

THE ROLE OF MARINE MACROPHYTES IN PROVIDING ESSENTIAL
ECOSYSTEM SERVICES: THEIR RELATIVE CONTRIBUTION AND
HOW SERVICES ARE IMPACTED BY EUTROPHICATION

by

Allison L. Schmidt

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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled “THE ROLE OF MARINE MACROPHYTES IN PROVIDING ESSENTIAL ECOSYSTEM SERVICES: THEIR RELATIVE CONTRIBUTION AND HOW SERVICES ARE IMPACTED BY EUTROPHICATION” by Allison L. Schmidt in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Supervisor: _____

Examining Committee: _____

Departmental Representative: _____

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*To Diego,
...for making me laugh. Siempre.*

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Abstract

Most coastal ecosystems are dominated by marine macrophytes that deliver a range of ecologically and economically important services such as carbon and nitrogen cycling and storage, and habitat provision to a range of associated species. The relative contribution of these services among different vegetated habitats, however, and their alteration due to anthropogenic stressors is little known. In this thesis, I first examined the within and between ecosystem structure and services of eelgrass (*Zostera marina*) and rockweed (*Ascophyllum nodosum*) beds in Atlantic Canada. Both habitats significantly enhanced the overall abundance and diversity of associated species, whereas differences in the species assemblages were attributed to differences in canopy structure within and between habitats. Changes in the canopy structure of the foundation species will affect associated food webs and ecosystem services. Next, I used large-scale field surveys to examine the effects of eutrophication on the structure and services of eelgrass beds. As eutrophication increased, plant dominance shifted from eelgrass to macroalgae and phytoplankton at a regional scale. The faunal community showed increases in filter feeders, detritivores and some herbivores, while sensitive species declined. These faunal changes can be linked to enhanced food availability and predation refuge offered by increased phytoplankton and opportunistic macroalgae. However, the loss of eelgrass and sensitive species highlight the negative consequences of eutrophication on eelgrass ecosystems and the services they provide. I also reviewed the global carbon and nitrogen storage and habitat services of mangroves, salt marshes, seagrass meadows and macroalgal beds. Despite only occupying 0.7% of the ocean area, together these ecosystems make up 12% of the oceanic carbon stock thereby playing an important role in global carbon and nitrogen storage. Moreover, these macrophyte habitats enhanced species richness and abundance of associated fauna and juvenile fishes. Overall, my findings indicate that each macrophyte habitat has its strengths yet all are essential in providing the full range of ecosystem services. Increasing human impacts along the coasts, however, are threatening macrophyte ecosystems worldwide, and their further decline will impair the provision of important services and human well-being. Lastly, I discuss the implications of my work for management and conservation.

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CHAPTER 1

Introduction

The normal functioning of terrestrial and aquatic ecosystems that form the Earth's life-support system directly and indirectly provide a range of essential goods and services (Daily 1997); yet we are just beginning to recognize the magnitude of the contribution of ocean ecosystems to human well-being. Ecosystem services fall under four broad categories: 1) provisioning services such as food, fuel and freshwater; 2) regulating services such as climate, water purification and erosion control; 3) supporting services such as habitat and nursery provision and 4) cultural services such as recreation, science and education (de Groot et al. 2002; Millennium Ecosystem Assessment 2005). The recent rise in ecological economics has led to a number of studies placing a price tag on ecosystem services in an attempt to raise awareness of their importance to scientists, economists, policy makers and the general public (Costanza et al. 1997; Balmford et al. 2002; Martínez et al. 2007). All of these studies have their limitations but they are useful in putting the life supporting services of ecosystems into perspective and examining the relative contribution of large biomes. For example, the total global value of the marine biome (\$21 trillion 1994USD yr⁻¹) has been estimated as almost double that of the terrestrial biome (\$12.3 trillion 1994USD yr⁻¹), with 60% of the marine total (\$12.5 trillion 1994USD yr⁻¹) coming from the coastal ocean (Costanza et al. 1997).

For centuries, humans have exploited, altered and polluted ocean ecosystems without considering their impacts on ecosystem functions and the ability of ecosystems to provide the goods and services we depend on (Jackson et al. 2001; Lotze and Milewski 2004; Lotze et al. 2006; Worm et al. 2006). The most heavily affected by anthropogenic activities, both past and present, are coastal ecosystems because of their proximity to human settlements and accessibility (Jackson et al. 2001; Lotze et al. 2006). One of the largest and most pervasive threats is nutrient enrichment and the consequent eutrophication of

coastal waters, which is only expected to increase with growing coastal human populations (Millennium Ecosystem Assessment 2005). Therefore, understanding the impacts of nutrient loading on coastal ecosystems and their consequences for the ocean and society is increasingly urgent.

The majority of coastlines around the world are dominated by vegetation, from intertidal and subtidal macroalgal and seagrass beds, to mangroves and salt marshes that provide a range of ecosystem services (Adam 2002; Alongi 2002; Steneck et al. 2002a; Schmidt et al. 2011). However, all of these ecosystems are currently faced with declining global populations (Valiela et al. 2009; Waycott et al. 2009; Wernberg et al. 2011) and an increasing number of threatened species (Polidoro et al. 2010; Short et al. 2011). The regional loss of coastal biodiversity is known to impair at least three critical ecosystem services; the number of viable target fisheries, provision of nursery habitat, and filtering and detoxification of coastal waters (Worm et al. 2006). In addition, quantifying carbon storage within these coastal ecosystems as well as how it changes with human stressors is imperative as we try to understand oceanic carbon sinks in the face of climate change (McLeod et al. 2011). Given the substantial contribution of the coastal ocean to human well-being, understanding the role that different coastal ecosystems play in the provision of carbon and nitrogen storage and habitat and nursery services, and how these services are affected by eutrophication is crucial for the effective conservation, management and restoration of coastal ecosystems and their services.

1.1. Outline of Thesis Chapters

In Chapter 2, I compare the ecosystem structure and services of two common yet contrasting coastal ecosystems of the northwest Atlantic; soft sediment beds of eelgrass (*Zostera marina*) and rocky shores dominated by rockweed (*Ascophyllum nodosum*). I use field survey data collected inside, along the edge and outside the macrophyte canopies to examine how the physical structure as well as the storage and habitat services vary within and between these two different ecosystems along the Atlantic coast of Nova Scotia. Previous works in this research field have compared specific ecosystem services be-

tween vegetated and unvegetated locations (e.g. Arrivillaga and Baltz 1999) or among ecosystems for specific taxonomic groups (e.g. Edgar 1990); making my study unique in examining multiple services and taxonomic groups. Moreover, I use a network modeling approach to examine differences in food-web structure between the two ecosystems and their respective vulnerability to simulated species loss. This chapter addresses an important knowledge gap since differences in basic habitat structure may affect the functions, services and resilience of an ecosystem with potentially wide-ranging consequences on associated species and human well-being.

In the third and fourth chapters, I used a large scale field survey across 12 estuaries in two provinces in Atlantic Canada to examine the effects of eutrophication on the structure, functions and services of eelgrass (*Zostera marina*) ecosystems. While Chapter 3 deals with the effects on the assemblage of primary producers, Chapter 4 focuses on the effects on the fish and invertebrate communities associated with eelgrass habitats. Eutrophication induced changes in phytoplankton biomass, benthic macroalgae and eelgrass bed structure have been previously documented in individual locations (e.g. Short et al. 1995; Hauxwell et al. 2001). However, little attention has been paid to the simultaneous changes in all of these components across multiple sites, or how changes in seagrass bed structure and primary producer abundance affect carbon and nitrogen storage services. Nor is there a detailed account of the species-specific response of benthic macroalgae which may have an important role in determining predator-prey interactions. Therefore, in Chapter 3, I attempt to address these knowledge gaps by examining the regional-scale effects of eutrophication on 1) the individual and combined abundances of phytoplankton, benthic macroalgae and eelgrass, 2) the structure and storage services of eelgrass beds and 3) the species-specific changes in benthic macroalgae. Changes in the structure of the eelgrass bed, the abundance of different primary producers as well as the identity and structural complexity of associated benthic macroalgae may affect the way in which different fauna species or functional groups use eelgrass habitats for foraging, shelter and settlement. Consequently, such changes will alter the pathway of nutrients through the benthic food web (Deegan et al. 2002). In addition, eutrophication can significantly alter water column and sediment chemistry, particularly through oxygen depletion and anoxia, creating a more hostile chemical environment that may lead to different responses in the

diverse mobile and sessile fauna (Gray et al. 2002) associated with eelgrass habitats. As such, in Chapter 4, I examine the species and functional group-specific responses in the abundance and habitat usage of juvenile and adult fishes and invertebrates with increasing eutrophication, as well as changes in overall community structure.

In Chapter 5, I use a literature review to examine the relative contribution of seagrasses, mangroves, macroalgae and salt marshes in binding carbon and nitrogen, and providing habitat and nursery services on a global scale. Although estimates of global carbon storage and sequestration have been made for seagrasses, mangroves and salt marshes (Nellemann et al. 2009; McLeod et al. 2011), they focus on local carbon burial thereby omitting macroalgal habitats because they inhabit rocky substrates. Yet, macroalgae produce large amounts of detritus that is exported to (Krumhansl and Scheibling 2011) and potentially buried in adjacent soft sediment habitats. In addition, unlike terrestrial estimates of carbon storage and sequestration (Del Grosso et al. 2008), marine estimates do not include standing stock biomass, a topic that I directly address by estimating the global standing carbon stock of each ecosystem, that I also compare to other oceanic and terrestrial biomes. Currently, there is no global comparison of the habitat and nursery services of coastal vegetated ecosystems. To date, most studies have focussed on one species or species group and are limited to local comparisons of one to two ecosystems with nearby unvegetated areas (e.g. Tupper and Boutilier 1995; Guidetti 2000). To address this knowledge gap, I use meta-analytical techniques to examine the enhancement effect of each macrophyte on the species richness and abundance of fishes, decapods crustaceans and infauna as well as juvenile fish abundance on a global scale. I also discuss the major threats to macrophyte ecosystems and identify important knowledge gaps that currently limit our full understating of the magnitude of the ecosystem services they provide.

Finally, in Chapter 6, I summarize my overall findings and propose future work to address some of the current knowledge gaps. I also discuss how existing and future knowledge can be used to inform the management process for coastal vegetated habitats.

CHAPTER 2

Ecosystem Structure and Services in Eelgrass *Zostera marina* and Rockweed *Ascophyllum nodosum* Habitats

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2.1. Introduction

Coastal ecosystems are among the most productive, diverse, and ecologically important habitats worldwide, and generate essential services that directly and indirectly benefit human well-being (De Groot et al. 2002, Millennium Ecosystem Assessment 2005a). Around the world, coastlines are dominated by structurally complex habitats created by intertidal or submerged aquatic vegetation that provide nutrient cycling, carbon storage, nursery, and juvenile habitat for a range of ecologically and economically important species (Adam 2002; Alongi 2002; Duarte 2002; Steneck et al. 2002a; Thompson et al. 2002). Despite their ecological importance, marine vegetated habitats are facing increasing anthropogenic impacts (e.g. harvesting, disturbance, pollution, climate change) leading to fragmentation, depletion, or localized extinction of the habitat and its dependent species (Millennium Ecosystem Assessment 2005; Lotze et al. 2006; Waycott et al. 2009)

Marine macrophytes use carbon and nitrogen as a function of their growth and are major contributors to net oceanic primary production stored in sediments (>30% of total ocean carbon storage; Duarte and Cebrián (1996)). However, humans have on average

doubled nitrogen loading (≥ 5 to 10 fold in many cases) to coastal waters around the world since pre-industrial times (Millennium Ecosystem Assessment 2005). Increased nutrient loading has been shown to change primary producer abundance and species composition (Duarte 1995) and impair the system's ability to store and cycle nutrients (Worm et al. 2000). Anthropogenic greenhouse gas emissions have also increased exponentially since 1750 resulting in a net warming effect (IPCC 2007). Increasing water temperature is predicted to change the distribution and productivity of seagrasses (Short and Neckles 1999) and shift the composition of rocky shore *Ascophyllum nodosum*-dominated habitats to mixed fucoid beds (Ugarte et al. 2010). The consequences of these shifts to the nitrogen retention and carbon storage capacity of coastal habitats are unknown.

Coastal vegetated habitats also play an important role as breeding, nursery, and foraging grounds, and provide shelter for associated species (Adam 2002; Alongi 2002; Duarte 2002; Steneck et al. 2002a; Thompson et al. 2002) including many commercially important fish and invertebrates (Rangeley 1994; Heck et al. 2003; Hughes et al. 2009). The depletion of many commercial fish stocks and non-recovery of others may at least partly be driven by the loss or degradation of marine vegetated habitats (Hughes et al. 2009). Determining the relative importance of different vegetated ecosystems as juvenile habitat and refuge is vital for the proper management of finfish and invertebrate fisheries that depend on these habitats.

The present study aims to assess the ecosystem structure and services of 2 common yet contrasting temperate habitats in the northwest Atlantic: seagrass and rockweed beds. Previous studies have compared specific ecosystem services (e.g. nursery habitat) between vegetated and unvegetated habitats (e.g. Perkins-Visser et al. 1996; Arrivillaga and Baltz 1999) or among vegetated habitats for one species or taxonomic group such as fish or invertebrates (e.g. Edgar 1990; Tupper and Boutilier 1997). Comparisons of multiple services among different habitats have been largely missing—an important knowledge gap as differences in habitat structure may affect the functions and services they provide (Beck et al. 2001; Bologna and Heck 2002). The objectives of the present study were to compare (1) canopy structure, nitrogen and carbon storage, (2) species abundance and diversity of associated communities, and (3) habitat usage of adults and juveniles within

and between eelgrass and rockweed canopies, based on extensive field surveys. Because biodiversity is essential for ecosystem functioning and services (Millennium Ecosystem Assessment 2005; Worm et al. 2006), we then used binary network models of predator–prey interactions to compare (4) differences in food-web structure and their robustness to simulated species loss. Together, the field surveys and food-web modeling proved a powerful approach in evaluating ecosystem structure and services in near-shore ecosystems.

2.2. Methods

2.2.1. Study Sites.

Study sites were located along the Atlantic coast of Nova Scotia, Canada (Fig. 2-1a, Table 2-1). Here, sheltered to moderately exposed intertidal and shallow subtidal rocky shores are dominated by extensive beds of rockweeds *Ascophyllum nodosum* and *Fucus* spp., while soft-sediment habitats are generally dominated by monospecific beds of eelgrass *Zostera marina*. We selected 4 sites dominated by *A. nodosum* beds (interspersed *Fucus vesiculosus* $\leq 35\%$ of canopy, hereafter rockweed; Fig. 2-1b) and 3 sites with *Z. marina* (hereafter eelgrass; Fig. 2-1c) that were sampled 16–26 September 2006, when most mobile species are abundant (Schmidt and Scheibling 2007). During the sampling period, sea surface temperature was $17.0 \pm 2.0^\circ\text{C}$ (SD) and significant wave height 1.4 ± 0.4 m (data acquisition in Halifax Harbour, buoy station 44258, $44^\circ 49' \text{N}$, $63^\circ 39' \text{W}$, 40–100 km from our study sites; Fisheries and Oceans Canada, Integrated Science and Data Management, <http://www.meds-sdmm.dfo-mpo.gc.ca>).

2.2.2. Sampling Design.

At each site, 3 transects were laid parallel to the shore inside (>10 m from the vegetation-bare substrate interface), along the edge (within the bed <1 m from the interface), and outside (>10 m away from any canopy-forming vegetation) of the eelgrass or rockweed bed. Transect depth at high tide ranged from 1 to 3 m, with outside transects generally deeper than inside transects, but differences between the transects were <1 m within each site. Highly mobile fauna were censused by the same observer swimming along

transects ($\sim 0.08 \text{ m s}^{-1}$) during the day- and nighttime high tides to capture diurnal patterns in species abundance and size. We used the transect size ($50 \times 4 \text{ m}$) recommended for underwater visual censuses of coral reefs (Mapstone and Ayling 1998). Due to constraints imposed by bed size or visibility, some transects had to be shortened or narrowed (Table 2-1), the effect of which we analyzed (see Community Structure and Habitat Services).

Canopy structure, abundance of mobile benthic species (hereafter quadrat macrofauna), and percent cover of sessile benthic and epiphytic organisms were assessed during the daytime high tide using $0.5 \times 0.5 \text{ m}$ quadrats, covered in alternating (every 25 cm) red and white electrical tape, placed at 5 m intervals along each transect. In the present study we consider the ‘phyte’ in epiphyte as referring to the host plant (eelgrass or rockweed), as recommended by Steel and Wilson (2003). The percent cover measures of the canopy and community were estimated to the nearest 2% using the coloured tape as a guide. We considered both sides of all the eelgrass blades in the quadrat as habitable space. Therefore, if both sides of all of the blades in the quadrat were covered with epiphytes, this would represent 100% cover. We first identified the species on the blades and then estimated the percent cover of each species on the collective, not each individual blade. All organisms were identified to the lowest possible taxon in the field where possible, or in the laboratory when the organisms needed further examination under a microscope. The smallest macrofauna individual sampled was 2 cm whereas epiphytes such as bryozoan colonies or spirorbid worms were typically 1 cm or less.

2.2.3. *Canopy Structure and Regulating Services.*

Our first objective was to compare the 3-dimensional canopy structure and nitrogen (N) and carbon (C) retention between the different canopy types (eelgrass, rockweed) and locations (in, edge, out). Canopy structure was assessed in each quadrat as % canopy cover, average canopy height (cm), and shoot (eelgrass) or holdfast (rockweed) density. The canopy cover was estimated using a $0.5 \times 0.5 \text{ m}$ quadrat by the same observer hovering just above the top of the canopy. The average canopy height was estimated by placing the zero end of a measuring tape on the bottom in the middle of the quadrat and extending it upwards until it reached the average height of the plants within the quadrat. Rockweed

holdfasts were counted in the 0.5×0.5 m quadrat and eelgrass shoots in a 0.25×0.25 m subset. Two samples of macrophyte tissue were collected on each end of the interior and edge transects for C-N analysis. Epiphytes were scraped from tissue samples prior to drying (70°C , 48 h) and homogenizing, and ~ 50 mg dry weight was analyzed with a Perkin Elmer CHN 2400 Analyser.

To estimate carbon and nitrogen storage at the canopy scale, we needed biomass estimates. We were unable to collect canopy biomass in 2006, but collected biomass together with associated % cover, shoot density, and canopy height for eelgrass in October 2007 and rockweed in September 2008 in order to reconstruct 2006 biomass. Stepwise multiple regression determined that the best combination of variables to predict rockweed biomass were shoot density and canopy height ($R^2_{\text{adj}} = 0.751$; $F_{2,20} = 31.1$, $p < 0.001$), while for above-ground eelgrass biomass, shoot density alone was the best predictor ($R^2_{\text{adj}} = 0.917$; $F_{1,11} = 121.8$, $p < 0.001$). The respective regression equations (rockweed biomass = $0.10 \times$ shoot density + $0.14 \times$ canopy height; eelgrass biomass = $0.003 \times$ shoot density) were then used to estimate 2006 biomass based on canopy structure. Dry weight of rockweed and eelgrass was 24.6% (± 0.5 SE) and 15.5% (± 0.4 SE) of wet weight, respectively. We then used the average % tissue carbon and nitrogen per location within each site to estimate the amount of carbon and nitrogen retained (kg m^{-2}) in eelgrass (aboveground only) and rockweed beds.

We used linear mixed-effects models (LMM) to examine differences in canopy structure (% cover, biomass, shoot density, canopy height), C-N tissue content and ratio, and carbon and nitrogen retention between canopy types (fixed factor with 2 levels: rockweed and eelgrass) and locations (fixed factor with 2 levels: in and edge) with sites as a random factor nested within canopy type. Canopy cover was arcsine-, and all other variables except canopy height and nitrogen retention were $\log(x + 1)$ -transformed to satisfy assumptions of normality and variance homogeneity. Where significant interactions were detected, we performed post-hoc comparisons using the Sidak correction. We used SPSS (version 15.0 for Windows) for all mixed-effects models.

2.2.4. *Community Structure and Habitat Services.*

Our second objective was to evaluate differences in associated species communities, including mobile and sessile flora and fauna, between canopy types and locations within canopies. We used a 3-factor multivariate permutational analysis of variance (PERMANOVA) to examine differences in biotic components (factors: Canopy, Location, Site(Canopy)) and diurnal differences in transect macrofauna (factors: Location, Site, Time of day). PERMANOVA was performed on the Bray-Curtis similarity matrix for (1) all species combined across collection methods using presence/absence and (2) separately for transect macrofauna, quadrat macrofauna, and sessile benthic and epiphytic species. Species abundance (density m^{-2} and percent cover) data were square-root transformed to down-weight the influence of highly abundant species and allow the rare species to influence the resemblance. We also used the zero-adjusted Bray-Curtis similarity matrix for the species abundance data to dampen the fluctuations of the metric for near-blank samples in an analogous way to the addition of a constant to the log transformation (Clarke and Gorley 2006). Using analogues of the ANOVA estimators, PERMANOVA also estimates the components of variation for both fixed and random factors (Anderson et al. 2008a). These estimators are directly comparable and useful in determining the relative importance of different terms in the model in explaining the overall variance. Since the estimates are in terms of squared units of the Bray-Curtis similarity, the square root (SQRT-V) is taken to put them back into % (Anderson et al. 2008a). Cluster analysis was used when PERMANOVA detected a significant diurnal, canopy, location, or interactive effect, and the SIMPER routine was used to identify those species that consistently contributed to the observed dissimilarities (dissimilarity / SD ≥ 1 ; Clarke and Warwick (2001)). We tested the effects of shorter transect lengths on our results by randomly removing between 1 and 6 quadrats (depending on the original transect length) from all transects to the minimum standard of 5 quadrats (Table 2-1) and re-running the PERMANOVA and SIMPER analyses on all assemblage components (quadrat macrofauna, sessile benthic, and epiphytic species) collected using quadrats. We then compared the results between the original and shortened data sets (Table A-1). All non-parametric permutation procedures and cluster analyses were performed using PRIMER (version 6.1.11) with PERMANOVA+ (version 1.0.1, PRIMER-E, Plymouth).

LMMs were also used to test for differences in overall species richness as well as total abundance, species richness, Shannon diversity, and Pielou's evenness indices of each assemblage component (transect and quadrat macrofauna, sessile benthic, and epiphytic species) between locations (three levels: in, edge, and out) and canopy types (two levels: rockweed and eelgrass) with sites as a random factor nested within canopy. The total abundances of sessile benthic and epiphytic species were arcsine-transformed to satisfy assumptions of normality and variance homogeneity.

2.2.5. *Juvenile Habitat and Nursery Services.*

Our third objective was to test whether adult and juvenile animals use the 2 canopies in different ways. The number (m^{-2}) and size (cm) of mobile fishes and decapod crustaceans (except hermit crabs) were estimated using transects for highly mobile species and quadrats for slower-moving and cryptic species. To separate juveniles from adults, we estimated individual total length of fishes and carapace width of decapods using a 15 cm scale bar with 1 cm graduations, and used published age at maturity data (Table A-2) to group species into their respective adult and juvenile categories. Where species-specific data were not available for our region, we used the minimum reported total length at maturity for the closest region for the same or a related species (same genus or family if necessary) with a similar maximum size. Because of the overabundance of zeros, we used regression tree models to summarize the habitat and nursery services data. Tree-based models were fitted by binary recursive partitioning and used as alternatives to linear and additive regression (Clark and Pregibon 1992). We grew a tree using the total abundance and abundance of each species observed at more than one site with life stage (adult, juvenile), canopy type (rockweed, eelgrass), and location (in, edge, out) as categorical predictors. All regression trees were grown using the statistical package R (version 2.8.0, R Foundation for Statistical Computing).

