprising that detritivores are not also more abundant in interior habitats. Detritus is created by live plants which are most abundant at the interior of seagrass beds, but instead of seeing a high presence of detritivores in this area, there is a comparable number of detritivores in bare areas. This may be due to the fact that the study sites were generally depositional areas high in organic matter, and many of the detritivores species are feeding on deposited organic materials.

Plant characteristics were different between bare, edge and interior. The species richness of edge and interior habitats are significantly different than that of bare habitats, but they are not different from each other. Figure 1 shows a trend towards an increase in richness from edge to interior, but the difference is not statistically significant. It seems that plant characteristics change gradually from bare to interior, but diversity only changes significantly between vegetated and unvegetated areas. This loose correlation makes it impossible to make conclusive statements about the direct relationship

between species richness and plant density and biomass in this study; however, the data suggests that further study on this matter is warranted. Future studies could look at plant characteristics from a wider variety of sample locations; my study only had one criterion for 'interior' samples, but a future study could look at seagrass characteristics from 5m, 10m, 15m, etc., from the bed's edge.

The BIOENV function of Primer6 tested which physical characteristic(s) best explained the macrofaunal community structure of habitats. The BIOENV test resulted in very low correlations of plant and faunal characteristics at both PH and PJ, indicating that no physical characteristic better explains the community structure than another. This is likely due to problems in the data; several plant samples were unfit for BIOENV testing because they were missing at least one of the above-ground, below-ground, or length measurements, which resulted in a low sample number in this test. Another reason that BIOENV came up with inconclusive results is the possible combined effect of biomass, length, density, number of leaves per shoot, and algal epiphyte biomass on faunal communities (Attrill *et al.* 2000). Attrill speculates that a method of improving seagrass studies would be to increase the sample size. This would increase the proportion of total individuals of all species, giving a better look at the true community structure, and better representing rare species.

One can conclude that there is no overall positive correlation between faunal abundance and plant density and biomass, but such a correlation may exist with species diversity. Further research that includes additional plant characteristics such as number of leaves per shoot, shoot density, and algal epiphyte biomass may produce more conclusive correlations between structural aspects of seagrass beds and their associate macrofaunal communities. Attrill *et al.* (2000) have found similarly confounding results concerning complexity and diversity. They found that structural complexity does not have an effect on the macroinvertebrate composition in different locations within the bed; however this complexity-diversity paradigm can be applied to differences between vegetated and non-vegetated areas.

5.3 Interior areas have highest plant biomass, density, and leaf length

This paradigm was almost entirely supported by the findings of my study. Below ground biomass and plant density show a statistically significant relationship with their distance from a bare area. There is an observed trend towards increasing above-ground biomass and leaf length (Figures 3&4) which is statistically supported after the removal of outliers (Table 3).

During sample analysis it was observed that many leaves were broken, and thus not used in calculating the average length of leaves in that sample. Authors speculate that the above-ground biomass and leaf length data could be unrepresentative of their true values. These leaves could have been broken by sampling errors which caused damage to the physical sample.

5.4 Macrofaunal density is highest at edges of bed

Macrofaunal density at PH is highest at the edge of the beds, but in PJ the abundance within bare and edge habitats were equally high (Table 1, Table 3). This result does not conclusively support the theory that macrofaunal density is highest at the edges of beds, nor does it reject the hypothesis.

The composition of species in bare samples in PJ was largely dominated by *Gemma gemma,* which comprised up to two thirds of the total abundance of some samples. This species is slightly less dominant in PH Bare, but not to the same extent as PJ Bare. Without the abundance of *Gemma gemma*, the average macrofaunal abundance in bare areas would fall from 263 ($\pm$46) to 102 ($\pm$26) in PJ Bare and from 186 ($\pm$49) to 99 ($\pm$34) in PH Bare.