2.2.6. *Food-web Structure and Functioning.*

Finally, we assembled the species lists into binary presence-absence food webs to compare food-web structure between rockweed and eelgrass habitats. Species lists were compiled from field surveys and trophic information from the scientific literature for the

study region (Table A-3). Food webs contained all species identified in the field including primary producers, benthic and pelagic invertebrates, and fishes. We also included marine mammals and birds that were observed in the field or are known to occur in these habitats in Nova Scotia (I. McLaren pers. comm.; Table A-3). Species that shared 100% of their links with other species were aggregated into trophic groups to account for potential differences in resolution and completeness of species lists between habitats (Cohen and Briand 1984; Dunne 2006). We used 16 properties to characterize food-web structure (Table 2-2, based on Dunne et al. 2004; Coll et al. 2008) that were estimated using previously developed software (Williams and Martinez 2000; Williams et al. 2002). Visualization was done using FoodWeb3D (R. J. Williams, Pacific Ecoinformatics and Computational Ecology Lab). We then compared the rockweed and eelgrass food webs to 18 other published aquatic food webs from temperate and tropical systems (Dunne et al. 2004) using MDS and cluster analysis on the normalized Euclidean distance matrix of 11 properties common to all food webs (Table 2-2).

To examine whether differences in structural properties affect the robustness of each food web to species loss, we explored the effects of simulated species removals on triggering secondary extinctions (Dunne and Williams 2009). A secondary extinction is defined as the loss of a species that occurs when a previous removal results in the loss of prey or when a cannibalistic species loses all of its prey except itself. Species loss was simulated sequentially by removing (1) the least connected species, the most connected species (2) including and (3) excluding primary producers (i.e. basal species), and (4) randomly chosen species (from 1000 random removal sequences) in each food web. We consider an ecosystem to be collapsed if all species have gone extinct.

2.3. Results

2.3.1. Canopy Structure

Canopy cover was significantly higher inside than at the edge of rockweed and eelgrass beds (Fig. 2-2a, LMM: $F_{1,127.9} = 18.2$, $p < 0.001$) without differences between canopy types. Biomass of rockweed was 8× that of eelgrass (Fig. 2-2b; $F_{1,4.88} = 55.3$, $p =$

0.001) with no differences between bed locations. Shoot density was 4× higher in eelgrass than rockweed (Fig. 2-2c; $F_{1,4.91} = 9.13$, $p = 0.03$) and canopy height double (Fig. 2-2d; $F_{1,5} = 9.16$, $p = 0.029$), with eelgrass blades reaching lengths of >1 m. In both habitats, shoot density and canopy height were greater inside than along the edge ($F_{1,128.2} = 4.78$, $p = 0.03$; $F_{1,127.2} = 4.06$, $p = 0.046$, respectively) with no interactions between canopy type and location.

2.3.2. Carbon and Nitrogen Retention

Tissue carbon content was similar in both canopy types (LMM: $F_{1,5.8} = 1.12$, $p = 0.33$) and across locations (Fig. 2-3a; $F_{1,28.2} = 1.12$, $p > 0.33$), while tissue nitrogen was almost double in eelgrass (Fig. 2-3b; $F_{1,4.84} = 22.03$, $p = 0.006$) but similar between locations. There was a significant interaction between canopy and location ($F_{1,127.5} = 5.56$, $p = 0.02$) for carbon storage, which was on average 14× greater in rockweed than eelgrass beds (Fig. 2-3c; post hoc: $p < 0.001$). Also, carbon storage inside rockweed beds was 2× that of their edges (post hoc: $p < 0.01$), while there was no difference within eelgrass beds (post hoc: $p = 0.941$). Nitrogen retention was 8× greater in rockweed beds (Fig. 2-3d; $F_{1,4.93} = 42.7$, $p = 0.001$) and about 1.5× greater inside both canopies than along the edge ($F_{1,128} = 3.8$, $p = 0.054$). Despite higher tissue nitrogen in eelgrass, the greater carbon storage and nitrogen retention of rockweed is related to its much higher biomass per unit area (Fig. 2-2b).

2.3.3. Diurnal Patterns in Macrofaunal Assemblage

Deteriorating weather conditions precluded nighttime sampling in 2 eelgrass sites, thus statistical tests for diurnal differences were performed for rockweed habitats only. Multivariate 3-factor PERMANOVA (Location, Site [random], and Time of day) detected a significant difference between sites (pseudo- $F_{3,6} = 3.17$, $p = 0.03$) and locations (pseudo- $F_{2,6} = 4.16$, $p = 0.007$) but not in the time of day or any of the interactions ($p > 0.11$). Nevertheless, some species were only observed at night (*Homarus americanus*, *Gadus morhua*, *Microgadus tomcod* in rockweed; *Cancer borealis* in eelgrass) or day (*Pholis gunnellus* in rockweed; Table A-4). Some were more frequently observed during night (e.g. *Anguilla rostrata*) or day (e.g. *Scomber scombrus*, *Sygnathus fuscus*, *Tautogo-*

labrus adspersus), and others had similar abundances during night and day (*Gasterosteus aculeatus* and *Carcinus maenas* in eelgrass). A few species were more abundant along habitat edges than the interior (*Sygnathus fuscus*, *T. adspersus* in rockweed). Because of unbalanced sampling of habitat types we only used daytime data hereafter.

2.3.4. Community Structure and Habitat Services

Overall, 44 species/genera (excluding canopy species unless epiphytes) were identified during field surveys, 3 of which were observed only at night, yielding a daytime total of 41 taxa. Of these, 33 species were found in rockweed and 23 in eelgrass habitats (Table A-5). Within rockweed beds, 48% of taxa were found inside and 78% along the edge, compared to 69% inside and 61% along the edge of eelgrass beds. Both eelgrass and rockweed had a similar percentage of taxa outside the canopy (35 and 39%, respectively). We did not find mobile transect macrofauna outside canopies during the day, and no epiphytes given the lack of foundation species (Table A-5). Eighteen taxa were found exclusively in rockweed and 7 in eelgrass. The canopy edges had the highest number of exclusive taxa (12) compared to 4 inside and 3 outside canopies.

We first evaluated whether different transect lengths had an effect on our data set. The abundance of mobile fauna in all transects was very low, highly variable, and lacked significant differences in any factor (see Habitat provision). Our comparison between the original and shortened transect lengths for the quadrat macrofauna, sessile benthic, and epiphytic species (Table A-1) indicated that most differences in composition and abundance were between sites and not driven by the number of quadrats used to collect the data. This was corroborated by previous studies examining the effect of transect length and width on highly mobile fishes and invertebrates (see Table A-1). Together, this permitted us to use the original data for all further analyses.

Species richness of the entire assemblages (Fig. 2-4a) was greatest along the edge of both canopy types (LMM: $F_{2,10} = 11.2$, $p = 0.003$) without differences between canopies. There was a significant interaction between canopy and location (PERMANOVA: pseudo- $F_{2,10} = 3.1$, $p = 0.007$) for community composition with significant differences between locations within rockweed beds, where inside and edge locations were similar (post hoc: $p = 0.16$) but both different from outside ($p < 0.031$). Cluster analysis revealed

distinct canopy groupings and similarities between inside and edges for both rockweed and eelgrass (Fig. 2-4b), while assemblages outside both canopies clustered together. SIMPER analysis identified *Lacuna vincta* and *Crangon septemspinosa* as occurring more often in eelgrass, and *Mytilus* sp. and *Chondrus crispus* in rockweed (Table A-5). The epiphytic invertebrates *Membranipora membranacea* and *Spirorbis* sp. and sessile benthic *Semibalanus balanoides* and *C. crispus* were more often inside or along the edge, whereas *Pagurus* sp., *Pseudopleuronectes americanus* and *Crangon septemspinosa* were more often outside.

Abundance and species richness patterns differed among different components of the assemblage (Fig. 2-5). The abundance of all mobile transect and quadrat macrofauna was higher inside and along the edge than outside (Fig. 2-5a,b), whereas sessile benthic and epiphytic species were most abundant along the edge (Fig. 2-5c,d). For highly mobile transect fauna (Fig. 2-5a), no significant differences in total abundance or community composition occurred between canopy types (LMM: $F_{1,5} = 0.78$, $p = 0.79$; PERMANOVA: pseudo- $F_{1,6} = 0.17$, $p = 1$, respectively) or locations within habitats ($F_{2,10} = 1.7$, $p = 0.22$; pseudo- $F_{1,6} = 0.18$, $p = 0.9$) nor was there an interaction ($F_{2,10} = 1.5$, $p = 0.28$; pseudo- $F_{2,6} = 0.44$, $p = 0.73$), likely due to low occurrences and large variability in the data. Species richness was similar within and between canopies, but no mobile species were observed outside (LMM: $F_{2,10} = 7.96$, $p = 0.009$; Fig. 2-5e).

For the quadrat macrofauna community, a significant interaction between location and site nested within canopy was detected in the PERMANOVA (Table 2-3), which was driven by significant differences in species abundance and composition between inside and edge locations in 3 of 7 sites (Table 2-4). The total abundance of quadrat macrofauna (Fig. 2-5b) inside eelgrass beds was double that inside rockweed beds, and while highest along the edge in rockweed was highest inside eelgrass beds (LMM Interaction: $F_{2,205} = 6.56$, $p = 0.002$; Fig. 2-5b). The significant effect of canopy and location on the community accounted for 23.8 and 18.8% of the variance, respectively (Table 2-3), which was lower than the residual (27.8%) but higher than the variance explained by the interaction Location x Site(Canopy) (18.1%). SIMPER analysis indicated that *Pagurus* sp., *Lacuna vincta*, and *Crangon septemspinosa* were more abundant in eelgrass, and *Littorina* spp. and *Carcinus maenas* in rockweed. Species consistently more abundant in the canopy in-

terior included *Lacuna vincta*, *Littorina* spp., *Asterias forbesii*, and *Carcinus maenas*, whereas *Crangon septemspinosa* and *Pagurus* sp. were more abundant outside. Quadrat macrofauna richness was higher inside and along the edge (LMM: $F_{2,200.3} = 5.91$, $p = 0.003$) without differences between canopies ($F_{1,5.0} = 0.45$, $p = 0.84$) or an interaction ($F_{2,200.3} = 2.66$, $p = 0.072$; Fig. 2-5f). Diversity was similar within and between canopies ($p > 0.260$), yet evenness increased from inside to edge to outside ($F_{2,145.2} = 2.93$, $p = 0.057$).

Sessile benthic species were on average 14× more abundant in rockweed than eelgrass, and within rockweed habitats 2 to 10× more abundant along the edge than outside or inside the canopy, respectively (LMM Interaction: $F_{2,200.4} = 4.08$, $p = 0.018$; Fig. 2-5c). The significant interaction Location x Site(Canopy) for the sessile benthic community (Table 2-3) was likely driven by the low number of species (denominator of post hoc *t*-test was 0) in 2 eelgrass sites and significantly different assemblages found along the edge at 2 rockweed sites (Table 2-4). SIMPER analysis identified *Chondrus crispus* and *Cladophora rupestris* as being more abundant along the edge in rockweed. Sessile benthic species richness was significantly greater along the edge of rockweed beds compared to other locations or eelgrass (LMM Interaction: $F_{1,200.4} = 31.5$, $p < 0.001$; Fig. 2-5g), yet this was the only location with >1 species.

Total epiphyte abundance was 10× greater along the edge than inside rockweed beds, while there was a more even distribution in eelgrass (LMM Interaction: $F_{2,200.3} = 3.0$, $p = 0.053$). The interaction Location x Site(Canopy) detected in the epiphytic species assemblage (Table 2-3) was due to the low number of species (denominator of post hoc *t*-test was 0) at 2 rockweed sites and the lack of significance when comparing the inside and edge locations in eelgrass (Table 2-4), but overall the significant effect of location on the epiphyte assemblage explained most of the variation after the residual and interaction with site (Table 2-3). SIMPER analysis identified *Spirorbis* sp. and *Membranipora membranacea* as more abundant along the edge in eelgrass and *Fucus vesiculosus* as more abundant inside rockweed. Epiphytic species richness and diversity were greatest along the edge of canopies, and richness was on average 14% greater in eelgrass than rockweed (LMM Diversity: $F_{2,200.4} = 14.0$, $p < 0.001$; Richness: Interaction, $F_{2,200.3} = 3.28$, $p = 0.040$; Fig. 2-5h).

2.3.5. *Juvenile Habitat and Nursery Services*

Overall, the abundance of adult and juvenile fishes and decapods in transects and quadrats was low and variable (Fig. 2-6). Transect species were found exclusively inside (adults and juveniles) or along the edge (juveniles) of rockweed and eelgrass beds (Fig. 2-6a,c). The regression tree indicated location within habitat as the most important splitting factor (Fig. 2-7). Within a canopy, life-stage further divided the tree into adult and juvenile groups, with further splits by location and canopy, respectively. Mackerel *Scomber scombrus* was the most abundant juvenile inside and along the edge of rockweed, and was only observed inside eelgrass (Fig. 2-6c). Both adult and juvenile quadrat species showed no clear patterns of habitat or location preference (Fig. 2-6b,d), and a regression tree did not split using total quadrat abundance. *Carcinus maenas* adults and juveniles were ubiquitous in rockweed, whereas in eelgrass adults occurred inside and along the edge and juveniles only along the edge (Fig. 2-6b,d). *Tautoglabrus adspersus* only occurred as juveniles along the edge and outside rockweed (Fig. 2-6d). Lastly, *Pseudopleuronectes americanus* was observed as adults and juveniles mainly outside both canopies (Fig. 2-6b,d).

2.3.6. *Food-web Structure and Functioning*

A total of 51 and 60 trophic groups were included to describe eelgrass and rockweed food webs, respectively (Fig. 2-8a,b, Table A-3). Seven food-web properties (%B, %H, maxTL, Chain, Path, %Omn, %Can; see Table 2-2 for values and abbreviations) were similar across both habitats; however, some properties were higher in eelgrass (C, L/S, %T, Vul) and others in rockweed (%I, Gen, %Loop, mTL), in agreement with differences in species assemblages between both habitats. MDS and cluster analysis comparing our and 18 published aquatic ecosystems grouped our rockweed and eelgrass webs within a larger cluster of temperate and tropical seagrass webs, and closer to 2 lakes and ponds and estuaries than to other freshwater and marine systems (Fig. 2-9).

Simulated species removals had similar consequences for rockweed and eelgrass food webs when the least connected, random, or most connected species excluding primary producers were removed (Fig. 2-8c). Removing the most-connected species resulted

in secondary extinctions after removal of 5 to 10% of species, while removing random or least-connected species resulted in intermediate to low levels of secondary extinctions (<14%). However, removing the most connected species including primary producers increased secondary extinctions 2-fold compared to excluding primary producers, and food webs collapsed after 25% of species removals in rockweed and 40% in eelgrass. Secondary extinctions are always high when primary producers are included in the deletion sequence; however, the rockweed food web was less robust than the eelgrass web. The robustness (proportion of primary species removals required to induce a total loss of $\geq 50\%$ of species) to the loss of the most connected species (including primary producers) was higher in eelgrass (24%) than in rockweed (18%).

2.4. Discussion

The ecosystem services provided by coastal vegetated habitats are essential to human well-being (Millennium Ecosystem Assessment 2005; Hughes et al. 2009) and linked to their habitat structure and functions (Heck et al. 1995; Gotceitas et al. 1997), yet the relative importance of different vegetated systems is not well studied. Our results show that both rockweed and eelgrass habitats strongly enhance the abundance and diversity of associated species, provide juvenile and adult habitat, and retain high amounts of nitrogen and carbon. Yet there were distinct differences within and between the 2 habitats that were linked to their architecture, highlighting their unique importance for ocean ecosystems and humans.

2.4.1. *Canopy Structure and Storage Capacity*

Most oceanic systems are dominated by phytoplankton with low biomass and high turnover rates (<1 mo; Smith 1981). In contrast, macrophytes have the highest primary producer biomass among marine ecosystems and turnover rates of >1 yr. Their effect on nutrient dynamics is closely coupled with primary production, as major plant nutrients are assimilated along with carbon in approximate C:N:P ratios of 800:49:1 for macroalgae and 435:20:1 for rooted macrophytes (Pedersen et al. 2004). The substantial carbon production and nutrient uptake by marine macrophytes provides a significant carbon sink

and nutrient retention through accumulation of biomass or detritus (Smith 1981; Cebrian 2002; Pedersen et al. 2004); however, we found interesting differences between eelgrass and rockweed habitats.

Most research on carbon sinks, fluxes, and sequestration has focused on net primary production ($\text{g C m}^{-2} \text{ yr}^{-1}$) and its main pathways through ecosystems (Duarte and Cebrián 1996; Cebrian 2002; Mateo et al. 2006), but doesn't directly take into account the existing standing stock. We estimated primary production of our rockweed and eelgrass (aboveground) beds as 1.3 and 1.6 $\text{kg C m}^{-2} \text{ yr}^{-1}$, respectively, using our biomass data and primary production measures for rockweed (Vadas et al. 2004) and eelgrass (Duarte and Chiscano 1999), and assuming a linear relationship between the 2 variables. Thus, eelgrass and rockweed may play similar roles as primary producers in coastal ecosystems. However, our rockweed had an order of magnitude greater standing biomass and thus greater nitrogen and carbon storage capacity. A notable omission in our storage estimates for eelgrass is its roots and rhizomes. In 2007 belowground biomass was 61% higher than aboveground biomass at our study sites (A. L. Schmidt unpubl. data); yet even after adding this, rockweed still had 5 and 9 \times more nitrogen and carbon per unit area, respectively.

Relatively little macroalgal and seagrass biomass is directly grazed compared to phytoplankton and microphytobenthos (Duarte and Cebrián 1996; Worm et al. 2000; Valentine and Duffy 2006). However, grazing may increase frond breakage (Viejo and Åberg 2003) and enhance export and detrital pathways. Turnover rates of rockweed beds in southwestern Nova Scotia range from 3 to 15 yr (Sharp 1987). Assuming an annual production of air bladders (Cousens 1984), our rockweed beds were >3 yr old, placing annual losses below 33% of standing biomass, consistent with 27% detrital losses for other rockweeds (Josselyn and Mathieson 1980). Average losses of eelgrass can range from 3 to 25% (Josselyn and Mathieson 1980), although these estimates considered mostly larger pieces of *Zostera* detritus, such as leaves or whole plants, and not smaller blade tips. Together, the low grazing and low turnover rates can lead to accumulation of biomass and detritus, and burial of carbon and nutrients in macrophyte habitats (Duarte and Cebrián 1996; Pedersen et al. 2004). Because macrophytes invest more, relative to annual algae, into structural components and chemical defenses against grazing, decomposition of exported and detrital material is slow (Duarte and Cebrián 1996; Moen et al.

1997; Pavia and Toth 2000). Eelgrass has much slower decomposition rates (76 to 190 d) than rockweed (22 to 26 d; Josselyn and Mathieson 1980), increasing the fraction of primary production stored in sediments, which is 40× greater for seagrasses than macroalgae (Duarte and Cebrián 1996). Thus, while rockweed has a higher storage capacity in its standing biomass, eelgrass enhances storage of primary production in sediments.

Tissue nitrogen content reflects the nutritional conditions where eelgrass and rockweed were collected, due to its link to water column nitrogen concentrations (Asare and Harlin 1983; Duarte 1990; Burkholder et al. 1992). All our study sites, except Musquodoboit Harbour, which had a fisherman's wharf, were isolated, with <3 houses in close proximity and the closest small town ≥ 10 km away. Inorganic nitrogen concentrations near many of our sites ranged from 0.005 to 0.009 mg l⁻¹ (Canadian Council of Ministers of the Environment 2007). In seagrass, tissue nitrogen <1.8% indicates strong nutrient limitation (Duarte 1990). Our eelgrass had tissue nitrogen of 0.99 to 1.5%, indicating severe nutrient limitation. Since both rockweed and eelgrass canopies occurred under the same nutrient-limiting conditions, the higher tissue nitrogen in eelgrass suggests it is more efficient at removing and retaining nitrogen than rockweed. Nevertheless, the sheer biomass of rockweed makes it an important nutrient reservoir.

2.4.2. *Habitat Provision*

Rockweeds and seagrasses create distinct 3-dimensional habitats that provide settlement, refuge, and foraging opportunities for a wide range of species (Rangeley and Kramer 1998; Heck et al. 2003; Fisheries and Oceans Canada 2009). In the present study, both canopies significantly enhanced abundance and diversity of associated species compared to non-vegetated habitats, as observed in other studies (Edgar 1990; Edgar and Shaw 1995a; Heck et al. 1995; Levin and Hay 1996). However, some notable differences between habitat types occurred that can be attributed to their different architecture as well as bottom type, rocky versus soft sediment. Overall, rockweed enhanced total macrofauna abundance 5-fold, comparable to eelgrass beds in the eastern United States (Summerson and Peterson 1984; Heck et al. 1995) and field experiments with *Sargassum filipendula* (Levin and Hay 1996). Yet at our sites, eelgrass enhanced total macrofauna abundance 9-fold, underscoring its importance in Nova Scotia.

Similar to Edgar (1990), most species in the present study showed little habitat specificity. However, those found exclusively in rockweed either need a hard substrate for attachment (*Semibalanus balanoides*) or feeding (*Crepidula fornicata*) or are typically more abundant on rocky reefs (*Tautoglabrus adspersus*) (Tupper and Boutilier 1997). In comparison, species exclusive to eelgrass were mainly detritivores (*Nassarius trivittatus*) or herbivores (*Lacuna vincta*) feeding on eelgrass and associated epiphytes.

Previous studies found higher faunal densities (Edgar 1990; Edgar and Shaw 1995b; Heck et al. 2003) and secondary production (Edgar et al. 1994) in seagrass beds than unvegetated areas, and at habitat edges compared to the interior (Bologna and Heck 2002). In the present study, all mobile species were generally more abundant inside than along the edge of eelgrass, while the reverse was observed for rockweed. This may be related to the habitat structure, which is considerably less complex in eelgrass than rockweed, allowing better maneuverability. In contrast, sessile benthic and epiphytic species were more abundant and diverse along the edges of both habitats, likely due to the damping effect of the canopy on water flow, concentrating their larvae and propagules at the edges (Bologna and Heck 2000; Bologna and Heck 2002).

The choice of location within and between habitat types is influenced by the abundance and distribution of prey and refuge from predation (Edgar 1990; Denno et al. 2005), which can be species- and habitat-specific. For example, one important predator in Atlantic Canada is the American lobster *Homarus americanus*, which supports the highest-value fishery in Canada (Fisheries and Oceans Canada 2008). They are typically nocturnal and may use rockweed beds as shelter during daytime (Karnofsky et al. 1989). Lobsters feed on species we found in rockweed (e.g. *Carcinus maenas*) and even on rockweed itself (Karnofsky et al. 1989). We observed lobsters along the edge of rockweed beds at night. Other mobile species found in eelgrass and rockweed habitats prey on sessile invertebrates (e.g. *Mytilus edulis*) and epiphytic algae (e.g. *Polysiphonia fucoides*) whose greater abundance along the edges enhances food availability for consumers.

Interestingly, juvenile and adult abundance of green crabs *Carcinus maenas* in rockweed habitats was inversely related, with higher adult abundance outside and along the edge and higher juvenile abundance inside the beds. Green crabs prey mostly on lit-

torinid snails and mussels but also cannibalize smaller individuals (see Table A-3 for diet references). Their increased predation efficiency along the edges and outside rockweed canopies together with other predators likely affected numbers of juvenile green crabs or forced them into the bed interior. In eelgrass, adult green crabs were highly abundant inside and along the edge, while juvenile abundance was low. The less-complex structure of eelgrass beds may enable better maneuverability of crabs and other predators inside eelgrass beds, reducing juveniles and other prey in the interior. We found complete absence of benthic juveniles and high abundance of adult predators inside eelgrass beds. These results highlight that associated species density and richness strongly depend on the presence of vegetated habitats, but different canopy structure, bottom types, and locations offer unique opportunities for settlement, refuge, and foraging.

2.4.3. *Nursery Services*

Some juvenile fishes (e.g. *Scomber scombrus*) were found only inside or along the edge of rockweed canopies, whereas others (e.g. *Tautogolabrus adpersus*) were found only along the edge or outside. Juvenile Atlantic cod *Gadus morhua*, once Canada's most important fishery species (Hutchings and Reynolds 2004), were observed along the edge of rockweed at night; they use rockweed and eelgrass beds as cover from predation (Tupper and Boutilier 1995; Laurel et al. 2003). In Nova Scotia, growth rates of juvenile cod were highest in eelgrass, but predation rates were lowest in rockweed (Tupper and Boutilier 1995), indicating that both habitats are important for post-settlement growth and survival. Even if significant differences in juvenile abundances between structurally complex habitats are lacking (Heck et al. 2003), the population structure of species that use these habitats is likely influenced by the trade-offs between energy gained and predation risk that determine the habitat-specific growth and mortality of juveniles, as in the case of cod (Tupper and Boutilier 1995). Increased juvenile growth and survival has been found in eelgrass and other vegetated habitats (Tupper and Boutilier 1995; Gotceitas et al. 1997; Tupper and Boutilier 1997), yet it is unclear whether canopies increase the recruitment of juveniles to adult populations. Like most coastal ecosystems, however, our beds have likely been severely altered by historical and current fishing (Jackson et al. 2001;

Hutchings and Reynolds 2004; Lotze et al. 2006), masking their true role as nurseries for commercially important species.

2.4.4. *Food-web Structure and Robustness*

The simplicity of binary models and their ability to detect fundamental changes in food-web structure due to changes in species composition make them good tools for comparing food-web structure and robustness across ecosystems (Dunne et al. 2004). In addition, when compared to more complex models they derive similar results for common food-web properties (Coll et al. 2008). Despite strong differences in 3-dimensional canopy structure and species composition between rockweed and eelgrass communities, the overall food-web structure of the 2 habitats was more similar to each other and to other temperate and tropical seagrass webs than to other aquatic and marine webs (Dunne et al. 2004; Fig. 2-9). The main structural differences were a 22% lower connectance in rockweed and a 44% higher fraction of top predators in eelgrass webs.

The higher connectance in eelgrass compared to rockweed webs likely contributed to their greater robustness to the removal of the most connected species including primary producers. Our findings are consistent with other estuarine food webs, where an increase in connectance of 14% can lead to a 35% increase in the number of species removals required to elicit a complete collapse of the food web (Dunne et al. 2002). Secondary extinctions reached 52% in rockweed, but only 14% in eelgrass for the same level of species removal (20%), and there was a complete food web collapse at a 15% lower species removal in rockweed than in eelgrass. These rapid declines in biodiversity are expected with the loss of functionally dominant species that are ecosystem engineers (Worm and Duffy 2003) such as rockweed and eelgrass. This may explain why, despite high connectance, the robustness of these habitats to the removal of the most-connected species, including primary producers, is among the lowest compared to other aquatic ecosystems (Dunne et al. 2004). Thus, our results emphasize the vulnerability of eelgrass and especially rockweed communities to disturbances that can cause the loss of primary producers, especially the foundation species, and highlight the fact that the link between connectance and robustness at larger spatial scales is not straightforward and may depend on the role of the species in an ecosystem. Although the numbers of secondary extinctions ap-

pears high, 29% of crustacean and 37% of fish species disappeared after the mass mortality of seagrass beds in Florida Bay in 1987 (Matheson et al. 1999). In Australia, 49% of fauna species present inside macrophyte-dominated habitats were not found in nearby unvegetated areas (Edgar 1990). Similarly, in our study 39% and 48% of fauna species (excluding epiphytes) were not observed outside rockweed and eelgrass canopies, respectively. Guidetti (2000) found that on average 50% of fish species on algal reefs and 58% in seagrass were absent in unvegetated habitats. These numbers are comparable to the secondary extinctions rates from our simulated species removals.

2.4.5. *Human Impacts on Ecosystem Services*

As human populations expand, so does our demand for and multiple impacts on the services that coastal ecosystems provide. Our work clearly shows that rockweed and eelgrass habitats play important roles in the coastal carbon and nitrogen cycles. Although marine vegetated habitats cover <2% of the global ocean, they contribute to almost half of the oceanic carbon burial, playing a major role in the oceanic carbon cycle (Duarte et al. 2005). Increased nutrient loading to coastal ecosystems is shifting the primary producer assemblage from long-lived macrophytes to phytoplankton, benthic micro-, and annual macroalgae, which can decrease the ecosystems' carbon and nitrogen retention (Worm et al. 2006; Antón et al. 2011). The projected increase in nutrient loading of another 10 to 20% by 2030 (Millennium Ecosystem Assessment 2005) will have profound repercussions on coastal ecosystems and their storage services.

Rockweed harvesting along the shores of Atlantic Canada removes large amounts of biomass (Ugarte and Sharp 2001). Harvesting does stimulate growth and canopy regeneration with a minimum of 85% biomass recovery within a year (Ugarte et al. 2006). This may offset the carbon removed during harvest; however, long-term burial of biomass or detritus and export will likely be reduced. The removal of nitrogen will affect nitrogen fluxes within and exports to adjacent ecosystems. Trophic transfer from seagrass meadows has been shown to subsidize distant habitats such as the deep sea and even terrestrial environments (Heck et al. 2008). Many trophic transfer processes observed in seagrass habitats, such as consumption by migratory waterfowl and beach wrack by amphipods (Heck et al. 2008), are also common in rockweed-dominated habitats (Behbehani and

Croker 1982; Blinn et al. 2008), indicating that rockweed production is also subsidizing other marine and terrestrial habitats.

Nutrient loading and harvesting can further alter, reduce, fragment, or completely remove macrophyte canopies with profound effects on associated species and food webs. Both rockweed and eelgrass beds provide important habitat to a wide range of species including at least 6 commercially important species such as American lobster and Atlantic cod (Anderson et al. 2008b; Fisheries and Oceans Canada 2008). The effect of patchy rockweed harvesting, as in Atlantic Canada, where 15 to 50% of a patch but no more than 17% of a bed may be harvested (Ugarte et al. 2006), may create more edge-like habitat. By decreasing the clump length and biomass (Ugarte et al. 2006), harvesting effectively creates a less dense interior and could increase the total abundance and richness of species within rockweed beds. However, the uncertainty around the effects of rockweed harvesting on the associated community necessitates further research.

The low abundances of juveniles in both rockweed and eelgrass habitats may be the result of historical and current overfishing (Jackson et al. 2001; Lotze et al. 2006). The magnitude of losses of large vertebrates such as cod was enormous (Hutchings and Reynolds 2004) and likely had profound impacts on species interactions and trophic transfer (Jackson et al. 2001; Coleman and Williams 2002). Continuous fishing pressure and expansion to lower trophic species (Anderson et al. 2008b) makes it nearly impossible to truly assess the nursery function of a habitat. Another confounding factor limiting our understanding of the nursery function is the use of alternative habitats. The extent to which species can switch among habitats or locations and remain productive would help to understand the short- and long-term buffering capacity of different habitats in the event of habitat degradation or loss in an area. The accelerating loss of seagrass habitats worldwide (Orth et al. 2006; Waycott et al. 2009) and concurrent impacts on alternative habitats (Adam 2002; Alongi 2002; Steneck et al. 2002a; Thompson et al. 2002; Hughes et al. 2009) could have serious implications for species using coastal vegetated habitats during any part of their life cycle. In addition, the strong response of eelgrass, and particularly rockweed, to the simulated loss of primary producers warrants further investigation, especially since regional losses of nearshore vegetation have been shown to strongly reduce the filtering and nursery services (Worm et al. 2006).

Overall, our results illustrate that rockweed and eelgrass have very different canopy structure and complexity and utilize different bottom types that support unique species assemblages. Therefore, one habitat cannot replace the other. Instead they simultaneously support coastal biodiversity and provide essential ecosystem services. The importance of eelgrass habitats in Atlantic Canada has recently been recognized by its designation as an ecologically significant species (ESS) by Fisheries and Oceans Canada (2009). Although not a tool for protection, it does officially recognize the important role of eelgrass in coastal ecosystems. On the other hand, the entire Atlantic coast of Nova Scotia and parts of the Bay of Fundy are open for rockweed harvesting (Ugarte and Sharp 2001). The present study illustrates that the lack of protection of sufficient habitat areas may seriously affect their ecological role and the services they provide.

Table 2-1. Details of exposure (Exp), canopy location (Loc), bottom type (BT), transect length (L) and width (W) in m, and number of quadrats (Q) per transect for each site sampled September 2006 in Nova Scotia, Canada. Sites are listed within canopy type from southwest to northeast corresponding to Fig. 2-1 (Rockweed n = 4; Eelgrass n = 3). Exposure included sites very sheltered (VS), sheltered (S), or moderately exposed (ME) to the predominant south-westerly winds. Canopy locations were inside (I), along the edge (E), and outside (O) the rockweed and seagrass beds. Bottom type included mud (M), mud and boulders (MB), cobble (C), cobble and boulders (CB), sand (S), and sand and boulders (SB). Numbers in **bold** indicate shorter transects (see 'Methods').

Canopy	Site	Exp	Loc	BT	L	W	Q
Rockweed	East Jeddore (EJ) 44°46'36"N, 63°00'26"W		I	MB	50	4	11
		S	E	MB	45	4	10
			O	M	50	4	11
	Necum Teuch (NT) 44°57'07"N, 62°10'99"W		I	MB	45	2	10
		S	E	MB	50	4	11
			O	M	50	2	11
	Port Dufferin (PD) 44°54'73"N, 62°23'76"W		I	CB	50	2	11
		ME	E	CB	50	4	11
			O	C	45	4	10
	Tangier (TG) 44°47'74"N, 62°41'06"W		I	MB	25	4	5
		VS	E	MB	50	4	11
			O	M	50	4	11
Eelgrass	False Passage (FP) 44°44'37"N, 62°47'45"W		I	S	40	4	9
		S	E	S	50	4	11
			O	S	50	4	11
	Musquodoboit Harbour (MH) 44°42'46"N, 63°04'50"W		I	M	40	2	9
		VS	E	M	50	4	11
			O	M	45	2	10
	Taylor's Head Provincial Park (TH) 44°49'26"N, 62°34'32"W		I	SB	30	2	6
		ME	E	SB	45	4	10
			O	S	50	4	11

Table 2-2. Food web properties for rockweed and eelgrass network models. Properties in bold were included in the MDS analysis comparing aquatic ecosystems (see Fig. 2-9)

Food web property	Symbol	Rockweed	Eelgrass
Species count	S	60	51
Linkage density	L/S	12.42	13.65
Connectance	C	0.21	0.27
Fraction of top predators	%T	15	22
Fraction of intermediate species	%I	70	63
Fraction of basal species	%B	15	16
Fraction of herbivores	%H	7	6
Generality—number of prey items per predator	Gen	0.93	0.88
Vulnerability—number of predators by prey	Vul	2.05	2.16
Fraction of species involved in looping	%Loop	8	4
Mean short-weighted trophic level	mTL	1.94	1.83
Maximum trophic level	maxTL	3.03	3.00
Mean number of links in every possible food chain or sequence of links connecting top to basal species	Chain	2.10	2.08
Fraction of omnivory	%Omn	83	82
Fraction of cannibalism	%Can	10	12
Mean trophic path length	Path	1.97	1.96

Table 2-3: PERMANOVA results on the effect of canopy, location, and site nested in canopy on the quadrat macrofauna, sessile benthic, and epiphytic species abundance collected using the original transect lengths (see Table A-1, for results using standardized shortened transects). SQR T-V are unbiased estimates of the components of variance for each of the fixed (F) and random (R) factors in the model. Negative SQR T-V values indicate that there is no evidence against the null hypothesis (Anderson et al. 2008a).

Source	DF	Quadrat Macrofauna			Sessile Benthic			Epiphytic		
		Pseudo-F	P	SQR T-V	Pseudo-F	P	SQR T-V	Pseudo-F	P	SQR T-V
Canopy (F)	1	6.04	0.021	23.8	2.69	0.072	4.68	0.07	0.97	-3.58
Location (F)	2	6.95	0.001	18.8	2.36	0.072	5.11	4.39	0.019	7.44
Site(canopy) (R)	5	14.62	0.001	18.9	6.61	0.001	6.33	5.25	0.001	6.18
Canopy x Location (F)	2	4.64	0.004	20.8	2.34	0.067	7.19	0.49	0.788	-4.08
Site(canopy) x Location (R)	10	5.25	0.001	18.1	6.23	0.001	10.5	4.19	0.001	9.21
Residual (R)	190			27.7			14.5			16.22
Total	210									

Table 2-4. Pairwise comparisons for significant interactions listed in Table 2-3. Letters refer to locations within each site (see Table 2-1 for abbreviations); -: denominator of the post-hoc t -test = 0

Canopy Type	Site	Macrofauna			Sessile Benthic			Epiphytic		
		I,E	E,O	I,O	I,E	E,O	I,O	I,E	E,O	I,O
Eelgrass	FP	0.242	0.001	0.001	-	-	-	0.222	0.011	0.001
	MH	0.082	0.001	0.001	-	-	-	0.613	0.008	0.028
	TH	0.022	0.001	0.001	0.638	0.507	0.328	0.169	0.001	0.038
Rockweed	EJ	0.346	0.001	0.001	0.002	0.001	0.054	0.001	0.001	-
	NT	0.153	0.001	0.001	0.064	0.242	0.238	0.047	0.007	0.092
	PD	0.001	0.001	0.001	0.001	0.001	0.471	0.002	0.003	0.031
	TG	0.007	0.001	0.005	0.721	0.178	0.314	-	-	-

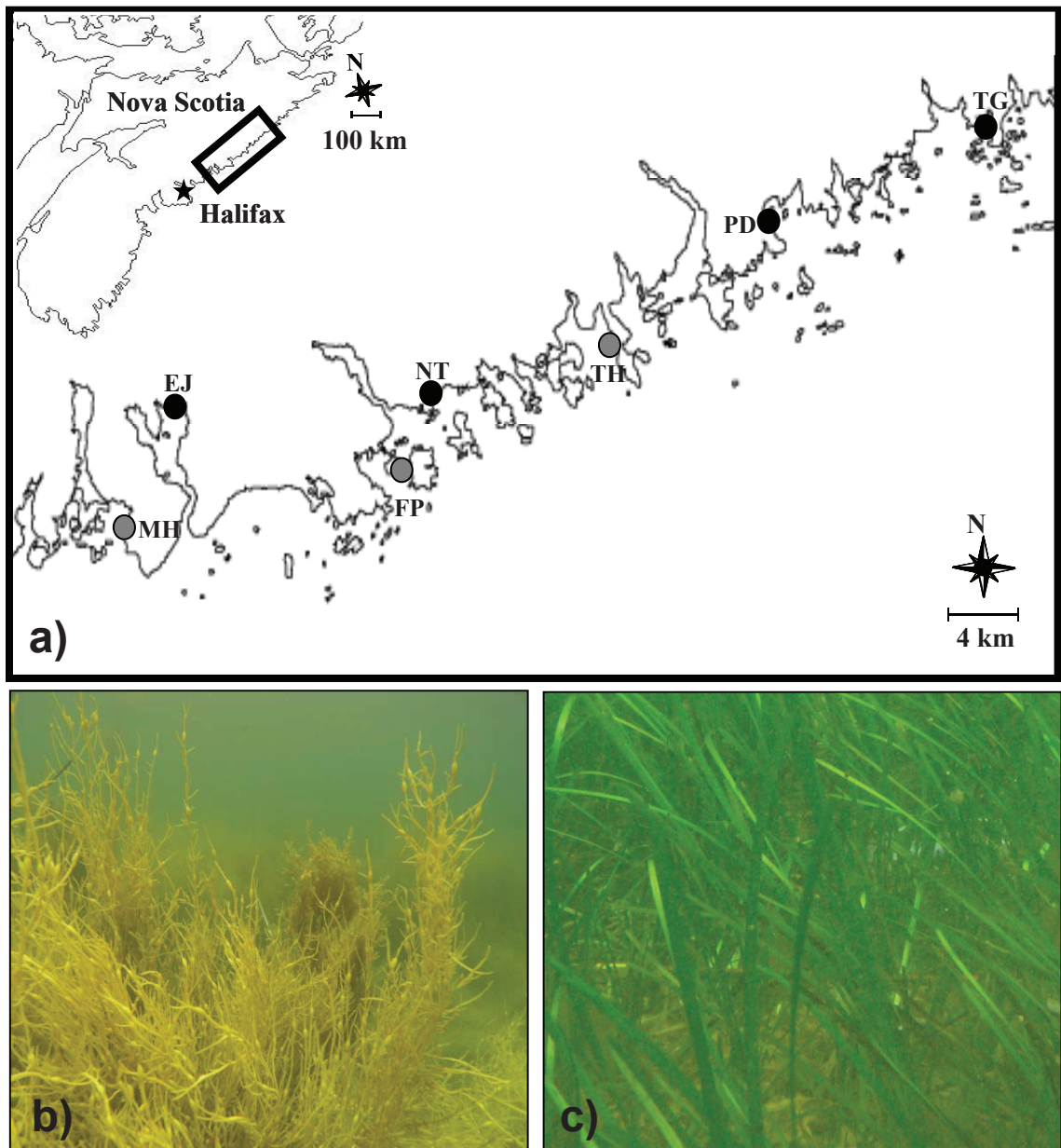


Figure 2-1. (a) Study sites along the Eastern Shore of Nova Scotia, Canada, with eelgrass (gray circles) and rockweed (black circles) beds. See Table 2-1 for abbreviations and site characteristics. (b) *Ascophyllum nodosum* in East Jeddore (EJ). (c) *Zostera marina* in Taylor Head Provincial Park (TH)

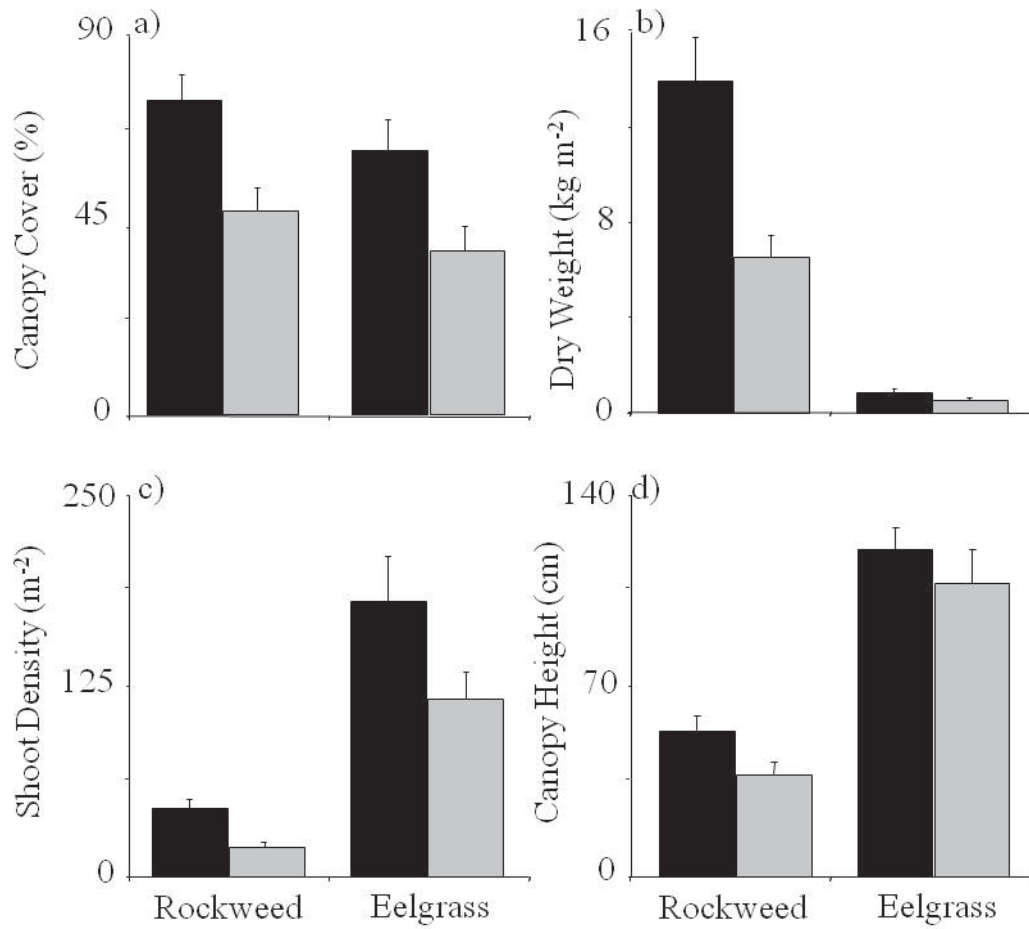


Figure 2-2. Canopy structure in the interior (black bars) and along the edge (grey bars) of rockweed and eelgrass beds. (a) percent cover, (b) dry weight (eelgrass \times 10), (c) shoot density, and (d) canopy height. Data are mean \pm SE