5.5 Faunal parameters are related to sediment properties

The channel leading to the study area at Port l'Hebert is narrower than that of Port Joli. This was expected to lead to restricted water flow and reduced capacity at Port l'Hebert, which would result in higher deposition of silts (>64µm particles) at Port l'Hebert than PJ. Because organic particles associate more frequently with silt than sand, PH was also expected to have more organic content in its sediments. Finally, it was expected that if any difference in sediment grain size was observed between

habitats, the silt fraction of interior samples would be larger than that of edge or bare samples due to the slowing of water that dense seagrass beds cause (Bowden *et al*. 2001).

However, quite the opposite was observed. Sediments at PJ had a higher silt fraction and organic content than sediments from PH. Additionally; edge habitats had significantly higher organic content than bare or interior samples. The unexpected silt fraction measurements may be due to low samples size, as only two silt samples from each habitat were analyzed for silt content for a total of six samples. The sample size was low due to time constraints on this project. The surprising results of the organic content measurements may be caused by the leeward edge effect discussed in section 5.1, as described by Bologna & Heck. Fast moving water above the seagrass canopy would keep particles in suspension until they hit the leeward edge of the bed, at which point water velocity would change and particles would settle out of the water column. Unfortunately, sediment size fraction data were not applied to BIOENV tests because there were only two data points per habitat. It is noteworthy that both PH and PJ study sites are highly depositional environments because the shapes and lengths of the bays change water velocity during tidal flow and cause suspended sediments to drop out of suspension.

The organic content of sediments was highest in edge habitats, and a notable maximum organic content was present in PH edge samples (Figure 5). This aligns with the increased density of all macrofauna seen in PH edge, as well as the increase in abundance in detritivores (Table 3). There is also an increase in the abundance of detritivores (deposit feeders) in PH Edge because of the increased availability of food in these locations. The reflection of faunal composition with changing organic sediments supports the hypothesis that macrofaunal parameters are related to sediment properties.

6. Conclusions

It was observed that some prevailing paradigms of seagrass beds and associated macroinvertebrate communities were supported by this study. It does indeed appear that the community structure within vegetated areas is different than that of unvegetated areas. There was no discrete positive relationship between faunal abundance and plant density and biomass; however there is indication that such a correlation may be observed in a study that measure more plant characteristics. Additionally, there seems to be a correlation between the species diversity and the plant characteristics measured here. The plant biomass, density and leaf length are certainly highest in interior habitats. Macrofaunal density in Port Joli seems to be highest in edge habitats, but this difference was not observed in Port l'Hebert and cannot be applied generally to all seagrass beds. The high organic content of sediments in PH edge samples aligns with the high macrofaunal density within this area; however, because there is low support for the relationship between sediment and macrofauna in this study and the parameters could not be tested using BIOENV, no firm conclusions can be drawn. Based on the conclusions of similar studies, I think that future studies should have higher sample sizes and different quantifications of 'interior' samples (cores taken from 5m from edge, 10m from edge, 15m from edge). This would further tease out subtle differences between locations within the bed and allow for more concrete conclusions to be drawn on the relationship between physical and biotic parameters of seagrass ecosystems.

Now that the abundance of macrofauna and their community structures have been identified in Nova Scotian seagrass beds, scientists can use this information to guide conservation and restoration projects. Using the data found in my study, researchers can calculate the services lost (biodiversity, carbon sequestration, etc.) in ecosystems that have sustained damages over a period of time, and use these calculations to restore ecosystem functions to their pre-damaged values. Similarly, this information can be used in conservation as a level at which ecosystem function should be maintained.

Further studies could calculate the biomass of macrofauna, as well as their abundance, to add to this body of information and make management plans that much stronger.

7. References

Abbott, R. Tucker. (1974). American Seashells, Second Edition. Litton Educational Publishing, Inc.: New York, NY.

Appy, Teresa D., Linkletter, Leslie E., & Dadswell, M.J. (1980). A Guide to the Marine Flora and Fauna of the Bay of Fundy: Annelida: Polychaeta. Fisheries and Marine Service Technical Report No. 920. Biological Station, St. Andrews, NB.

Attrill, M. J., Strong, J. A. and Rowden, A. A. (2000). Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography, 23*: 114–121.

Beer, Sven & Koch, Evamaria. (1996). Photosynthesis of marine macroalgae and seagrasses in globally changing CO_2 environments. *Marine Ecology Progress Series, 141*: 199-204.