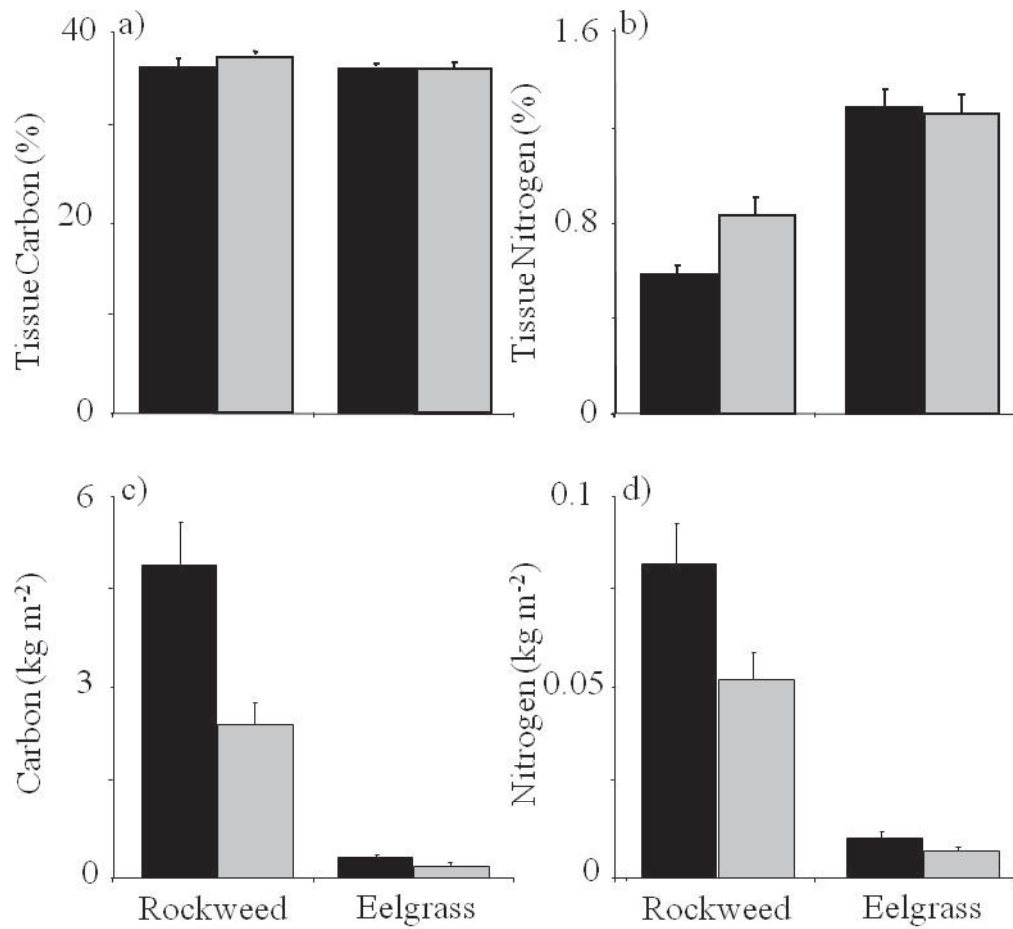


Figure 2-3. Regulating services in the interior (black bars) and along the edge (grey bars) of rockweed and eelgrass beds. (a) tissue carbon and (b) tissue nitrogen content (% dry weight), and (c) carbon storage and (d) nitrogen retention per unit area. Data are mean \pm SE

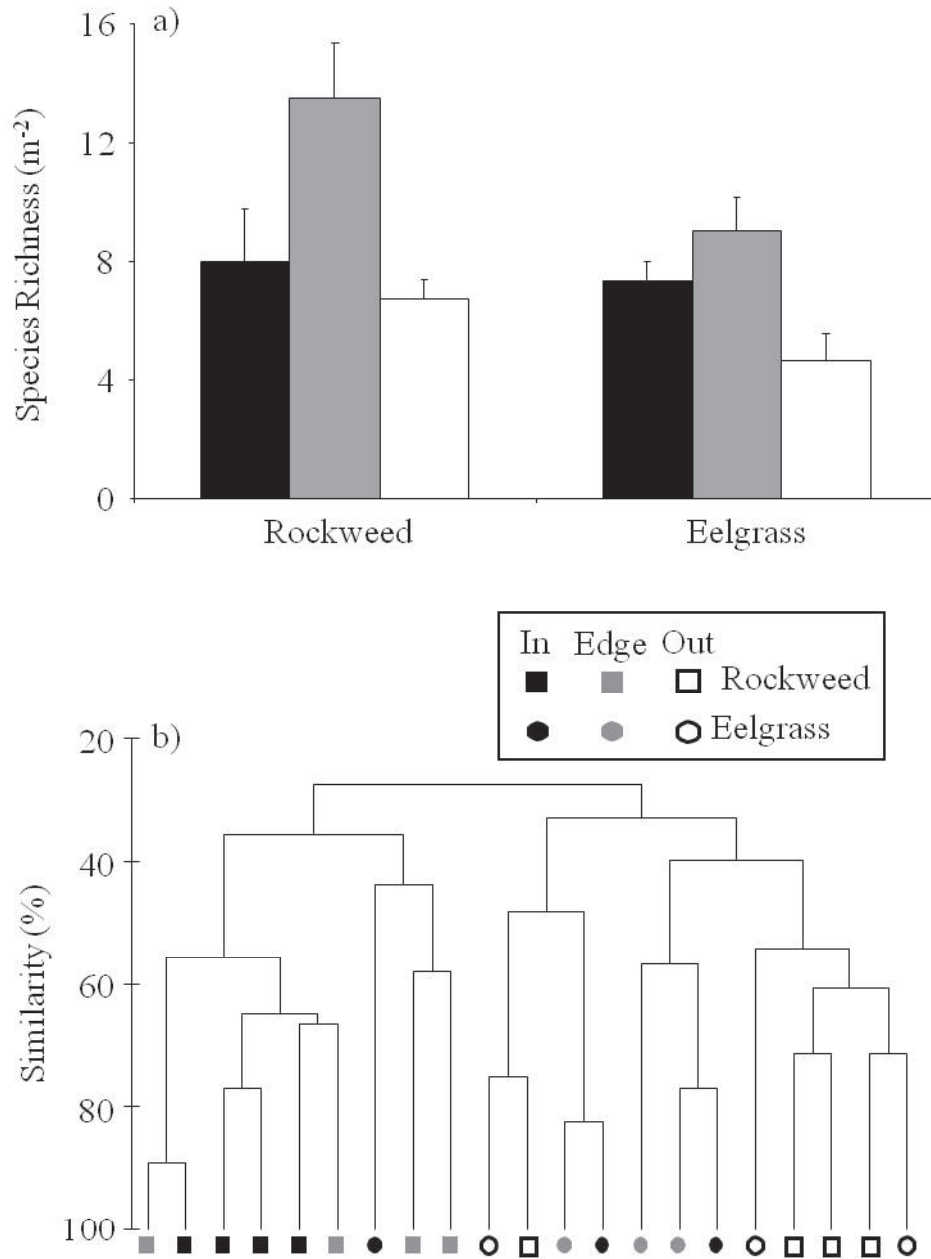


Figure 2-4. Total community structure. (a) mean (\pm SE) species richness and (b) similarity of the communities between canopy species and locations. Both graphs are based on species presence/absence of all macrofauna, sessile benthic, and epiphytic species

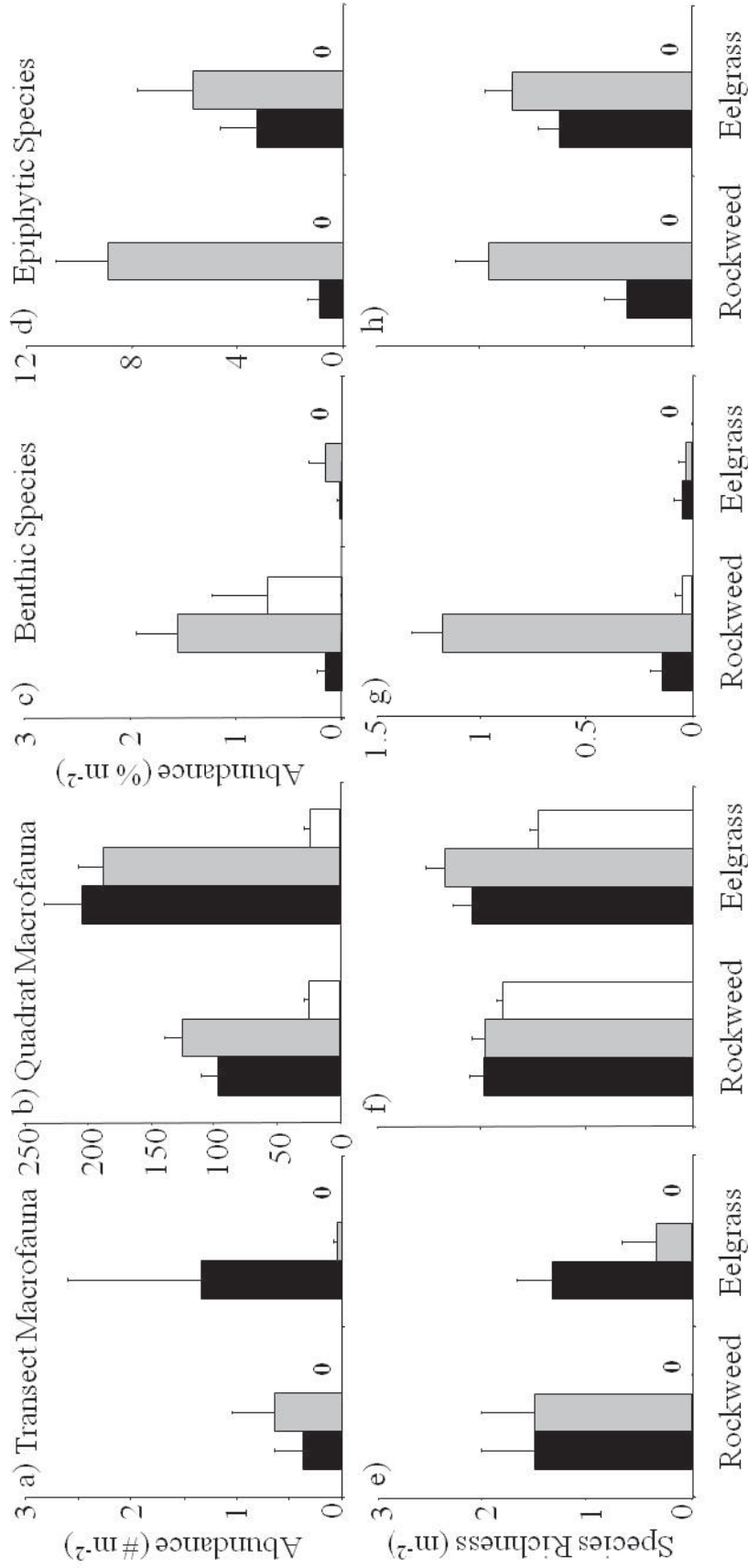


Figure 2-5. Mean (\pm SE) total abundance and species richness of mobile macrofauna surveyed using transects (a,e) and quadrats (b,f), and sessile benthic (c,g) and epiphytic (d,h) flora and fauna surveyed using quadrats in the interior (black bars), along the edge (grey bars), and outside (white bars) of rockweed and eelgrass beds. Zero values are indicated.

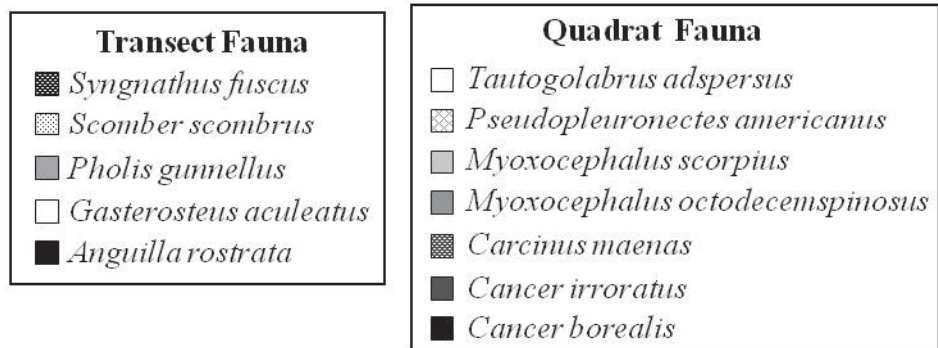
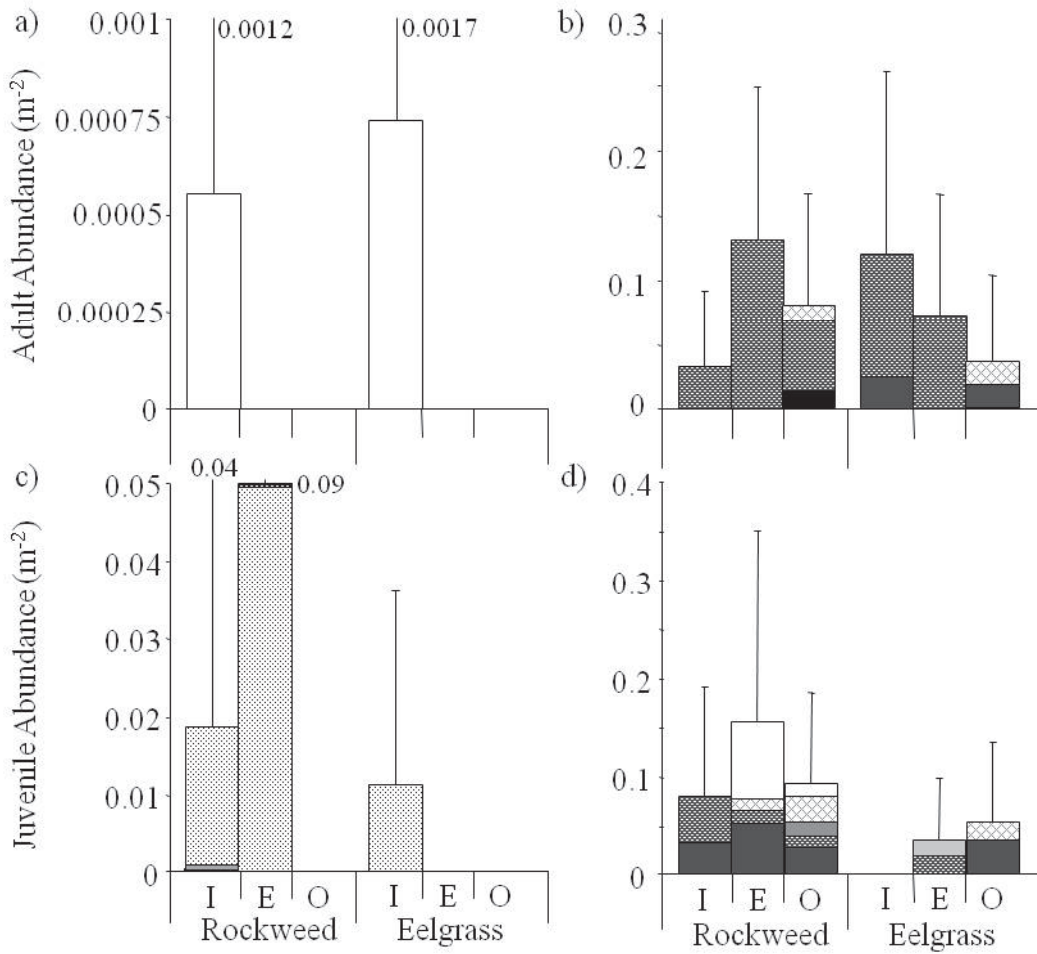


Figure 2-6. Mean abundance (\pm SE) of adults and juveniles of the macrofauna species whose life stages could be distinguished based on size sampled using transects (a,c) and quadrats (b,d) in the interior (I), along the edge (E) and outside (O) of rockweed and eelgrass beds. Numbers above or to the right of error bars indicate the numerical SE values. The order of the species in the legends corresponds to the vertical order in the bars

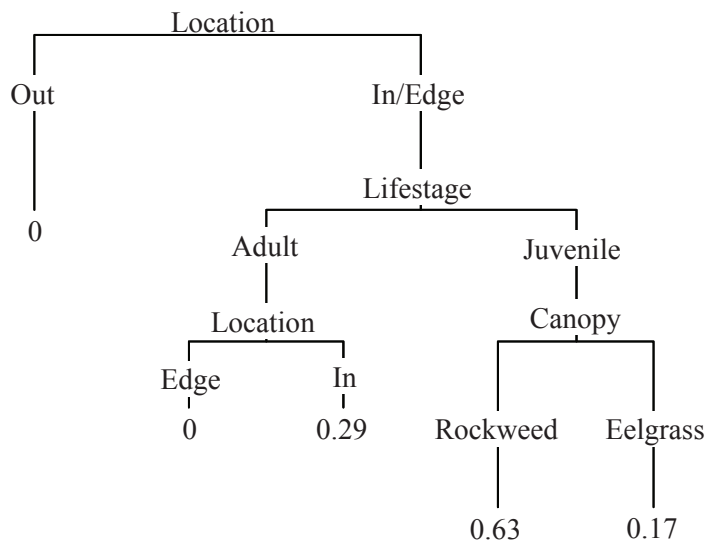


Figure 2-7. Regression tree model for abundance data from transects for all species combined. Species abundance (m^{-2}) was the response variable and life stage (adult, juvenile), canopy type (rockweed, eelgrass), and location (in, edge, out) were categorical predictors. The numbers represent the total abundance of each branch

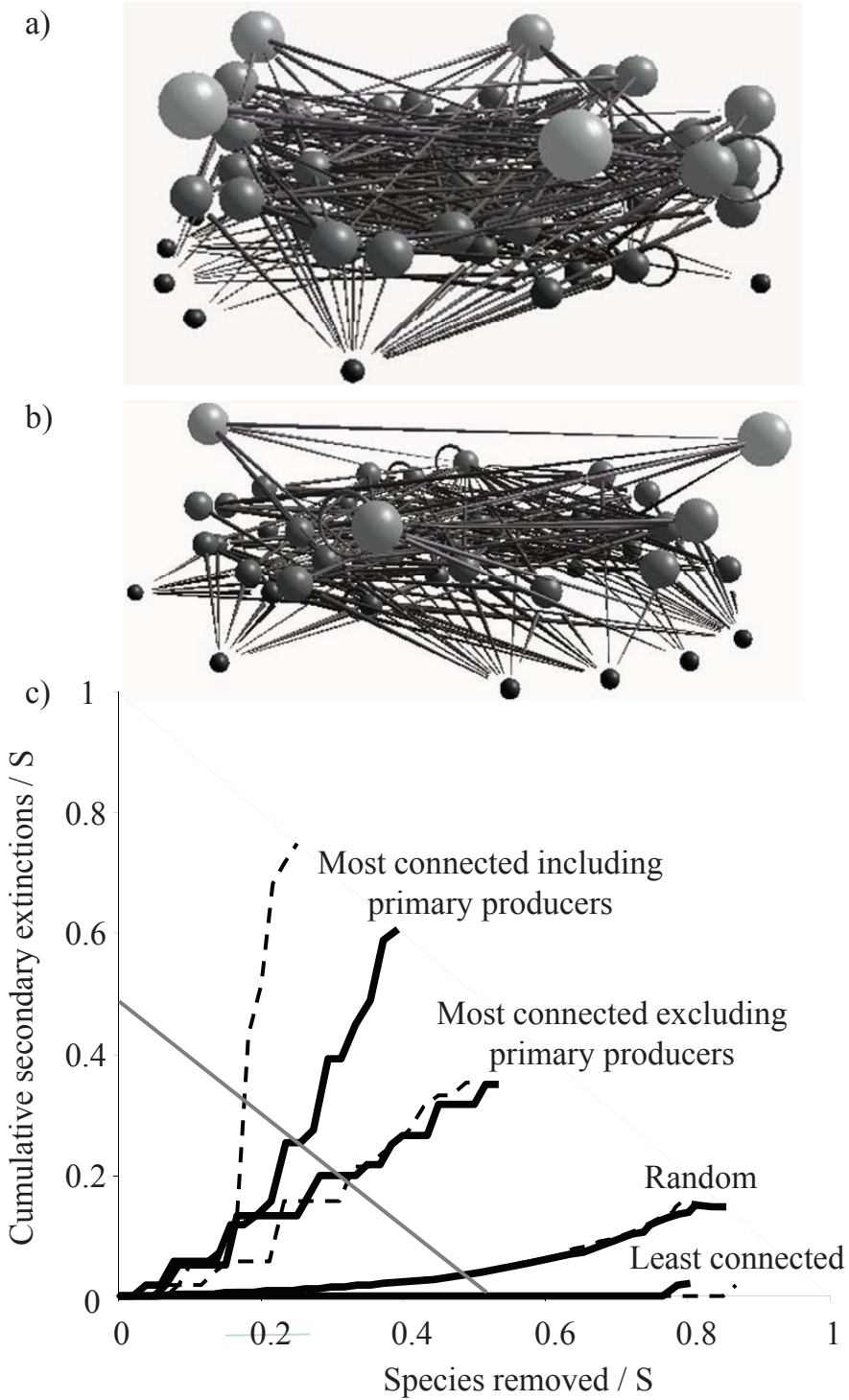


Figure 2-8. Visualization of food webs in (a) rockweed and (b) eelgrass habitats, and (c) secondary extinctions in eelgrass (solid line) and rockweed (dashed line) food webs resulting from the simulated removal of species that are least connected, random, most connected excluding, and most connected including primary producers. In (a) and (b), small dark balls represent primary producers, medium grey balls represent intermediate consumers, and large light balls represent top predators. S: species count (see Table 2-2)

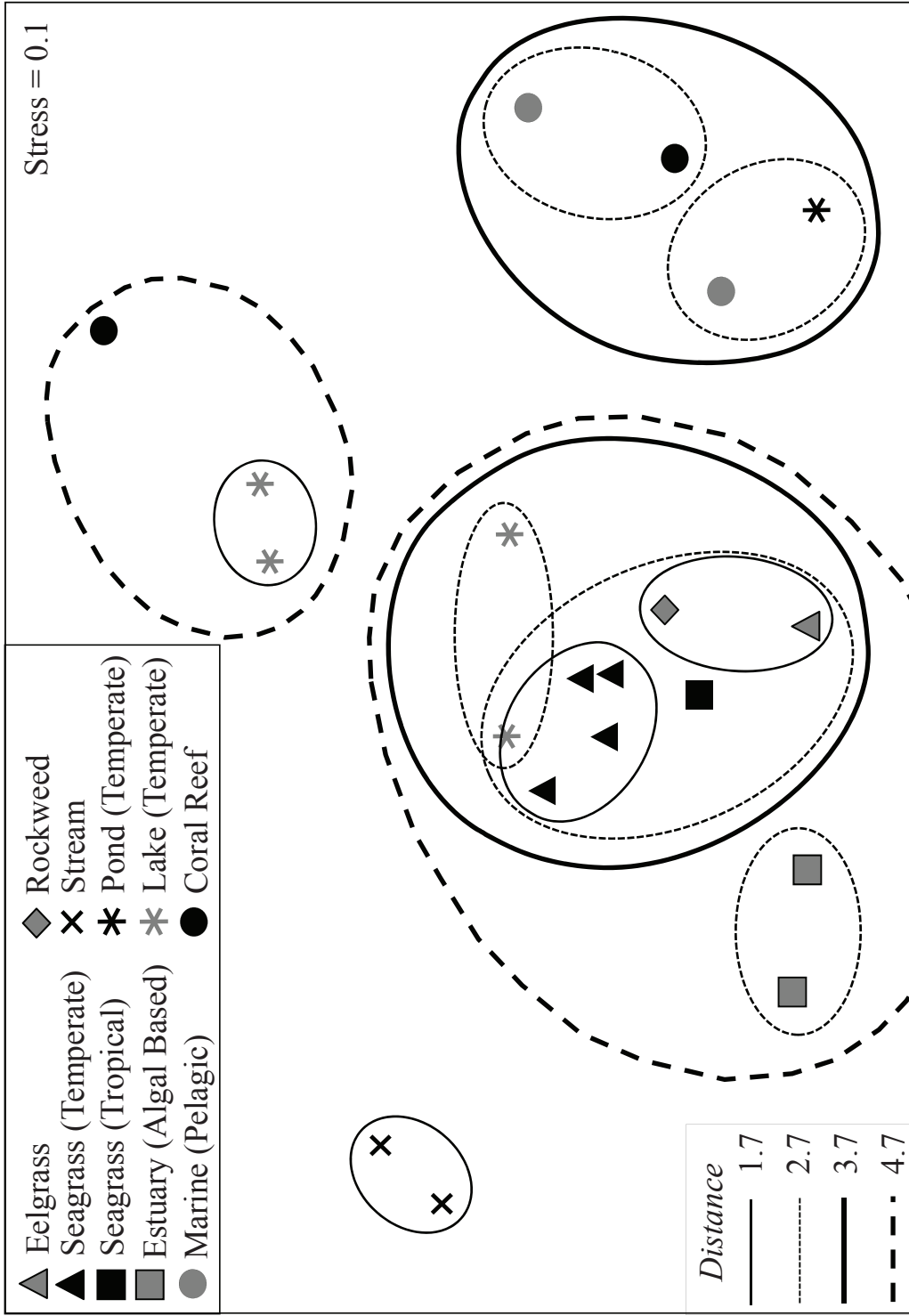


Figure 2-9. Multidimensional scaling analysis overlaid with Euclidean distances from cluster analysis based on 11 food web properties (see Table 2-2) of 14 aquatic (Dunne et al. 2004), 4 temperate seagrass (Coll et al. 2011), and the 2 rockweed and eelgrass food webs from the present study. The marine pelagic, algal-based estuarine, and stream food webs are all from temperate systems.

CHAPTER 3

Regional-scale Effects of Eutrophication on Ecosystem Structure and Services of Seagrass Beds

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3.1. Introduction

Seagrasses are among the most productive habitats in the world (Larkum et al. 2006) and their functions provide essential nutrient cycling (Duarte 2002; Romero et al. 2006), climate regulation (Nellemann et al. 2009; McLeod et al. 2011), sediment stabilization (Orth et al. 2006) and nursery and habitat services (Duarte 2002; Schmidt et al. 2011) that contribute directly and indirectly to human well-being. Despite their ecological importance, anthropogenic activities are increasingly affecting seagrass ecosystems around the world leading to fragmentation, depletion or localized extinction of the habitat (Lotze et al. 2006; Waycott et al. 2009). Already one third of global seagrass area has disappeared since 1879 (Waycott et al. 2009), while losses in highly affected estuaries and coastal seas have been estimated at 65% of historical abundance (Lotze et al. 2006). With loss rates 14 times greater than those of tropical rainforests (Nellemann et al. 2009) seagrass

habitats are among the most threatened ecosystems in the world (Duarte 2002; Waycott et al. 2009).

In the early 1970s, coastal eutrophication was identified as one of the major contributors to seagrass declines in estuaries (Howarth and Marino 2006) and continues to be one of the largest contemporary threats to seagrasses on a global scale (Duarte 2002; Orth et al. 2006; Waycott et al. 2009). Anthropogenic nitrogen loading is the main driver of eutrophication in most temperate estuaries and coastal seas (Howarth 1988; Howarth and Marino 2006) and is viewed as one of the most pervasive effects humans have on estuaries around the world (Vitousek et al. 1997). Human activity, particularly agricultural fertilizer use, sewage and wastewater discharges and burning of fossil fuels, has doubled the reactive nitrogen entering the global nitrogen cycle with 67% of the nitrogen currently entering coastal waters and a projected 10-20% increase by 2030 (Vitousek et al. 1997; Millennium Ecosystem Assessment 2005). The main effects of nitrogen enrichment of shallow coastal waters on primary producers include a shift in community dominance from perennial seagrasses to phytoplankton and fast growing opportunistic macroalgae, a change in benthic (Duarte 1995; Short et al. 1995; Borum and Sand-Jensen 1996) and pelagic species composition (Howarth and Marino 2006) and impairment of the system's ability to store and cycle nutrients (McGlathery 2001).

Under low nutrient conditions, eelgrass beds are associated with abundant and diverse benthic and epiphytic micro- and macroalgae (Coleman and Burkholder 1994; Jaschinski et al. 2009; Schmidt et al. 2011), where the benthic macroalgae are typically distributed in scattered patches (Hauxwell et al. 2001). Together, epiphytic micro- and macroalgae can contribute up to 36% of the biomass and 18-51% of the production in eelgrass beds (Penhale 1977; Borowitzka et al. 2006). Nutrient enrichment, however, shifts the dominance from predominantly red macroalgae and unicellular diatoms to annual green and brown macroalgae and cyanobacteria (Coleman and Burkholder 1994; Hauxwell et al. 2001; Johnson et al. 2005). The loss of the seagrass coupled with a shift in the composition of the algal assemblage, changes the quality and production of live and detrital food resources available to consumers effectively changing the pathway and turnover of carbon and nitrogen through benthic and pelagic food webs, potentially re-

ducing ecosystem stability (McClelland and Valiela 1998; Deegan et al. 2002; Olsen et al. 2011).

For temperate seagrasses such as eelgrass, light availability is the most important factor controlling growth (Dennison and Alberte 1985). Thus, the primary cause of eelgrass loss under increasingly eutrophic conditions is reduced light penetration due to increased abundance of phytoplankton and total suspended solids (Moore et al. 1996), epiphytic algae on eelgrass blades (Short et al. 1995), drift macroalgal blooms or any combination of the three (Hauxwell et al. 2001; Hauxwell et al. 2003). Other mechanisms, such as ammonia toxicity, low oxygen concentration, increased sediment sulfides and anoxia (Pregnall et al. 1984; Goodman et al. 1995) also contribute to reduced growth and production of temperate seagrasses (Hauxwell et al. 2001; Havens et al. 2001), especially when coupled with increased shading (McGlathery 2001).

Our study aimed to examine the effects of eutrophication on the combined and species-specific structure of the phytoplankton and macroalgal assemblage in eelgrass beds as well as eelgrass' canopy structure, nutrient and carbon storage services in Atlantic Canada. Previous studies have assessed eutrophication-induced changes in phytoplankton biomass (Borum and Sand-Jensen 1996), epiphytic (Coleman and Burkholder 1995), and benthic macroalgae (Neckles et al. 1993; Hauxwell et al. 2001) in eelgrass beds as well as eelgrass bed structure (Short et al. 1995) usually at individual locations. What has received little attention are the simultaneous changes in all of these primary producer components across regional scales, which is key to our understanding of the general as well as province-specific and variable effects of eutrophication. Also, the species-specific responses of macroalgae have been little studied, an important knowledge gap as they can affect predator-prey interactions (Sunda et al. 2006) and the cycling of carbon and nitrogen through benthic food webs (Olsen et al. 2011) in turn altering fish and invertebrate communities (Deegan et al. 2002). Finally, understanding the effects of nutrient loading on eelgrass habitats and their carbon and nitrogen storage capacity is becoming increasingly urgent because of the importance of coastal vegetated habitats (blue carbon) in mitigating anthropogenic carbon dioxide emissions (McLeod et al. 2011). Therefore, the objectives of our study were to examine 1) phytoplankton biomass and particulate matter, 2) the abundance and composition of benthic and epiphytic macroalgal assemblages, 3)

eelgrass canopy structure, and 4) the carbon and nitrogen storage of eelgrass beds across a gradient of eutrophication on a regional scale in Atlantic Canada.

3.2. Methods

3.2.1. Study Sites

We sampled 12 sites located within larger estuaries in the Provinces of New Brunswick (NB) and Prince Edward Island (PEI), Canada from 27 July to 08 August 2007 (Fig. 3-1, Table 3-1). All estuaries contained mostly soft sediment substrate and eelgrass beds as the dominant structuring vegetation. Sites were chosen a priori based on the range and severity of human uses that would contribute nitrogen to the estuary (Coll et al. 2011) and annual mean nutrient concentrations in PEI rivers (M. van Heuvel unpub. data) and then grouped into low (L) and high (H) eutrophication a posteriori using % tissue nitrogen concentrations in eelgrass blades and roots (*see* Eelgrass Canopy Structure and Storage Services for collection methods). We used the % tissue nitrogen because it is a more integrated measure of nutrient conditions than short-term water column nitrogen concentrations (Duarte 1990; Lee et al. 2004).

3.2.2. Sampling Design

At each site, one 50 x 4 m transect was laid parallel to the shore inside the eelgrass bed ≥ 10 m from the vegetation-bare substrate interface. To assess water column integrated phytoplankton abundance, we manually collected three 1 L water samples over the transect center using a pipe sampler (weighted tubing 2 m long x 2.5 cm diameter) at 3 times of the tide to capture at least one high and low tide at each site. Samples were kept in opaque thermos bottles, filtered on site within an hour of collection and frozen for storage (*see* below). To assess the eelgrass canopy and benthic and epiphytic (on eelgrass) macroalgae, we sampled eleven quadrats (0.5 x 0.5 m, with 0.25 m subsections) placed every 5 m along the transect during high tide.

3.2.3. *Phytoplankton Abundance*

To assess the abundance of the phytoplankton community and other particles in the water column we measured concentrations of chlorophyll *a* (Chl *a*) and phaeopigments ($\mu\text{g L}^{-1}$), total particulate matter concentration (TPM; mg L^{-1}) and its organic (POM; mg L^{-1}) and inorganic (PIM; mg L^{-1}) components. We used a Pall filtration rig with three 200 mL polysulfone filter funnels with a 19.1 mm effective diameter attached to a Welch piston vacuum pump (Model 2522) to filter the three water samples per site. For Chl *a* and phaeopigments, two replicate 70 mL subsamples were filtered through 0.7 μm Whatman GF/F filters (2.5 cm diameter). All filters were placed in cryovials and stored in liquid nitrogen. Particles from another two replicate subsamples were captured by filtering through a pre-combusted (6 h at 450°C) and weighed 0.7 μm Whatman GF/F filters to estimate TPM, POM, and PIM, but the volume filtered was judged by the appearance of color on the filter and depended on the study site. The volume filtered ranged from 50-150 mL but remained constant within a site. The filters were washed twice with 5 mL of 2% ammonium formate to remove salt, placed in a petri dish and stored on ice.

In the laboratory, Chl *a* concentrations were determined using the Welschmeyer technique (Welschmeyer 1994) by extracting particulate matter retained on the GF/F filters in 90% acetone at -20°C for 24 hours and measuring the extract in a Turner Designs 10-005R fluorometer. To convert all Chl *a* to phaeopigment, 5 μL of 10% HCl was added to the extract. Phaeopigment concentration was then estimated by measuring the fluorescence from the acidified extract (Strickland and Parsons 1972). TPM filters were dried (60°C, 24 h), weighed (dry weight), combusted (450°C, 6 h) and weighed again (combusted weight) to estimate POM and PIM.

3.2.4. *Benthic and Epiphytic Macroalgae*

To evaluate changes in benthic and epiphytic algal community structure the same observer estimated the percent cover of benthic and epiphytic algae in each 0.25 m² quadrat by hovering just above the top of the canopy. Using the 0.25 m subsections as a guide, the percent cover of each algal species on the bottom and on the eelgrass blades was estimated with respect to the bottom to the nearest 2% whereby the sum of benthic and epi-

phytic cover could exceed 100%. All algae were identified to the lowest possible taxon in the field, and used to calculate species richness (S).

3.2.5. *Eelgrass Canopy Structure and Storage Services*

To examine changes in the canopy structure we used a 0.25 x 0.25 m inset of the sampling quadrat to count shoot density and measure canopy height of four haphazardly selected shoots from the substrate to the tip of the longest blade to the nearest millimeter. We also examined changes in eelgrass above (blades) and below (roots and rhizomes) ground biomass. We used a sediment core (0.2 m diameter; 0.2 m deep) to collect the above and below ground biomass at three locations (0, 25, and 50 m) along each transect. First, we gently pressed the core in the collection location to leave an outline on the sediment and then cut and removed all of the above ground tissue from within the outline. Next, we took the entire core sample to estimate below ground biomass. Any above ground tissue in the core sample itself was added to the weight of all cut blades, which may have led to a slight overestimation of above ground biomass (~1-2 shoots) in locations of high shoot density.

In the laboratory, all visible epiphytes were scraped from the blades prior to weighing above ground wet weight to the nearest milligram. All of the blades and roots and rhizomes from 2-5 shoots from each core sample were weighed prior to drying (70°C, 48 h) and re-weighed to estimate the wet:dry weight ratio. After weighing, the dried above and below ground tissue samples were homogenized separately and a 50 mg dry weight subsample was analyzed using a Perkin Elmer Carbon Hydrogen Nitrogen 2400 Analyzer to estimate tissue carbon (C) and nitrogen (N) content. We used the average above and below ground percent tissue C and N and biomass per site to estimate the amount of C and N stored (kg m^{-2}) in above and below ground eelgrass beds.

3.2.6. *Statistical Analysis*

For all analyses we used a fully crossed two-factorial design with a fixed province (two levels, NB and PEI) and eutrophication factor (two levels; L and H). Where possible we used parametric statistics and compared the results with the non-parametric technique; however, since the results were the same we only present the non-parametric analyses for

consistency across all results. We used univariate permutational analysis of variance (PERMANOVA) on the Euclidean distance matrix of species richness as well as the zero-adjusted Bray-Curtis similarity matrix of the square root transformed total abundance of benthic and epiphytic primary producers. Permutational post-hoc *t*-tests were used where significant effects were detected (Anderson et al. 2008a).

Since some variables were not independent, we used multivariate PERMANOVAs to examine the effects of province and eutrophication on the Euclidean distance matrix of normalized 1) Chl *a* and phaeopigments, 2) PIM and POM, 3) eelgrass shoot density and canopy height, 4) above and below ground biomass, 5) %C and %N tissue content, and 6) overall C and N storage. Where differences were significant we followed up with protected univariate PERMANOVA and post hoc *t*-tests.

Analogous to ANOVA, PERMANOVA also estimates the components of variation for both fixed and random factors as sums of squared fixed effects (divided by the appropriate degrees of freedom) and actual variance components (Anderson et al. 2008a). These estimators are directly comparable and useful in determining the relative importance of different terms in the model in explaining the overall variance. Since the estimates are in squared units of either Euclidean distance or Bray-Curtis similarity, the square root (\sqrt{V}) is taken to put them back into their original units (Anderson et al. 2008).

Multivariate PERMANOVA was also used to assess the community composition of the benthic and epiphytic algae. We used the zero-adjusted Bray-Curtis similarity matrix of the dispersion weighted algal cover to dampen the fluctuations of the metric for near-blank samples in an analogous way to the addition of a constant to the log transformation (Clarke and Gorley 2006). Dispersion weighting divides the cover of each species by their variance to mean ratio calculated from replicate quadrats within a site and then averaged across sites. This only downweights numerically dominant spatially clustered species decreasing the influence of their erratic cover estimates on the similarity coefficients (Clarke and Gorley 2006). When a significant effect was detected, we used similarity percentages analysis (SIMPER) to identify the species that consistently contributed (dissimilarity/SD ≥ 1) to the observed dissimilarities (Clarke and Warwick 2001). We used

cluster analysis on the zero-adjusted Bray-Curtis similarity matrix of the square root transformed site-averaged benthic and epiphytic cover to identify more general patterns in the community.

Finally, to assess changes in the overall primary producer assemblage, we used principal component analysis (PCA) on the site-averaged concentration of Chl *a*, combined above and below ground eelgrass biomass and the total cover of benthic and epiphytic macroalgae to evaluate the overall response of the phytoplankton-macrophyte-eelgrass assemblage to eutrophication. We then used regression analysis of the first principal component axis as well as the individual components Chl *a*, benthic and epiphytic algal cover and eelgrass biomass against percent tissue nitrogen to examine the effect of eutrophication on a regional scale.

3.3. Results

3.3.1. Eutrophication Levels

The % tissue nitrogen (%N) in eelgrass blades and roots identified two different eutrophication levels in our a priori selected sites (Table 3-1, Fig. 3-2). The average of the above and below ground %N ranged by 0.22% and 0.27% within the low and high eutrophication levels, respectively and there was a significant difference in both above and below ground %N between eutrophication levels (Table 3-2).

3.3.2. Phytoplankton Abundance

Chl *a* and phaeopigments, phytoplankton degradation products, increased significantly in the water column with eutrophication (Fig. 3-3; Table 3-3) and there was no province effect or interaction between factors. Despite the apparent increase in PIM with eutrophication (Fig. 3-3), there was a no significant effect of eutrophication, province or their interaction in the multivariate analysis with POM (Table 3-3) likely because of the high variability under eutrophied conditions. However, the effect of eutrophication explained the greatest amount of variance in PIM and POM after the residual.

3.3.3. *Benthic and Epiphytic Macroalgae*

Overall, 16 species or genera of benthic and epiphytic macroalgae were identified during field surveys: four red (*Ahnfeltia plicata*, *Chondrus crispus*, *Cystoclonium purpureum*, *Rhodochorton purpureum*), eight green (*Chaetomorpha linum*, *Cladophora rupestris*, *Codium fragile* ssp. *tomentosoides*, *Rhizoclonium* sp., *Spongomorpha* sp., *Ulva intestinalis*, *U. lactuca*, *Ulothrix speciosa*) and four brown algal species (*Fucus evanescence*, *F. vesiculosus*, *Pilayella littoralis*, *Sphaerotrichia divaricata*). Of these, six were annuals and only *Ulothrix speciosa* was an epiphyte on eelgrass.

Total abundance (% cover) of the benthic and epiphytic macroalgae was significantly affected by a province by eutrophication interaction (Table 3-4); however, eutrophication explained the greatest amount of the variation. Overall, total abundance strongly increased with eutrophication across as well as within provinces (Fig. 3-4). Species richness significantly increased with eutrophication with no effect of province nor was there an interaction between factors (Fig. 3-4, Table 3-4). Because of overall low species richness, with often only one species per site, we did not further examine diversity patterns.

Cluster analysis of the community composition, based on the average percent cover (mean of 11 quadrats per site) of each benthic and epiphytic species, revealed that sites with low levels of eutrophication were more similar to each other (73.3%) than to high sites (except one high site in NB) within the same province (Fig. 3-4 insert). It also showed that the different responses of the communities to high levels of eutrophication were driving the differences between provinces (Fig. 3-4 insert). The most important factor in explaining the variance in benthic and epiphytic community composition (multivariate PERMANOVA) was the eutrophication level (Table 3-4). In NB, community composition significantly differed between low and high levels (Post Hoc: $p = 0.001$) largely driven by the increase in *Ulothrix speciosa* (Fig. 3-4). In PEI, the significant differences between low and high ($p = 0.001$) were driven by the increase in both *Ulva lactuca* and *U. speciosa*.

3.3.4. *Eelgrass Canopy Structure*

Overall, eelgrass shoot density declined with increasing eutrophication (Fig. 3-5) but there was a significant province by eutrophication interaction (Table 3-5). In both provinces, shoot density significantly declined from low to high levels (Post Hoc: $p \leq 0.023$; Fig. 3-5) and the interaction is one of magnitude because shoot density declined more in PEI than NB. Across provinces, the canopy was similarly short under low levels of eutrophication ($p = 0.69$); however, the increase in height from low to high levels was more pronounced in PEI (Fig. 3-5), resulting in a significant interaction between eutrophication and province (Table 3-5).

There was a reduction in total eelgrass biomass with increasing eutrophication (Fig. 3-5). The decline was significant in above ground biomass in both provinces (Fig. 3-5; Table 3-5) but below ground biomass only decreased in PEI (Post Hoc: $p = 0.001$) leading to a significant interaction between province and eutrophication (Table 3-5). In addition, the below ground biomass under low levels of eutrophication did not differ between provinces ($p = 0.08$) but was significantly lower in PEI under highly eutrophic conditions ($p = 0.001$).

3.3.5. *Carbon and Nitrogen Storage*

While the tissue nitrogen content showed a clear increase with eutrophication (*see above, Eutrophication levels*), the tissue carbon content in above and below ground eelgrass was similar across eutrophication levels but was significantly higher in PEI (Table 3-2, Fig. 3-2). The overall carbon and nitrogen storage in above and below ground eelgrass biomass was significantly affected by the province by eutrophication interaction as were the below ground carbon and nitrogen storage when examined individually (multivariate and protected PERMANOVAs; Table 3-5). Despite the increase in tissue carbon content (%) across provinces, carbon storage (g m^{-2}) showed a similar pattern to eelgrass biomass whereby total carbon storage declined with eutrophication (Fig. 3-5). There was no effect of province or eutrophication on above ground carbon storage (Table 3-5), nor was there a difference in below ground storage between levels in NB (Post Hoc: $p = 0.28$) or across provinces under low levels of eutrophication ($p = 0.09$). However, there was significantly more carbon stored in the below ground tissue in NB under high eutrophica-

tion levels ($p = 0.001$) and the overall decline in total carbon storage was driven by the significant decrease in below ground storage in PEI ($p = 0.001$). Total nitrogen storage was similar across eutrophication levels likely because tissue nitrogen increased with eutrophication causing nitrogen storage to differ from the pattern observed in biomass (Fig. 3-5). There was no change in above ground nitrogen storage across provinces or eutrophication levels (Table 3-5), whereas below ground nitrogen storage significantly declined in PEI (Post Hoc: $p = 0.009$) but not in NB ($p = 0.11$). However, similar to the pattern in below ground biomass, nitrogen storage was significantly lower in PEI under levels of high eutrophication ($p = 0.001$) but was not different between provinces for low eutrophication levels ($p = 0.14$).

3.3.6. Overall Community

Principal component analysis of the entire primary producer assemblage showed clear distinctions between the levels of eutrophication (Fig. 3-6a). There was a negative correlation between overall eelgrass biomass (principal component (PC) 1 eigenvectors: -0.556) and the percent cover of benthic and epiphytic macroalgae (0.645) and Chl *a* concentration (0.524) in the first principal component separating the low and highly eutrophied conditions. The first principal component explained 70.6% of the variation. The second principal component was divided between the effect of eelgrass biomass (PC2 eigenvector: 0.657) and Chl *a* (0.753) and explained an additional 22.7% of the variation for a cumulative of 93.3%. Despite the variability in the response of some of the sites in PC1, there was a significant positive relationship (Linear regression, $F_{1,10} = 17.0$, $p = 0.002$) between the PC1 scores and average (blades and roots) tissue nitrogen (Fig. 3-6b).

We also examined the response of each component of the PCA across the regional scale (Fig. 3-7). There was a significant positive relationship between average tissue nitrogen and Chl *a* (Linear regression, $F_{1,10} = 7.7$, $p = 0.02$; Fig. 3-7a) and the strongest relationship was with the cover of benthic and epiphytic algae ($F_{1,10} = 21.4$, $p < 0.001$; Fig. 3-7b). However, the negative relationship between average tissue nitrogen and overall eelgrass biomass was not significant ($p = 0.10$; Fig. 3-7c).

3.4. Discussion

Our large-scale field surveys revealed a general regional shift from perennial eelgrass to opportunistic macroalgae and phytoplankton with increasing eutrophication in Atlantic Canada, but also some province- and species-specific responses. We further showed that carbon and nitrogen storage of eelgrass habitats declined with increasing eutrophication. Overall, our results demonstrate that eutrophication alters the structure and services of eelgrass beds with potentially wide-ranging consequences on coastal ecosystems and human well-being (Millennium Ecosystem Assessment 2005; Hughes et al. 2009).

3.4.1. *Changes in Phytoplankton*

Due to their short life-history, phytoplankton respond quickly to enhanced nutrient availability by increasing their biomass and can maintain a high biomass under sustained enrichment conditions (Sunda et al. 2006). Like previous studies in seagrass beds (Short et al. 1995; Moore et al. 1996), we documented an increase in phytoplankton biomass (Chl *a*) and phaeopigments, the degradation products of Chl *a*, with increasing nutrient loading. Increase in phytoplankton biomass is a major contributor to particle light attenuation in the water column and has been linked to eelgrass decline (Olesen 1996). Indeed, in our study, eutrophied sites with higher Chl *a* had reduced eelgrass density and biomass and enhanced canopy height, all indicating shading. In addition, increased benthic re-suspension because of the decrease in sediment stabilization due to the decline in eelgrass (Christiansen et al. 1981; Olesen 1996) can create a positive feedback loop further promoting eelgrass loss (Duarte 1995).