Bell, J. D. and Westoby, M. (1986). Variation in seagrass height and density over a wide spatial scale: effects on fish and decapods. *Journal of Experimental Marine Biology and Ecology, 104*: 275–295.

Berkenbusch, Katrin & Rowden, Ashley A. (2007). An examination of the spatial and temporal generality of the influence of ecosystem engineers on the composition of associated assemblages. *Aquatic Ecology, 41*:129–147.

Birch, WR, and Birch, M.. (1984). Succession and pattern of tropical seagrasses in Cockle Bay, Queensland, Australia: A decade of observations. *Aquatic Botany, 19*: 343-367.

Bologna, Paul A. X. and Heck, Kenneth L. Jr. (2000). Impacts of seagrass habitat architecture on bivalve settlement. *Estuaries, 23*(4); 449-457.

Boström, C., Jackson, E. L., & Simenstad, C. A. (2006a). Seagrass landscapes and their effects on associated fauna: A review. *Estuarine, Coastal and Shelf Science, 68*(3), 383-403.

Boström, C., O'Brien, K., Roos, C., & Ekebom, J. (2006b). Environmental variables explaining structural and functional diversity of seagrass macrofauna in an archipelago landscape. *Journal of Experimental Marine Biology and Ecology, 335*, 52-73.

Boström, Christoffer & Bonsdorff, Erik. (2000). Zoobenthic community establishment and habitat complexity — the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series, 205*: 123–138.

Boström, Christoffer & Mattila, Johanna (1998). The relative importance of food and shelter for seagrass-associated invertebrates: a latitudinal comparison of habitat choice by isopod grazers. *Oecologia, 120*(1): 162-170.

Bricker SB, Ferreira, J.G., & Simas, T. (2003). An integrated methodology for assessment of estuarine

trophic status. *Ecological Modelling, 169*: 39–60.

Carman, M. R., & Grunden, D. W. (2010). First occurrence of the invasive tunicate *Didemnum vexillum* in eelgrass habitat. *Aquatic Invasions, 5*(1), 23-29.

Chambers, Patricia A., DeWreede, Robert E., Irlandi, Elizabeth A., & Vandermeulen, Herbert (1999). Management issues in aquatic macrophyte ecology: a Canadian perspective. *Canadian Journal of Botany, 77*: 471–487.

Commito, John A.; Currier, Carol A.; Kane, Laura R.; Reinsel, Kathleen A.; and Ulm, Irene M. (1995). Dispersal Dynamics of the Bivalve *Gemma gemma* in a Patchy Environment. Ecological Monographs, 65(1):1-20.

Connolly, Rod M. (1997). Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. *Hydrobiologia, 346*: 137–148.

Davis, R. C., Short, F. T., & Burdick, D. M. (1998). Quantifying the effects of green crab damage to eelgrass transplants. *Restoration Ecology, 6*(3), 297-302.

Deegan, L. A., Wright, A., Ayvazian, S. G., Finn, J. T., Golden, H., Rand Merson, R., & Harrison, J. (2002). Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquatic Conservation, 12*(2), 193-212.

Dennison, W.C., Orth, R.J., Moore, K.A., Stevenson, J.C., Carter, V., Kollar, S., Bergstrom, P.W., & Batiuk, R.A. (1993). Assessing water quality with submersed aquatic vegetation. *BioScience, 43*: 86–94.

Duarte, C.M , Middelburg, J., & Caraco, N. (2005).Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences, 2*: 1–8.

Duarte, C.M., & Chiscano, C.L. (1999). Seagrass biomass and production: A reassessment. *Aquatic Botany, 65*: 159–174.

Duarte, Carlos M. (2002). The future of seagrass meadows. *Environmental Conservation, 29*(2): 192-206.

Duffy, Emmett J., MacDonald, Kenneth S., Rhode, Jennifer M., & Parker, John D. (2001). Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology, 82*(9): 2417–2434.

Edsel, A. Caine (1989). Caprellid amphipod behaviour and predatory strikes by fish. *Journal of Experimental Marine Biology and Ecology,* 126(2): 173-180.