3.4.2. *Changes in Benthic and Epiphytic Macroalgae*

To date, much of the work on algae in eelgrass beds has focused on the overall increase in macroalgal abundance with nutrient loading emphasizing problematic species (Hauxwell et al. 2001; McGlathery 2001) while studies at the species level have focussed on species presence and absence (Johnson et al. 2005) and benthic and epiphytic microalgae (Neckles et al. 1993; Coleman and Burkholder 1995; Jaschinski et al. 2009). Our study is the first to document species-specific changes in epiphytic and benthic macroal-

gal abundance in eelgrass beds across different levels of eutrophication on both local and regional scales.

Typically, macroalgal assemblages in temperate seagrass beds with limited nutrient availability are dominated by rhodophytes whereas those experiencing nutrient loading are dominated mainly by filamentous and foliose chlorophytes (McGlathery 2001; Johnson et al. 2005; Schmidt et al. 2011). In our study, we identified one epiphytic and 15 benthic macroalgal species across all sites, and under high levels of eutrophication the assemblage was dominated by both filamentous and foliose green algal species. Although no work has examined the shifts in benthic macroalgal species assemblages specifically in eelgrass beds, research on ephemeral algae showed changes from predominantly red corticated algae (e.g., *Ceramium* spp., *Polysiphonia* spp.) to foliose (e.g., *Ulva* spp., *Porphyra* spp.) and uniseriate filaments (e.g., *Ulothrix* spp., *Pilayella* spp.) under increasing nutrient enrichment (Karez et al. 2004). Our results showed a clear increase in ephemeral epiphytic and benthic macroalgal cover but there was a difference in the responding species between provinces. In New Brunswick, the uniseriate filamentous epiphyte *Ulothrix speciosa* increased 40-fold in cover and in Prince Edward Island, the benthic foliose *Ulva lactuca* increased 670-fold reaching up to 61% cover. Despite using different metrics, our results are consistent with the observed 6-fold increase in benthic macroalgal biomass (Valiela et al. 1997), 38-fold increase in macroalgal canopy depth (Hauxwell et al. 2001) and 100-fold increase in epiphyte biomass (Wright et al. 1995) between estuaries with low and high nutrient loading.

The differences in the dominant species between provinces may be driven by a combination of factors, including differences in environmental conditions, climate, propagule supply, interactions between algal species and consumers as well as differences in nutrient loading (Lin et al. 1996; Johnson et al. 2005). Short et al. (1995) found that under identical nutrient enrichment conditions, phytoplankton, epiphytes and macroalgae each independently dominated a mesocosm tank which was attributed to differences in top-down control. Moreover, foliose macroalgae require higher loading rates than filamentous algae to bloom because they maintain higher individual biomass, have longer turnover times and lower nutrient uptake rates (Duarte 1995; Havens et al. 2001). This may suggest that, despite similar eelgrass tissue nitrogen content, the eutrophied estuaries in

Prince Edward Island may have higher nitrogen inputs than New Brunswick. Overall, the changes in macroalgal species composition and abundance will likely have a profound effect on associated animal communities as they provide food and habitat for a variety of species (Deegan et al. 2002; Schmidt et al. 2011).

3.4.3. *Changes in Eelgrass Canopy Structure*

Eelgrass can show both a physiological and morphological response to nutrient loading and light limitation (Short 1987; Moore et al. 1996; Romero et al. 2006). As nutrient enrichment and light attenuation increase, eelgrass responds by increasing leaf length and decreasing shoot density, biomass and growth leading to changes in canopy structure and ultimately eelgrass loss (van Lent et al. 1995; Moore et al. 1996; Short and Burdick 1996). Using mesocosm experiments, Short et al. (1995) teased apart the effects of nutrient enrichment and light limitation on eelgrass and found that shoot density and above ground biomass both decreased by 50% in all treatments whereas leaf length only increased by 29% with shade. We found a 45% decline in shoot density, 53% increase in leaf length and a 27% decline in above below ground biomass, which is consistent with the effects of shading. Light limitation has been attributed as the main cause of eelgrass decline in increasingly eutrophic estuaries by inhibiting growth and recruitment (Short et al. 1995; Hauxwell et al. 2001; Hauxwell et al. 2003).

The increases in phytoplankton biomass, and epiphytic and benthic macroalgal abundance observed in our study have all been documented to increase water column light attenuation (Hauxwell et al. 2001; Brush and Nixon 2002; Carroll et al. 2008). Both water column and epiphyte shading are detrimental for established shoots, whereas shading by macroalgal mats was more detrimental for newly recruiting eelgrass shoots (Hauxwell et al. 2001; Hauxwell et al. 2003). This suggests that the light limitation imposed by the large increases in phytoplankton biomass, epiphyte cover in New Brunswick and benthic macroalgal cover in Prince Edward Island contributed to the observed changes in canopy structure of established shoots but may also have a severe effect on the recruitment of new shoots.

Other potential factors that have been implicated in eelgrass decline, whose effects are exacerbated under low light conditions and high temperatures, include alterations in

oxygen and ammonium concentrations resulting from the presence of macroalgal canopies (McGlathery et al. 1997; Hauxwell et al. 2001; Havens et al. 2001) and increased sediment sulfides and anoxia (Pregnall et al. 1984; Goodman et al. 1995; Pulido and Borum 2010). Although we did not measure sulfides, sediments from cores collected at each of our study sites smelled increasingly of hydrogen sulfide with eutrophication, especially in Prince Edward Island. In addition, we observed extensive leaf bleaching at two of the highly eutrophied sites in Prince Edward Island which is indicative of water column anoxia (Pulido and Borum 2010). Once a shoot dies, so does the ramet and since eelgrass does not have dormant buds on their rhizomes to form new shoots it can only recolonize from the seed bank (Greve et al. 2005). Over time with persistent or re-occurring periods of extended anoxia this would lead to a decline in the below ground tissue due to inhospitable growing conditions and recurring die-offs of the new ramets to eventual extirpation as the seed bank is exhausted. This is likely what is happening in Prince Edward Island since we had an 82% decline in below ground biomass. However, in New Brunswick there was no significant change in below ground biomass, indicating that changes in sediment and water column chemistry were less severe which was likely due to the differential response of the macroalgal community between provinces: epiphytic macroalgae in New Brunswick compared to extensive benthic algal mats in Prince Edward Island.

3.4.4. *Changes in Eelgrass Carbon and Nitrogen Storage*

Eelgrass tissue nitrogen is known to reflect the nutrient availability of the surrounding waters (Short 1987; Duarte 1990; Lee et al. 2004) and we did document a significant increase in tissue nitrogen across study sites. However, despite this increase in tissue nitrogen, our values were all below the 1.8% benchmark established by Duarte (1990) indicating that eelgrass at our sites was still nitrogen limited. Macroalgae and phytoplankton compete strongly with eelgrass for nutrients (Duarte 1995) which can lead to nutrient limitation even under enriched conditions. Their increased abundance can initially benefit eelgrass by acting as a nutrient ‘sponge’ (Harlin 1978); however, these benefits are quickly outweighed by the adverse effects of biogeochemical changes in the sediment and light limitation (Burkholder et al. 1992).

Coastal rooted macrophytes, like eelgrass, are increasingly being recognized as significant carbon sinks for anthropogenic CO₂ and their global decline seriously threatens the ability of the coastal ocean to sequester carbon (Nellemann et al. 2009; McLeod et al. 2011). As the vegetation changes from eelgrass- to macroalgae- and phytoplankton-dominated, carbon and nitrogen cycling accelerates via increased herbivory and decomposition and long term storage declines (Duarte 1995; McClelland and Valiela 1998). These changes are reflected in our results where the decline in eelgrass biomass with increasing eutrophication led to an overall reduction of the carbon storage capacity of the habitat. The 82% decrease in below ground carbon storage in Prince Edward Island may have more serious long term repercussions because it was not offset by the 30% increase in below ground storage in New Brunswick and below ground storage has the greatest potential for long term carbon sequestration via burial (Mateo et al. 2006). Although total nitrogen storage did not change with eutrophication because of the increase in tissue nitrogen, there was a significant decrease in below ground nitrogen storage in Prince Edward Island. Therefore, the shift in the dominant primary producer from perennial eelgrass to ephemeral benthic and epiphytic macroalgae and phytoplankton will have profound implications not only for carbon and nitrogen cycling, storage and sequestration but also the trophic structure of associated food webs in New Brunswick and Prince Edward Island.

3.4.5. *Overall Community Changes and Indicators of Eutrophication*

Our study is the first to integrate changes in different primary producer components with increasing eutrophication into one analysis. Our PCA results clearly distinguished between the two eutrophication levels and show that all three primary producer components were needed to explain the variation in the response between provinces. Previous studies have reported positive relationships between total water column nitrogen and benthic and epiphytic macroalgal abundance, Chl *a* and a negative relationship with eelgrass biomass (Borum 1985; Short et al. 1995; Carroll et al. 2008). In our study, we found similar relationships with eelgrass tissue nitrogen but it was clear that the combination of the three different primary producer components best reflected the overall effect of eutrophication highlighting the variable response of individual ecosystems to nutrient loading.

There were two notable omissions in our study on primary producers, benthic and epiphytic microalgae. Benthic microalgal biomass and production frequently equal or exceed the biomass and production of phytoplankton in shallow coastal habitats (Webster et al. 2002) and epiphytic microalgae can, on average, contribute 18% of the productivity of an eelgrass bed (Penhale 1977). Increases in biomass and productivity, a concurrent decrease in diversity as well as a shift from large sized diatoms to small diatoms and cyanobacteria with increasing eutrophication have been documented for both epiphytic and benthic microalgal species (Neckles et al. 1993; Coleman and Burkholder 1994; Hillebrand and Sommer 1997). Both types of microalgae play a significant role in the uptake, cycling and trophic transfer of both carbon and nitrogen (Neckles et al. 1993; Sundbäck and Miles 2002; Webster et al. 2002) and, along with their significant contribution to estuarine production warrants further research into the effects of eutrophication on these two microalgal components which is essential for a complete picture of the changes in primary producer assemblages in eelgrass ecosystems under increased nutrient loading.

Our large-scale field surveys clearly show that eutrophication of coastal estuaries is profoundly altering the primary producer assemblage, eelgrass canopy structure and carbon and nitrogen storage capacity of coastal ecosystems at local and regional scales. These results highlight that management responses to eutrophication can be outlined on a regional scale, yet may need to be refined on a more local scale where natural variation between estuaries and differences in human activities can modify an ecosystem's response to eutrophication. Without nutrient management, the projected increase in nitrogen loading into coastal waters coupled with warming ocean temperatures, expanding bivalve and finfish aquaculture as well as other human activities could push increasingly stressed eelgrass populations in the Canadian Maritimes into a slow decline and ultimately loss of an essential coastal habitat with potentially severe consequences for associated plant and animal communities as well as human well-being.

Table 3-1. Name (ID), location, and eutrophication level (Level) for each study site as well as bottom depth (Depth) at high tide, mean water temperature (Temp.), and salinity. Also listed is the average of the above and below ground eelgrass (*Zostera marina*) tissue nitrogen content (%N). Temperature and salinity are the mean of 3 measurements with an SE range of 0.1-0.8 and 0.1-1.2, respectively.

Site	ID	Location	Level	Depth (m)	Temp. (°C)	Salinity	% N
New Brunswick							
Tabusintac Bay	TB	N 47.37 W 64.94	low	0.80	25.8	27.5	0.76
Baie St. Simon Sud	SS	N 47.73 W 64.77	low	1.00	23.7	26.8	0.90
Kouchibouguac Bay	KB	N 46.84 W 64.94	low	0.75	22.7	27.2	0.91
Baie de Lamèque	LM	N 47.79 W 64.67	high	1.50	22.7	27.0	1.14
Cocagne Harbour	CG	N 46.37 W 64.62	high	1.00	27.7	28.8	1.12
Baie de Bouctouche	BT	N 46.50 W 64.68	high	0.75	27.5	27.7	1.20
Prince Edward Island							
Stanley-Trout River Estuary	ST	N 46.47 W 63.46	low	1	24.7	27.0	0.72
Freeland River Estuary	FL	N 46.66 W 63.91	low	0.8	23.2	30.1	0.89
Mill River Estuary	MR	N 46.77 W 64.08	low	0.8	23	31.3	0.94
Midgell River Estuary	MD	N 46.42 W 62.63	high	1.5	22.7	24.5	1.13
Southwest River Estuary	SW	N 46.48 W 63.50	high	0.8	24.4	27.3	1.21
Kildare River Estuary	KD	N 46.84 W 64.05	high	0.3	27.5	27.0	1.39

Table 3-2. Multivariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on the above and below ground tissue carbon and nitrogen content (% CN) and univariate results for each component of tissue carbon and nitrogen (below black line). sqrt-V are unbiased estimates of the components of variance for each of the factors in the model. Negative sqrt-V values indicate that there is no evidence against the null hypothesis (Anderson et al. 2008a). Total degrees of freedom (df) = 30 and RES is the residual. Significant effects are in bold.

	Source	PR	EUTRO	PR X EUTRO	RES
	df	1	1	1	27
	<i>pseudo-F</i>	10.4	0.74	2.49	
Above and below %CN	<i>p</i>	0.002	0.41	0.11	
	sqrt-V	1.60	-0.27	0.90	1.99
% Nitrogen above	<i>pseudo-F</i>	0.33	52.8	0.63	
	<i>p</i>	0.58	0.001	0.43	
	sqrt-V	-0.003	0.25	-0.003	0.13
below	<i>pseudo-F</i>	0.29	67.0	0.43	
	<i>p</i>	0.58	0.001	0.53	
	sqrt-V	-0.002	0.22	-0.003	0.10
% Carbon above	<i>pseudo-F</i>	10.4	0.74	2.49	
	<i>p</i>	0.004	0.39	0.12	
	sqrt-V	1.60	-0.27	0.90	1.99
below	<i>pseudo-F</i>	10.5	0.33	2.51	
	<i>p</i>	0.005	0.55	0.13	
	sqrt-V	0.97	-0.26	0.55	1.20

Table 3-3. Multivariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on water column chlorophyll *a* and phaeopigment (Chl *a* and Phaeo) and particulate organic and inorganic matter (POM and PIM) concentrations as well as the univariate results for each component (below black line). sqrt-V are unbiased estimates of the components of variance for each of the factors in the model. Negative sqrt-V values indicate that there is no evidence against the null hypothesis (Anderson et al. 2008a). Total degrees of freedom (df) = 35 and RES is the residual. Significant effects are in bold.

	Source	PR	EUTRO	PR X EUTRO	RES
	df	1	1	1	32
	<i>pseudo-F</i>	1.60	6.60	0.78	
Chl <i>a</i> and Phaeo	<i>p</i>	0.18	0.003	0.48	
	sqrt-V	0.24	0.73	-0.21	1.31
	<i>pseudo-F</i>	1.20	1.87	0.24	
POM and PIM	<i>p</i>	0.28	0.16	0.80	
	sqrt-V	0.15	0.31	-0.41	1.41
Chl <i>a</i>	<i>pseudo-F</i>	2.84	10.8	1.77	
	<i>p</i>	0.11	0.002	0.20	
	sqrt-V	0.27	0.63	0.25	0.85
Phaeo	<i>pseudo-F</i>	0.65	3.38	0.003	
	<i>p</i>	0.52	0.03	0.92	
	sqrt-V	-0.14	0.36	-0.32	0.99

Table 3-4. Multivariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on the community composition (Community) and univariate results for total cover (%) and richness (S) of benthic and epiphytic macroalgae associated with eelgrass beds. sqrt-V are unbiased estimates of the components of variance for each of the factors in the model. Negative sqrt-V values indicate that there is no evidence against the null hypothesis (Anderson et al. 2008a). Total degrees of freedom (df) = 131 and RES is the residual. Significant effects are in bold.

	Source	PR	EUTRO	PR X EUTRO	RES
	df	1	1	1	128
	<i>pseudo-F</i>	39.1	92.2	34.6	
Community	<i>p</i>	0.001	0.001	0.001	
	sqrt-V	22.4	34.6	29.7	29.5
	<i>pseudo-F</i>	3.82	207.9	7.25	
Cover	<i>p</i>	0.019	0.001	0.003	
	sqrt-V	4.69	40.1	9.86	22.7
	<i>pseudo-F</i>	0.049	70.6	1.22	
Richness	<i>p</i>	0.84	0.001	0.26	
	sqrt-V	-0.09	0.81	0.06	0.79

Table 3-5. Multivariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on eelgrass characteristics: 1) shoot density (SD) and canopy height (CH), 2) above and below ground biomass (BIOMASS) and 3) above and below ground carbon and nitrogen storage (CN). Protected univariate PERMANOVA of individual eelgrass characteristics are shown below the dark line. sqrt-V are unbiased estimates of the components of variance for each of the factors in the model. Negative sqrt-V values indicate that there is no evidence against the null hypothesis (Anderson et al. 2008a). Total degrees of freedom (df) = 131 and RES is the residual. Significant effects are in bold.

	SOURCE	PR	EUTRO	PR X EUTRO	RES
	df	1	1	1	128
	<i>pseudo-F</i>	8.37	46.0	21.9	
SD and CH	<i>p</i>	0.001	0.001	0.001	
	sqrt-V	0.37	0.94	0.90	1.13
Above and below biomass	<i>pseudo-F</i>	2.94	3.87	4.22	
	<i>p</i>	0.058	0.028	0.018	
	sqrt-V	8.55	10.4	15.6	25.6
Above and below CN	<i>pseudo-F</i>	0.49	1.29	4.86	
	<i>p</i>	0.62	0.29	0.015	
	sqrt-V	-0.33	0.24	1.26	1.90
	<i>pseudo-F</i>	19.6	100.7	57.5	
SD	<i>p</i>	0.001	0.001	0.001	
	sqrt-V	0.35	0.81	0.86	0.65
	<i>pseudo-F</i>	2.72	18.6	3.99	
CH	<i>p</i>	0.09	0.001	0.05	
	sqrt-V	0.15	0.48	0.28	0.92
Biomass above	<i>pseudo-F</i>	2.20	4.15	2.16	
	<i>p</i>	0.11	0.03	0.12	
	sqrt-V	6.57	10.6	9.13	25.1
below	<i>pseudo-F</i>	4.07	5.40	10.1	
	<i>p</i>	0.03	0.004	0.001	
	sqrt-V	9.38	11.2	22.9	22.4

	SOURCE	PR	EUTRO	PR X EUTRO	RES
	df	1	1	1	128
Carbon above	<i>pseudo-F</i>	0.0005	2.17	0.40	
	<i>p</i>	0.98	0.14	0.54	
	sqrt-V	-0.24	0.26	-0.26	1.01
below	<i>pseudo-F</i>	0.36	3.24	11.1	
	<i>p</i>	0.54	0.07	0.002	
	sqrt-V	-0.17	0.31	0.93	0.86
Nitrogen above	<i>pseudo-F</i>	0.07	0.002	0.12	
	<i>p</i>	0.77	0.96	0.74	
	sqrt-V	-0.24	-0.25	-0.33	1.04
below	<i>pseudo-F</i>	1.85	0.007	11.4	
	<i>p</i>	0.19	0.81	0.001	
	sqrt-V	0.19	-0.20	0.96	0.88

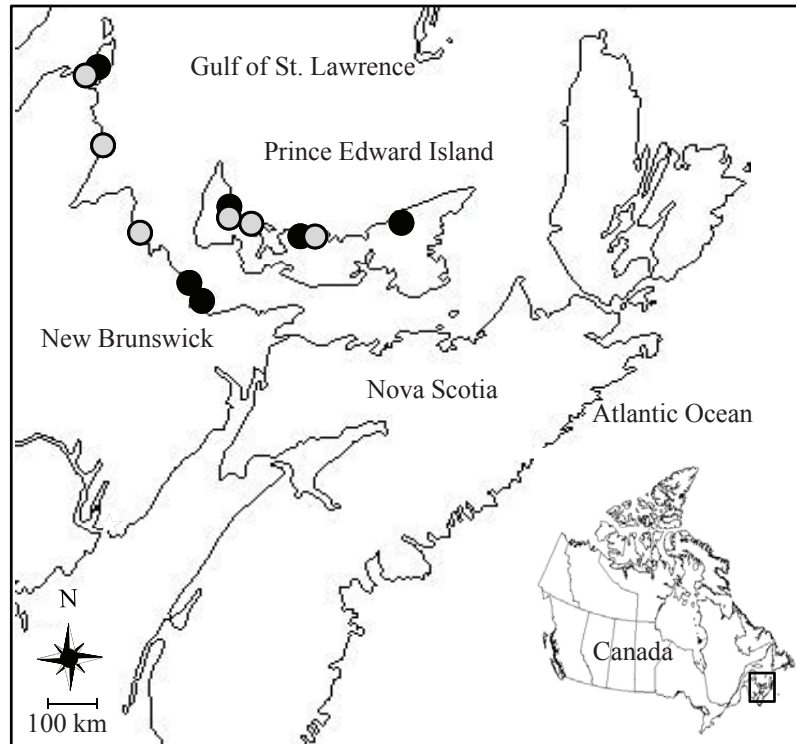


Figure 3-1. Map of study sites experiencing low (grey circle) and high (black circle) levels of eutrophication in the provinces of New Brunswick and Prince Edward Island in Atlantic Canada (see Table 3-1 for more details on each site and Coll et al. (2011) for photos).

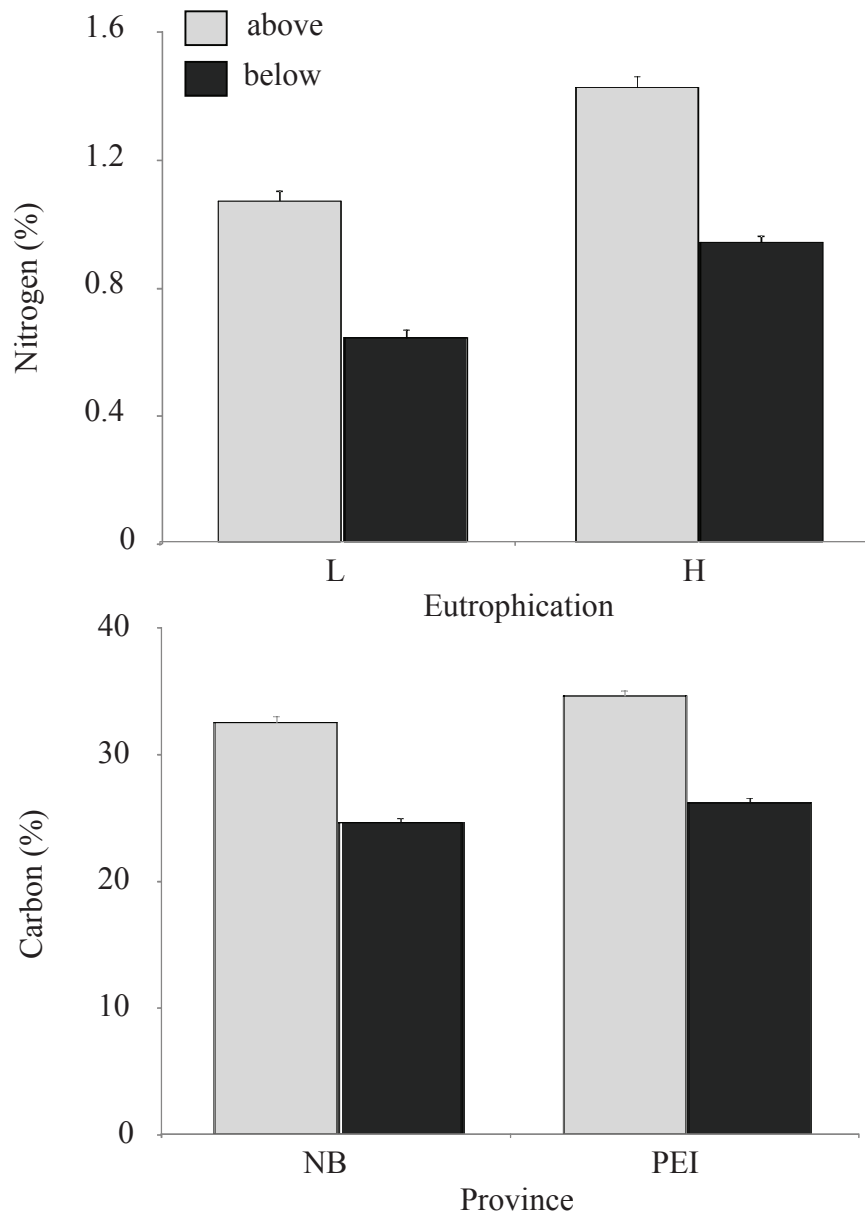


Figure 3-2. Mean above and below ground tissue nitrogen and carbon content (%) of eelgrass (\pm SE) across low (L) and high (H) eutrophication levels and the provinces of New Brunswick (NB) and Prince Edward Island (PEI), respectively.