Erftemeijerb, Paul L. A., & Middelburg, Jack J. (1995). Mass balance constraints on nutrient cycling in tropical seagrass beds. *Aquatic Botany,* 50(1): 21-36.

Fonseca, M.S., Kenworthy, W.J. & Whitfield, P.E. (2000). Temporal dynamics of seagrass landscapes: A preliminary comparison of chronic and extreme disturbance events. *Biologia Marina Mediterranea,* 7: 373–376.

Forman, R. T. T. (1995). Some general principles of landscape and regional ecology. *Landscape Ecology,* 10(3), 133-142.

Frederiksen, M., Krause-Jensen, D., Holmer M., & Laursen, J. Sund (2004). Long-term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters. *Aquatic Botany,* 78: 167-181.

Glemarec M., LeFaou Y., & Cuq F. (1997). Long-term changes of seagrass beds in the Glenan Archipelago (South Brittany). *Oceanologica Acta,* 20: 217-227.

Gordon, D.M., Grey, K.A., Chase, S.C., & Simpson, C.J. (1994). Changes to the structure and productivity of a *Posidonia sinuosa* meadow during and after imposed shading. *Aquatic Botany,* 47**:** 265-275.

Gosner, Kenneth L. (1971). Guide to Identification of Marine and Estuarine Invertebrates. John Wiley and Sons, Inc.: Newark, New Jersey.

Hauxwell, J., Cebrián, J., & Valiela, I. (2003). Eelgrass *Zostera marina* loss in temperate estuaries: Relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series,* 247(1), 59-73.

Hauxwell, Jennifer, Cabrian, Justin, Furlong, Christopher, & Valiela, Ivan (2001). Macroalgal Canopies Contribute to Eelgrass (*Zostera marina*) Decline in Temperate Estuarine Ecosystems. *Ecology,* 82(4):1007-1022.

Healey, D., & Hovel, K. A. (2004). Seagrass bed patchiness: Effects on epifaunal communities in san diego bay, USA. *Journal of Experimental Marine Biology and Ecology,* 313:155-174.

Hemminga M, & Duarte, C.M. (2000). Seagrass Ecology. Cambridge (United Kingdom): Cambridge University Press.

Hovel, K. A. (2003). Habitat fragmentation in marine landscapes: Relative effects off habitat cover and configuration of juvenile crab survival in California and North Carolina seagrass beds. *Biological Conservation,* 110, 401-412.

Howard, R. K. (1987). Diel variation in the abundance of epifauna associated with seagrasses of the Indian River, Florida, USA. *Marine Biology,* 96(1):137-142.

Kaldy, J. E., & Dunton, K. H. (2000). Above- and below-ground production, biomass and reproductive ecology of thalassia testudinum (turtle grass) in a subtropical coastal lagoon. *Marine Ecology Progress Series,* 193(1), 271-283.

Larkum, A. W. D., Orth, R. J., & Duarte, C. M. (2006). *Seagrasses: Biology, ecology, and conservation*. Dordrecht, Netherlands: Springer.

Lewis, F. Graham (1984). Distribution of macrobenthic crustaceans associated with *Thalassia, Halodule* and bare sand substrata. *Marine Ecology Progress Series,* 19:101-113.

Marbà, N., Santiagoa, R., Díaz-Almelaa, E., Álvarezb, E., & Duarte, C. M.Seagrass (*Posidonia oceanica*) vertical growth as an early indicator of fish farm-derived stress. *Estuarine, Coastal and Shelf Science,* 67(3), 475-487.

McRoy, C. Peter, Barsdate, Robert J., and Nebert, Mary (1972). Phosphorus cycling in an eelgrass (*Zostera marina)* ecosystem. Limnology and Oceanography,17(1): 58-67.

Milewski, Inka (2004). Nutrient Pollution: A survey of eelgrass beds in estuaries and coastal bays in northern and eastern New Brunswick. Conservation Council of New Brunswick Inc. Accessed online on October 11 2010 at <http://www.elements.nb.ca/theme/invasive_species/inka/research.htm>.