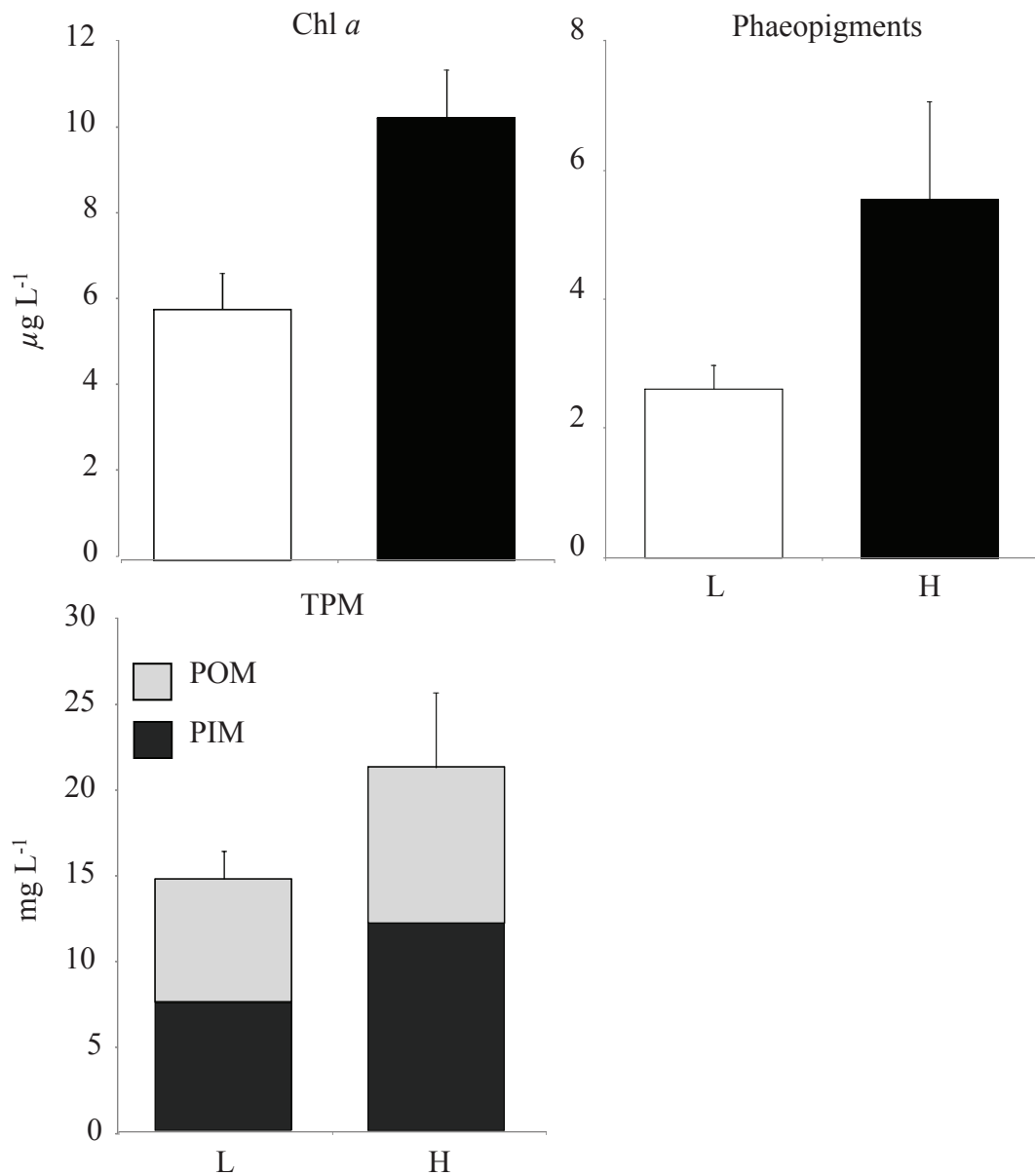


Figure 3-3. Concentrations (mean \pm SE) of chlorophyll *a* (Chl *a*), phaeopigments, and total particulate matter (TPM) with its organic (POM) and inorganic (PIM) components for water samples collected at sites experiencing low (L, white) and high (H, black) levels of eutrophication.

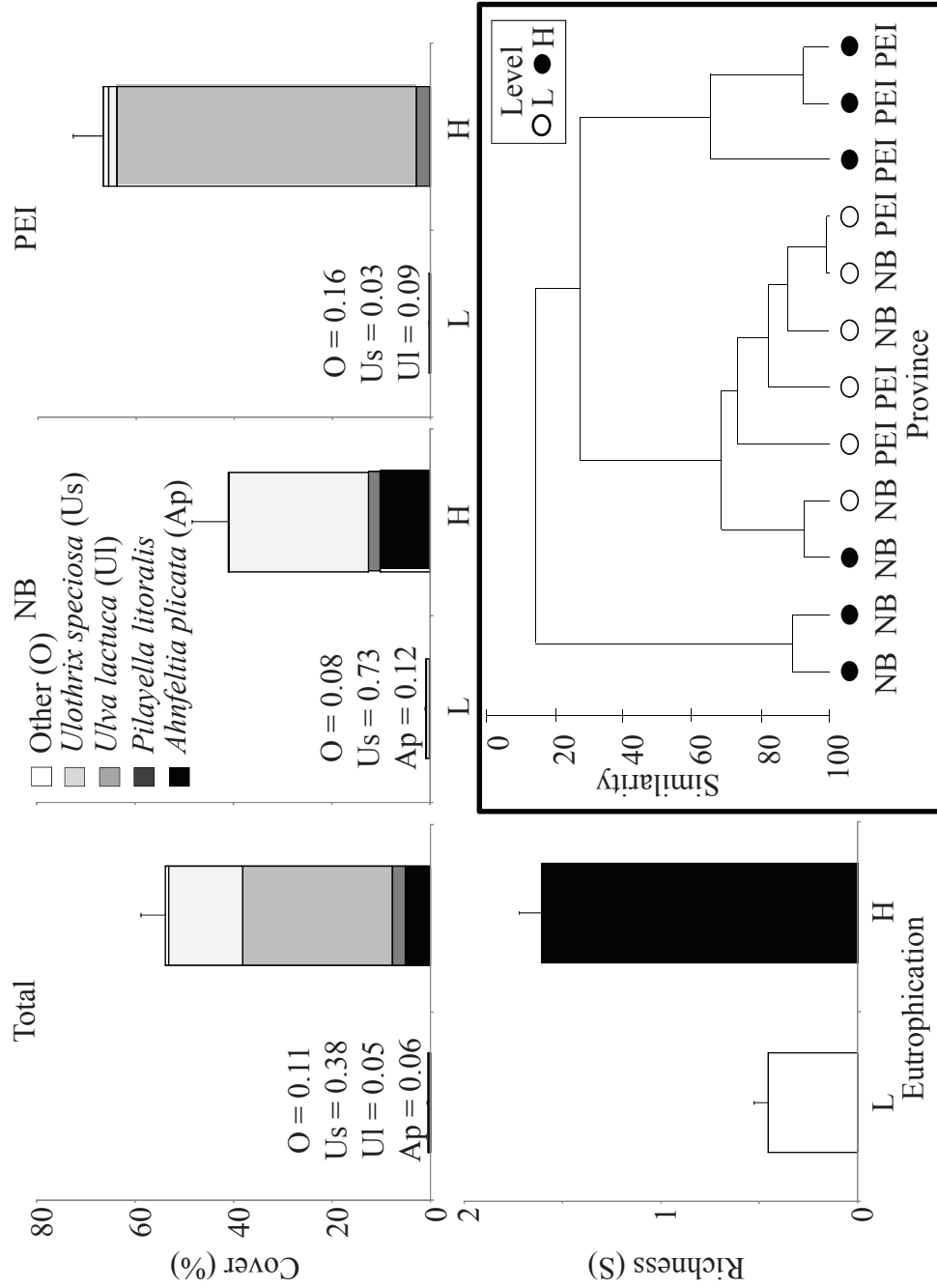


Figure 3-4. Abundance (% cover, \pm SE) of individual benthic and epiphytic macroalgae, species richness and inset cluster dendrogram on their community composition in eelgrass beds across low (L) and high (H) levels of eutrophication in New Brunswick (NB) and Prince Edward Island (PEI). The order in the color legend is the order that the macroalgae appear in the bars. Numbers above small bars indicate the percentage of species (abbreviations in legend) with low abundance. White and black bars in the species richness plot represent low and high eutrophication levels, respectively.

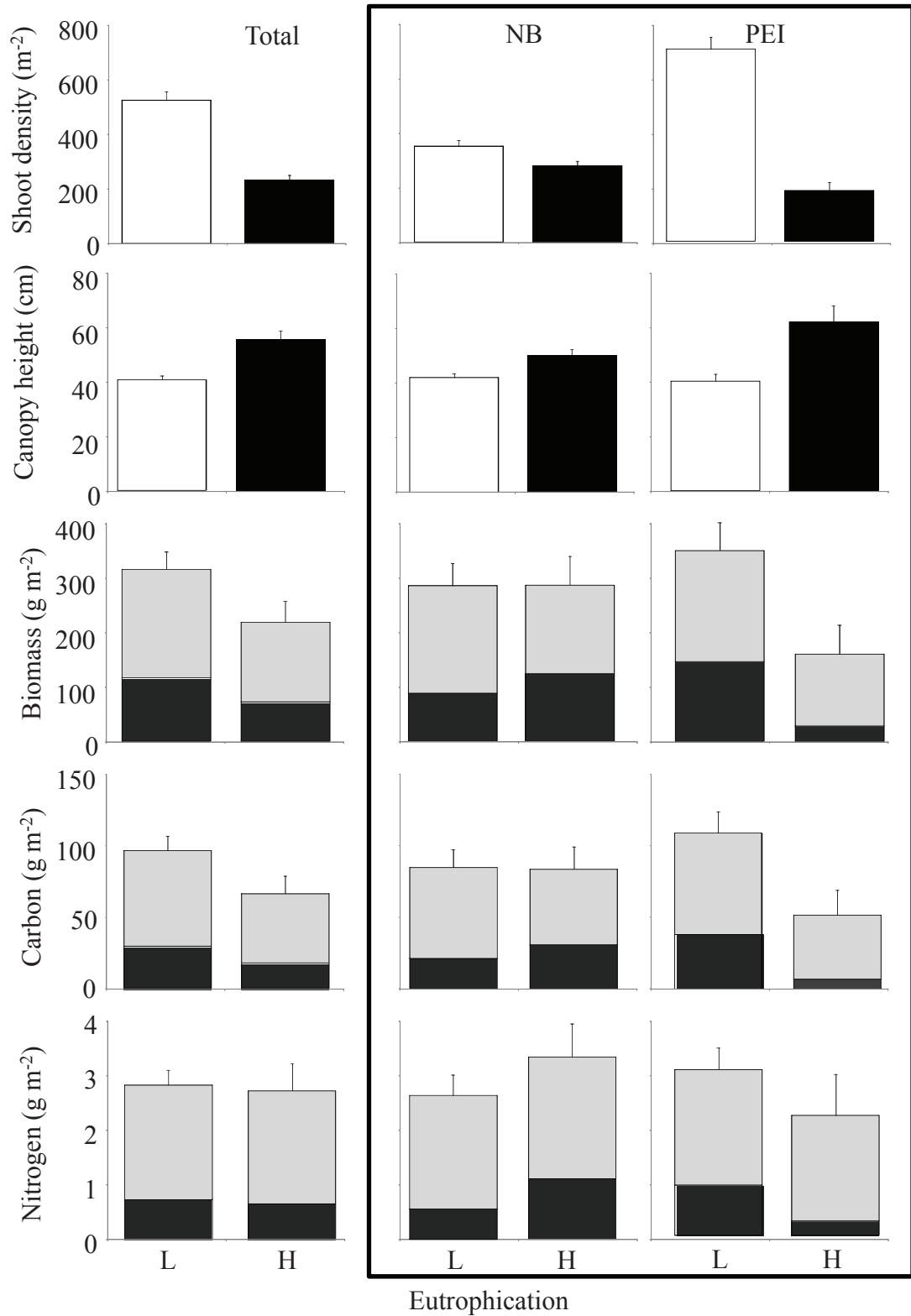


Figure 3-5. Canopy structure (shoot density and canopy height, \pm SE) of eelgrass beds across low (L, white) and high (H, black) levels of eutrophication in New Brunswick (NB) and Prince Edward Island (PEI) as well as biomass, carbon, and nitrogen storage in the above (light grey) and below (dark grey) ground component of the eelgrass beds.

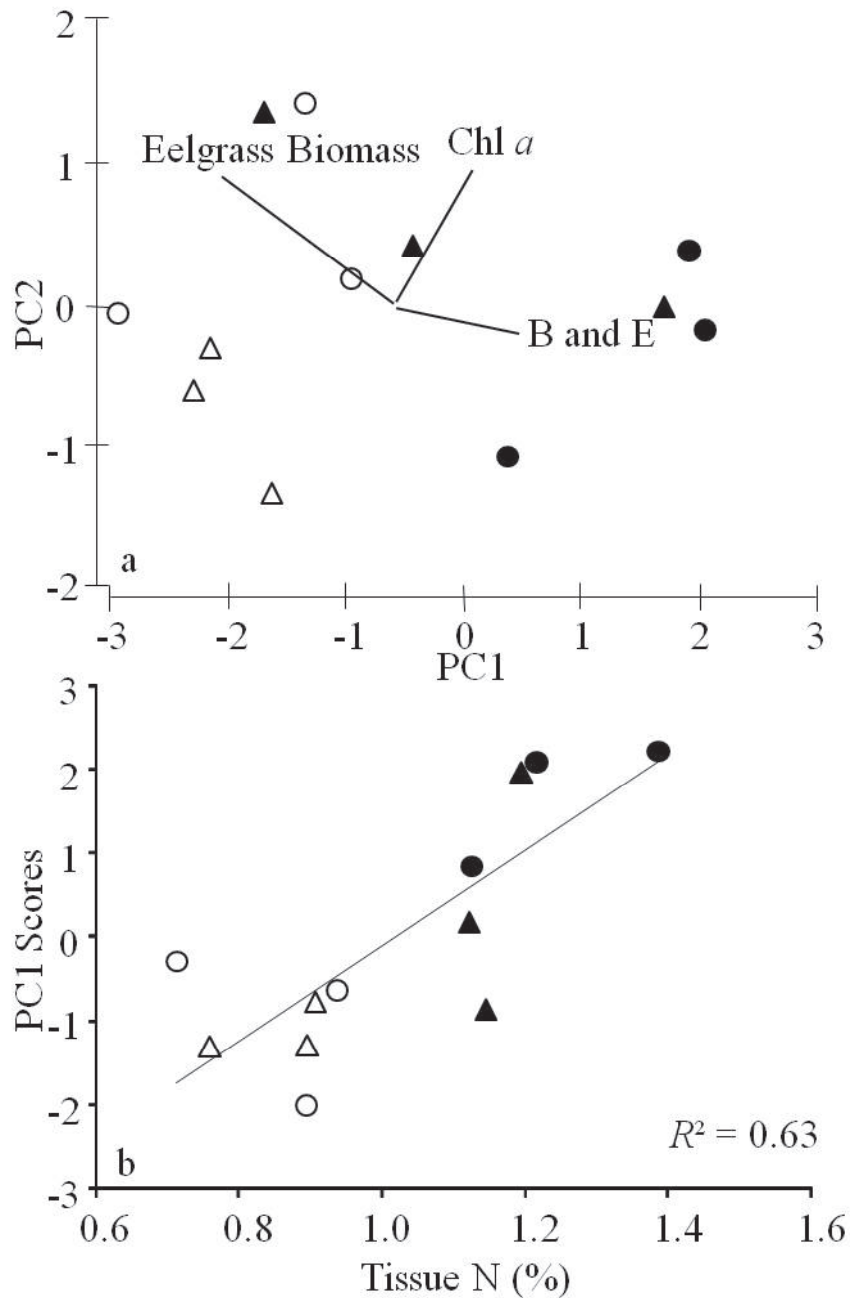


Figure 3-6. (a) Principal component analysis using overall above and below ground eelgrass biomass, phytoplankton chlorophyll *a* (Chl *a*) concentration and the total percent cover of benthic and epiphytic macroalgae (B and E) across low (white) and high (black) levels of eutrophication in New Brunswick (triangles) and Prince Edward Island (circles) and (b) linear regression of principal component 1 (PC1) scores against average (blades and roots) eelgrass tissue nitrogen content (%N) across all sites in both provinces.

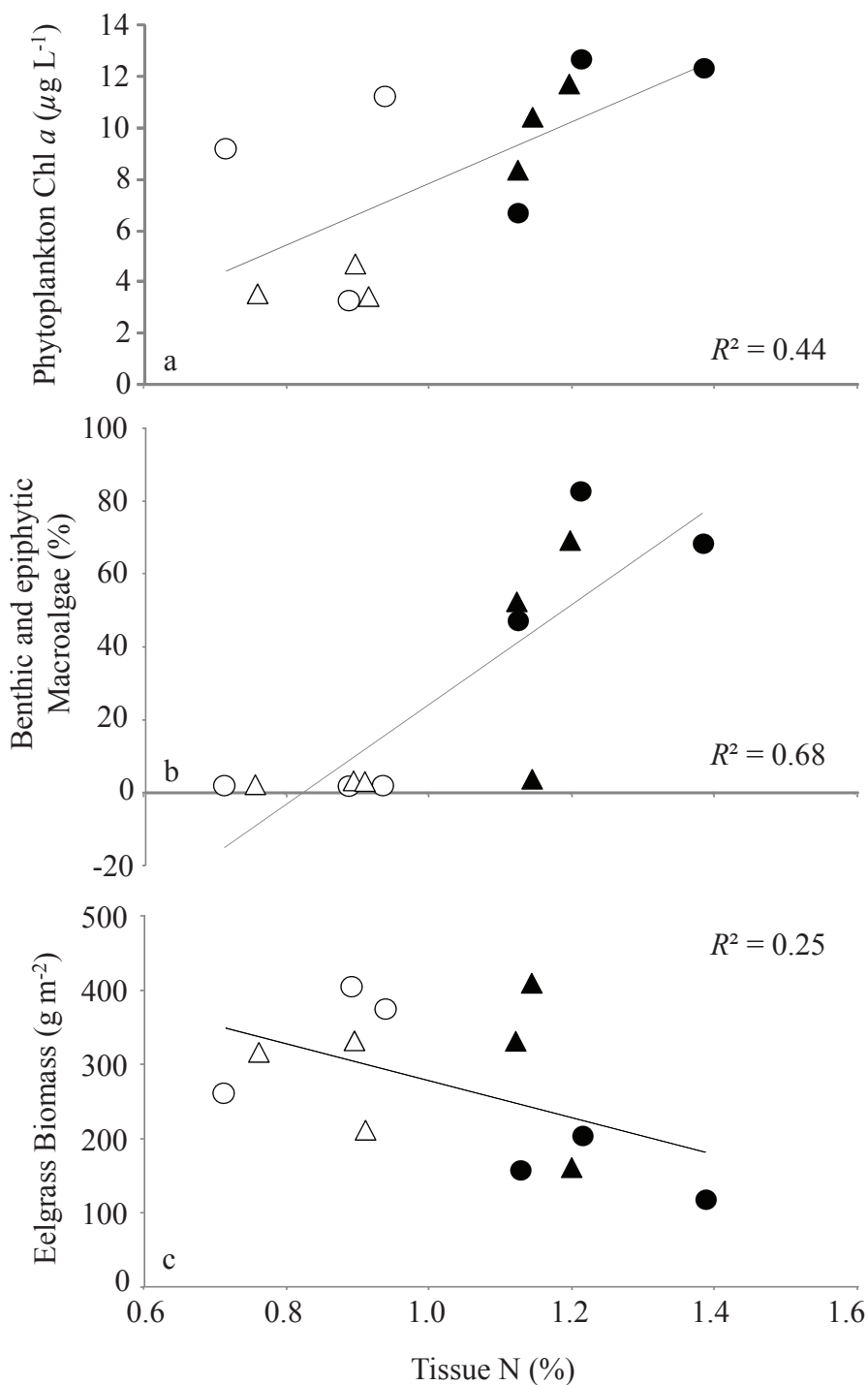


Figure 3-7. Regression analysis of (a) chlorophyll *a* (Chl *a*) concentration, (b) the total percent cover of benthic and epiphytic macroalgae, and (c) overall eelgrass biomass against average eelgrass tissue nitrogen (%N) content across all sites in New Brunswick (triangles) and Prince Edward Island (circles). Eutrophication levels are indicated with colors (low = open; high = black).

CHAPTER 4

Effects of Eutrophication on Fish and Invertebrate Communities in Seagrass Habitats

4.1. Introduction

The coastal ocean harbors some of the most diverse and productive habitats on the planet and is increasingly threatened by multiple anthropogenic activities (Duarte 2002; McClanahan 2002; Steneck et al. 2002b). The most universal threat to estuaries and coasts is nutrient pollution leading to the eutrophication of marine ecosystems (Jackson et al. 2001; Tilman et al. 2001; Kennish 2002). Estuaries are particularly sensitive to nutrient loading because they are semi-enclosed and have more limited flushing than an open coast (Kennish 2002; Dolbeth et al. 2003; Powers et al. 2005). In addition, riverine input to the estuary can deliver nutrients from human activities far upstream adding to those entering locally via direct discharge, land runoff, groundwater and atmospheric deposition (Vitousek et al. 1997; Kennish 2002). Nitrogen, the main driver of estuarine eutrophication in temperate regions (Howarth 1988; Howarth and Marino 2006), has increased in rivers between 2- to 20-fold for most regions surrounding the North Atlantic Ocean since pre-industrial times (Howarth et al. 1996) and is projected to continue increasing with coastal population density, agriculture and fossil fuel combustion (Vitousek et al. 1997; Tilman et al. 2001; Millennium Ecosystem Assessment 2005).