Moore, Kenneth A, Neckles, Hilary A., & Orth,Robert J. (1996). *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. *Marine Ecology Progress Series,* 142:247-259.

Niklas, Karl J. (2005). Modelling Below- and Above-ground Biomass for Non-woody and Woody Plants. Annals of Botany, 95(2): 315-321.

Olesen, Birgit and Sand-Jensen, Kaj (1994). Demography of Shallow Eelgrass (Zostera Marina) Populations--Shoot Dynamics and Biomass Development. Journal of Ecology, 82(2): 379-390.

Orth, R. J., & Van Montfrans, J. (1984). Utilization of a seagrass meadow and tidal marsh creek by blue crabs (*Callinectes sapidus*): seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Marine Ecology Progress Series,* 41:283-294.

Orth, Robert, J., Carruthers Tim J. B., Dennison, William C., Duarte, Carlos M., Fourqurean, James W., Heck, Kenneth L. Jr., … and Williams, Susan L. (2006). A Global Crisis for Seagrass Ecosystems. *BioScience,* 56(12): 987- 996.

Peterson, C. H., Wong, M., Piehler, M. F., Grabowski, J. H., Twilley, R. R., & Fonseca, M. S. *Estuarine habitat productivity ratios at multiple trophic levels.* Unpublished manuscript.

Pollock, Leland W. (1998) A Practical Guide to the Marine Animals of Northeastern North America. Rutgers University Press: Piscataway, New Jersey.

Reusch, T.B.H., Ehlers, A., Hammerli, A, & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences of*

the United States of America, 102: 2826-2831.

Robbins, B. D., & Bell, S. S. (1994). Seagrass landscapes: A terrestrial approach to the marine subtidal environment. *Trends in Ecology & Evolution,* 9(8), 301-304.

Seymour, Norman R., Miller, Anthony G. & Garbary, David J. (2002). Decline of Canada geese (*Branta canadensis*) and common goldeneye (*Bucephala clangula*) associated with a collapse of eelgrass (*Zostera marina*) in a Nova Scotia estuary. *Helgoland Marine Research,* 56:198–202.

Short, Frederick T. & Burdick, David M. (1995). Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina. Limnology and Oceanography,* 40(4): 740-749.

Stoner, A. W. (1980). The role of seagrass biomass in the organisation of benthic macrofaunal assemblages. *Bulletin of Marine Science,* 30: 537–551.

Suchanek T.H., Williams, S.W., Ogden, J.C., Hubbard, D.K., Gill, I.P. (1985).Utilization of shallow-water seagrass detritus by Caribbean deep-sea macrofauna: δ 13C evidence. *Deep Sea Research,* 32: 2201–2214.

Taylor, D., S. Nixon, S. Granger, and B. Buckley (1995). Nutrient limitation and the eutrophication of coastal lagoons. *Marine Ecology Progress Series,* 127: 235–244.

Tolan, J. M., Holt, S. A., & Onuf, C. P. (1997). Distribution and community structure of ichthyoplankton in laguna madre seagrass meadows: Potential impact of seagrass species change. *Estuaries,* 20(2), 450-464.

Trans-Canada Highway. Nova Scotia Map. Accessed online November 17 2010 at <http://transcanadahighway.com/novascotia/map.htm>

Watanabe, Masako, Nakaoka, Masahiro, & Mukai, Hiroshi. (2005). Seasonal variation in vegetative growth and production of the endemic Japanese seagrass *Zostera asiatica*: a comparison with sympatric *Zostera marina*. *Botanica Marina,* 48(4): 266-273.

Weiss, Howard M. (1995). Marine Animals of Southern New England and New York: Identification Keys to Common Nearshore and Shallow Water Macrofauna. Hartford, Connecticut.

Zieman, J.C, Wood, E.J.F. (1975). Effects of thermal pollution on tropical-type estuaries with emphasis on Biscayne Bay Florida. Chapter 5. In: Wood EJF, Johannes RE. (eds.). Tropical marine pollution. Elsevier Publishing Co. New York.