Seagrasses are found in estuaries around the world and eutrophication is one of the major contributors to the 33% decline in global seagrass area over the last century (Hughes et al. 2009; Waycott et al. 2009). Higher nitrogen concentrations stimulate the

growth of phytoplankton and opportunistic epiphytic and free-floating macroalgae effectively shading seagrass plants, which, in temperate estuaries, is the primary cause for seagrass loss (Hauxwell et al. 2001; Hauxwell et al. 2003). In addition, the decomposition of the increased amount of sinking particulate organic matter enhances oxygen depletion and the development of water column hypoxia and sediment anoxia (Gray et al. 2002), which alone can lead to the loss of seagrass beds (Pregnall et al. 1984; Goodman et al. 1995) but when combined with reduced light penetration is especially lethal (McGlathery 2001).

Seagrass beds play a vital role as breeding, nursery and foraging grounds and shelter for associated species including many commercially important fish and invertebrates (Duarte 2002; Heck et al. 2003; Hughes et al. 2009). However, changes in or loss of the seagrass canopy can have serious repercussions on the associated community which can lead to changes in trophic structure (Deegan et al. 2002; Pihl et al. 2006; Hughes et al. 2009). Yet, it is not simply the loss of the seagrass habitat that affects the associated fauna (Pihl et al. 2006; Schmidt et al. 2011) but also the biogeochemical processes that contribute to the shift in primary producers as eutrophication proceeds (Gray et al. 2002; Paerl 2006). The increase in phytoplankton and ephemeral algae associated with nutrient enrichment enhances the food resources available to filter feeders and herbivores (Diaz and Rosenberg 1995) which alters the pathway of nutrients through the benthic food-web, ultimately affecting the habitat's ability to support higher trophic levels (Deegan et al. 2002). In addition, the presence of an algal canopy may initially mitigate the effects of seagrass decline by providing an alternative habitat (Norkko et al. 2000; Salovius et al. 2005) but it also decreases the oxygen concentration at the sediment interface (Hauxwell et al. 2001) and mass accumulations may lead to frequent episodes of water column hypoxia (McGlathery 2001). Hypoxia in the water column and anoxic sediments can have negative effects on growth, metabolism and survivorship of finfish, shellfish and other invertebrates (Pihl et al. 1991; Rosenberg et al. 2001; Gray et al. 2002) and has been deemed the main driver of changes in benthic fauna associated with eutrophication (Gray et al. 2002).

In Atlantic Canada, many bays and estuaries are dominated by the eelgrass *Zostera marina* (Gotceitas et al. 1997; Seymour et al. 2002; Coll et al. 2011). However, estuarine

eutrophication in this region has already led to a shift in dominance of the primary producer assemblage from eelgrass under low nutrient conditions to phytoplankton and opportunistic macroalgae under high nutrient conditions (Schmidt et al. 2012). This study aims to examine the effects of eutrophication on the fish and invertebrate community associated with eelgrass beds as well as the species- and functional group-specific responses of the fauna and their habitat usage. Much of the work in temperate seagrass beds has focused on temporal changes within and between estuaries (e.g. Bonsdorff et al. 1997; Bachelet et al. 2000; Boström et al. 2002), spatial changes within an estuary across a gradient of eutrophication (e.g. Deegan et al. 2002; Cardoso et al. 2007) or on one component of the faunal assemblage such as infauna (e.g. Dolbeth et al. 2003) or fishes (e.g. Schein et al. 2012). The faunal patterns in many of these studies showed a decline in the total abundance and species richness and a shift towards small opportunistic and hypoxia tolerant species. Understanding these patterns across faunal groupings and at an estuary level is essential for regional scale management and decision making. Therefore, the main objectives of our study was to assess the local and regional-scale effects of increasing eutrophication on the faunal community as a whole as well as the response of specific species and functional groups and the habitat usage by adults and juveniles of mobile macrofauna using a large scale field survey in Atlantic Canada.

4.2. Methods

4.2.1. Study Sites

Our sites were located within 12 estuaries across the Provinces of New Brunswick (NB) and Prince Edward Island (PEI), Canada, and sampled from 27 July to 08 August 2007 (Fig. 4-1). All estuaries were sheltered from oceanic waves and contained soft sediment substrate dominated by monospecific beds of eelgrass as the main structuring vegetation. Sites were chosen based on the severity of land-based human activities contributing nitrogen to the estuary (Lotze et al. 2003; Coll et al. 2011), nutrient concentrations in PEI rivers (M. van Heuvel, unpublished data) and then confirmed by % nitrogen

concentrations in eelgrass tissue (Schmidt et al. 2012). For more details on the physical conditions of the study sites see Table 3-1.

4.2.2. *Sampling Design*

At each site, one 50 x 4 m transect was laid parallel to the shore inside the eelgrass bed ≥ 10 m from the vegetation-bare substrate interface. Sampling depth at high tide ranged from 0.3-1.5 m (Schmidt et al. 2012). Highly mobile and pelagic species (hereafter mobile and pelagic fauna) were censused by the same observer swimming along transects (~ 0.08 m s⁻¹) during the day- and night-time high tides to capture diurnal patterns in species abundance and size. We used the recommended transect size for underwater visual censuses of coral reefs (Mapstone & Ayling 1998). The abundance of mobile benthic species (hereafter benthic fauna) and percent cover of sessile benthic and epiphytic fauna (hereafter sessile fauna) were assessed during the day-time high tide by the same observer using eleven quadrats (0.5 x 0.5 m, with 0.25 m subsections identified with colored tape) placed every 5 m along the transect. The percent cover measures were estimated to the nearest 2% using the colored tape as a guide. For epiphytic fauna, we considered both sides of all the eelgrass blades in the quadrat as habitable space and as such 100% cover would mean that both sides of all of the blades in the quadrat were covered with epiphytes. We estimated the percent cover of each species on the collective, not each individual blade. Infauna were sampled using a sediment core (0.2 m diameter; 0.2 m deep) in 3 quadrats (at 0, 25, and 50 m) along the transect line. Core samples were processed in the field using a 0.5 μ m sieve. All organisms were identified to the lowest possible taxon in the field where possible or kept on ice to be identified in the laboratory when the organisms needed further examination under a microscope.

4.2.3. *Community Structure and Habitat Use*

The objective of our study was to evaluate the effects of eutrophication on the mobile and sessile faunal community associated with eelgrass beds and the habitat usage of adult and juvenile fishes and large decapod crustaceans. To separate juveniles from adults, we estimated individual total length of fishes and carapace width of decapods using a 15 cm scale bar with 1 cm graduations and used published age at maturity data (Table 4-1) to

group species into their respective adult and juvenile categories. Where species-specific data were not available for our region, we used the minimum reported total length at maturity for the closest region for the same or a related species (same genus or family if necessary) with a similar maximum size. To examine general patterns in the faunal assemblage we also classified species into functional groups: large and small demersal and small pelagic for highly mobile fishes censused using transects and herbivores, detritivores, filter feeders and predators for the quadrat fauna and infauna as well as filter feeders for sessile fauna.

4.2.4. *Statistical Analysis*

We used fully crossed two-factorial multivariate permutational analysis of variance (PERMANOVA) with a fixed province (two levels; NB, PEI) and eutrophication (two levels; L, H) factor to separately assess the overall community composition (presence/absence across all faunal groups) and functional group abundance and species composition for each component of the community (quadrat fauna, sessile fauna and infauna) as well as the adult and juvenile fishes and decapods. A fixed time of day factor (2 levels: Day, Night) was added to assess diurnal differences in the mobile and pelagic fauna. To examine habitat usage by adult and juvenile fishes and large decapods crustaceans across the levels of eutrophication and region, we added a fixed lifestage factor (2 levels: Adult, Juvenile) and focused our interpretations on the 2- and 3-way interactions. We used the zero-adjusted Bray-Curtis similarity matrix of the dispersion weighted functional group and species composition for the benthic fauna, sessile fauna and infauna to dampen the fluctuations of the metric for near-blank samples in an analogous way to the addition of a constant to the log transformation (Clarke and Gorley 2006). Dispersion weighting down-weights the influence of the numerically dominant, spatially clustered species on the similarity coefficients by dividing the abundance of each species by their variance to mean ratio calculated from replicate quadrats within a site and then averaged across sites (Clarke and Gorley 2006). Since there was no replication at the transect level, species abundance data were square-root transformed to down-weight the influence of highly abundant species and allow the rare species to influence the resemblance. Where differ-

ences were significant we followed up with protected univariate PERMANOVA for each functional group and post hoc t-tests.

For differences in species composition, we used cluster analysis within each province and similarity percentages (SIMPER) analysis to identify the species that consistently contributed to the differences for benthic fauna, sessile fauna and infauna, separately (Clarke and Warwick 2001). Species identified by SIMPER were examined individually using univariate PERMANOVA and post hoc t-tests and then grouped for presentation (e.g. small pelagics in Fig. 4-2). No corrections for multiple comparisons were made to the post hoc t-tests because the permutation p -values provide an exact test of each individual null hypothesis whereas experiment-wise corrections, such as Bonferroni, are inexact and known to be overly conservative (Anderson et al. 2008a). In addition, more than 30% of the comparisons had significant results indicating that they are less likely to be because of random chance. PERMANOVA also estimates the components of variation as sums of squared fixed effects and were used to determine the relative importance of different terms in the model in explaining the overall variance when no significant effects were detected (Anderson et al. 2008a).

To examine changes in overall species richness and total abundance (m^{-2} or % cover), we used univariate PERMANOVA on the Euclidean distance matrix of species richness of the entire community (presence/absence) as well as zero-adjusted Bray-Curtis similarity matrix of the square root transformed data of each assemblage component (mobile and pelagic, benthic, sessile, infauna). Finally, we used rarefaction curves to examine structural changes in each community component across the eutrophication levels because they are better at teasing out the changes than the Shannon diversity index when the number of species and individuals is low (Pearson and Rosenberg 1978).

4.3. Results

4.3.1. Diurnal Patterns in Mobile and Pelagic Fauna

Multivariate 3-factor PERMANOVA (province, eutrophication, time of day) did not detect a significant effect of any factor ($p > 0.20$) on the assemblage of mobile and pe-

lagic fauna. Therefore, we averaged the data collected at the different times of day at each site for the analysis of community structure. Nevertheless, some species were only observed during the day (*Alosa pseudoharengus*, *Aurelia aurita*, *Tautoglabrus adspersus*, *Urosalpinx cinerea*) or at night (*Cerebratulus lacteus*, *Clupea harengus harengus*, *Pseudopleuronectes americanus*). Some fish species were more frequently observed at night (*Anguilla rostrata*, *Gasterosteus aculeatus*) or during the day (*Menidia menidia*) while *Syngnathus fuscus* had a similar abundance at both times of day.

4.3.2. Overall Community Structure

We observed a total of 52 species or genera across all sites and eutrophication levels (Table 4-2). Of these, ten were exclusively found at low and twelve at highly eutrophied sites. Eighteen species were only observed at sites in Prince Edward Island (PEI), while six were exclusively in New Brunswick (NB; Table 4-2). The overall community composition and species richness based on the presence/absence of the entire assemblage differed between provinces (PERMANOVA: $pseudo-F_{1,8} = 2.7$, $p = 0.013$; $pseudo-F_{1,8} = 18.0$, $p = 0.005$, respectively) whereby richness was significantly higher in PEI (mean \pm SE: 21 ± 1.1) than NB (13.2 ± 1.6) but there was no difference across levels of eutrophication nor was there an interaction ($p \geq 0.11$).

4.3.3. Mobile and Pelagic Fauna

The mobile and pelagic fauna consisted mostly of fishes (Fig. 4-2) as well as two species of jellyfish (*Cyanea capillata*, *Aurelia aurita*), the oyster drill *Urosalpinx cinerea* and the large nemertean *Cerebratulus lacteus* (Table 4-2). We found no significant effects of province or eutrophication on the composition of the mobile and pelagic fauna or their total abundance (PERMANOVA: $p \geq 0.09$), nor was there an effect when aggregated into individual functional groups ($p \geq 0.17$) likely due to low abundances and high variability (Fig. 4-2). However, there was a tendency for an increase in total abundance with eutrophication, driven by increases in small demersal (mainly threespine stickleback *Gasterosteus aculeatus*) and small pelagic fishes (mainly Atlantic silverside *Menidia menidia*) (Fig. 4-2). In contrast, Atlantic herring *Clupea harengus harengus* and winter flounder *Pseudopleuronectes americanus* only occurred at low sites. Rarefaction analysis

showed that overall species richness was greater under low than high eutrophication conditions (Fig. 4-3).

4.3.4. *Benthic Fauna*

The benthic fauna consisted mainly of invertebrates, including gastropods, crustaceans, echinoderms and bivalves (Fig. 4-4), as well as two small fish (Table 4-2). We detected a significant block by eutrophication interaction in total abundance as well as functional group and species composition (Table 4-3). Total abundance increased with eutrophication in both provinces (Post Hoc: $p \leq 0.05$) but the increase in NB was greater than in PEI (Fig. 4-4). In addition, total abundance was significantly higher in PEI than NB in both the low and high levels of eutrophication ($p = 0.001$). Rarefaction showed consistently greater species richness under low than high eutrophication (Fig. 4-3). Overall, detritivores were more abundant in PEI than in NB ($p \leq 0.021$) and increased with eutrophication in PEI ($p = 0.001$) but not in NB ($p = 0.59$; Fig. 4-4). As a group filter feeders did not show any significant differences in abundance across provinces or levels of eutrophication (Table 4-3; Fig. 4-4). Predators on the other hand were significantly more abundant in PEI than NB and herbivores were more abundant under high levels of eutrophication (Table 4-3; Fig. 4-4). Cluster analysis of species abundance clearly showed distinct groupings with eutrophication in both provinces with minor overlap (data not shown), which was reflected in the highly significant difference ($p = 0.001$) in the assemblages between levels of eutrophication in both provinces. In addition, the assemblages present under each level of eutrophication were different between provinces ($p = 0.001$).

SIMPER analysis identified the species in Table 4-4 as consistently contributing to the differences between either levels of eutrophication or provinces. Among gastropods, the mud whelk *Nassarius obsoletus* declined with eutrophication in NB and increased in PEI (Fig. 4-4) although these effects were not statistically significant (Table 4-4). Both periwinkle species *Littorina saxatillis* and *L. littorea* declined with eutrophication, which was stronger in NB than PEI ($p \leq 0.041$). In contrast, the horn snail *Bittium alternatum* increased with eutrophication in NB ($p \leq 0.008$) but showed no significant difference across levels in PEI ($p \geq 0.19$; Fig. 4-4). Among crustaceans, isopods were most abundant under low levels of eutrophication in both provinces ($p \leq 0.013$, Fig. 4-4) but higher in

NB than PEI under eutrophied conditions ($p = 0.001$). Similarly, the sand shrimp *Cran-
gon septemspinosa* declined with increasing eutrophication in both provinces ($p \leq 0.035$)
but was more abundant in PEI than NB under low levels ($p = 0.005$; Fig. 4-4). There was
an increase in both the hermit crab *Pagurus acadiensis* and mysid shrimp *Mysis stenole-
pis* with eutrophication in NB, which was only statistically significant for the hermit crab
(Table 4-4), and both species were absent under highly eutrophied conditions in PEI ($p \leq$
0.003; Fig. 4-4). Among predators, there was a significantly higher number of Forbes
seastar *Asterias forbesii* in PEI but no effect of eutrophication (Table 4-4) despite the ap-
parent decline with eutrophication in PEI (Fig. 4-4). The fourspine stickleback *Apeltes
quadracus* was more abundant in PEI and under highly eutrophied conditions (Table 4-4;
Fig. 4-4) and the mummichog *Fundulus heteroclitus* also increased with eutrophication in
PEI ($p = 0.007$). Finally, the American oyster *Crassostrea virginica* was significantly
more abundant under eutrophic conditions in NB ($p = 0.047$) while it declined with eu-
trophication in PEI (Fig. 4-4).

4.3.5. Sessile Fauna

The sessile benthic and epiphytic fauna were all filter feeders and consisted of
sponges, tunicates, hydroids and bryozoans (Fig. 4-5; Table 4-2). There was no effect of
eutrophication on total sessile fauna abundance but it was significantly greater in PEI
than NB (Table 4-5; Fig. 4-5). Mean rarefaction showed consistently higher species rich-
ness under eutrophic conditions but there was large variability and the error bars of both
curves overlapped (Fig. 4-3). There was a significant interaction between province and
eutrophication on sessile species composition (Table 4-5; Fig. 4-5). Because sessile fauna
were almost completely absent in NB there was no difference in the assemblage across
levels of eutrophication (Post Hoc: $p = 0.059$) and it was different from PEI ($p = 0.001$),
where the assemblage differed across levels of eutrophication ($p = 0.001$; Fig. 4-5). These
findings were supported by cluster analysis; however, the dendograms are not shown due
to low abundances in NB. The hydroid *Sertularia pumila* was only observed under low
conditions in PEI ($p = 0.003$), whereas the sponge *Cliona celata* only at high levels in NB
(Fig. 4-5, Table 4-5). The tunicate *Botryllus schlosseri* ($p = 0.065$) and bryozoans *Electra
pilosa* ($p = 0.001$) and *Tegella unicornis* ($p = 0.12$) were only at highly eutrophied sites in

PEI (Fig. 4-5). There was also a significant decline in the epiphytic sponge *Amphilectus lobatus* ($p = 0.004$) mirrored by an increase in other hydroid species (Table 4-5; Fig. 4-5).

4.3.6. Infauna

The infauna consisted mostly of bivalves, amphipods and polychaetes (Fig. 4-6; Table 4-2). There was no significant effect of province or eutrophication on the total infauna abundance (Table 4-6) despite the increasing trend with eutrophication in Figure 4-6. Rarefaction revealed no difference in richness between levels of eutrophication (Fig. 4-3) likely due to the low sample size and high variability. There was also no effect on functional group composition (Table 4-6), likely because of the variable responses of the species within a group but also between groups (Fig. 4-6). However, detritivores were significantly more abundant in PEI than NB and filter feeders significantly increased with eutrophication in both provinces, whereas predators and herbivores showed no significant effects (Table 4-6; Fig. 4-6). In addition, we found a significant difference in the species composition between provinces and eutrophication (Table 4-6) which was reflected in the distinct low and high groupings in the cluster dendrogram of each province (data not shown). SIMPER identified all of the species in Figure 4-6 as consistently contributing to differences between provinces or eutrophication levels. Bivalves (other bivalves) and predatory polychaetes of the genus *Glycera* significantly increased in abundance with eutrophication (Table 4-6). Although the results were not significant, the bivalve *Petricola pholadiformis* and amphipods also increased with eutrophication, which was the factor that explained the most variation (Table 4-6; Fig. 4-6). The only infaunal gastropod that was collected declined as eutrophication increased as did the deposit feeding bamboo worm *Clymnella torquata*. In addition both *C. torquata* and the predatory polychaetes of the genus *Nereis* were both more abundant in PEI than NB (Table 4-6; Fig. 4-6).

4.3.7. Juvenile Versus Adult Habitat Usage

A total of twelve fish and large decapod crustacean species were observed as either adult or juvenile life stages in eelgrass beds in NB and PEI. Eight fish species were identified along transects; however, there was no significant effect of province or eutrophication level on the adult and juvenile abundance of these mobile and pelagic species

(PERMANOVA, $p \geq 0.33$), which are therefore not shown in the figures. Only four benthic fauna species were observed in either adult or juvenile lifestages, two fishes and two large decapod crustaceans (Fig. 4-7). Overall, there was a significant interaction between province and eutrophication levels for both adults and juveniles (Table 4-7). Adults increased in abundance with eutrophication driven by the significant increase in the mud crab *Dyspanopeus sayi* in NB (Post hoc: $p = 0.024$), which was also much more abundant in NB than in PEI ($p = 0.033$; Fig. 4-7). There was also an increase in the fourspine stickleback *Apeltes quadracus* and mummichog *Fundulus heteroclitus* and decline in rock crab *Cancer irroratus* in PEI (Fig. 4-7) but none of these effects were statistically significant (Table 4-7). For juveniles, SIMPER identified the two fishes as consistently contributing to the differences between provinces or eutrophication levels. The fourspine stickleback *A. quadracus* significantly increased in abundance in both provinces with eutrophication and was six times more abundant in PEI (Table 4-7; Fig. 4-7). The mummichog *F. heteroclitus* was only observed in PEI ($p = 0.011$) and increased in abundance by eight times from low to high levels of eutrophication but variability precluded a significant result ($p = 0.062$).

To directly compare the habitat usage of adults and juveniles for the four benthic fauna species we focussed on the significant 2- and 3-way interactions between lifestage and eutrophication and province. Overall, there was a significant effect of all factors and their interactions (multivariate PERMANOVA: $p \leq 0.005$) on species composition with the exception of the 3-way interaction ($p = 0.069$). Similarly, at the species level, there was a significant interaction between lifestage and eutrophication (univariate PERMANOVA: $pseudo-F_{1,256} = 3.95$, $p = 0.047$; $pseudo-F_{1,256} = 4.27$, $p = 0.026$, respectively) and lifestage and province ($pseudo-F_{1,256} = 3.95$, $p = 0.047$; $pseudo-F_{1,256} = 7.32$, $p = 0.005$) but no 3-way interaction ($p \geq 0.15$) on the abundance of both the fourspine stickleback and mummichog, respectively. There were more juveniles than adults of both species in PEI (Post Hoc: $p \leq 0.004$) and no difference in NB ($p \geq 0.05$; Fig. 4-7). Juveniles were also more abundant at highly eutrophied sites ($p \leq 0.026$) relative to low sites where they were more abundant than adults ($p \leq 0.022$), while adult abundance was not significantly affected by eutrophication ($p \geq 0.70$). There was no effect of any factor on the abundance of adult and juvenile rock crabs *C. irroratus* (univariate PERMANOVA: p

≥ 0.108) whereas the significant 3-way interaction ($pseudo-F_{1,256} = 6.10, p = 0.003$) best explained the complete absence of juvenile mud crabs and the presence of adults only at highly eutrophied sites in NB (Post Hoc: $p = 0.027$; Fig. 4-7).

4.4. Discussion

Our large-scale field surveys of eelgrass beds clearly show changes in the faunal community with eutrophication that differ between provinces. This is consistent with the differential response of the primary producer assemblage (Schmidt et al. 2012) that would influence the faunal community in terms of food and habitat availability and is summarised in Figure 4-8. Both provinces experienced a significant increase in phytoplankton abundance but New Brunswick saw an increase in the filamentous epiphytic macroalgae *Ulothrix speciosa*, whereas in Prince Edward Island there was an increase in the mat-forming benthic macroalgae *Ulva lactuca* (Schmidt et al. 2012). The higher algal abundance increases the flux of organic matter to the bottom thereby providing more food for filter feeders, herbivores and deposit feeders as well as refuge in the algal mats (Pearson and Rosenberg 1978; Raffaelli et al. 1998; Christie et al. 2009). However, these benefits can be quickly outweighed by the negative consequences of the increase in oxygen demand and hydrogen sulphide resulting from organic matter decomposition (Diaz and Rosenberg 1995; Raffaelli et al. 1998; Gray et al. 2002). Although we did not measure water and sediment chemistry, a decrease in oxygen and increase in sulphides was evident in the increasing sulfide smell with eutrophication in both provinces. This coupled with the decline in below ground eelgrass biomass and tissue bleaching in Prince Edward Island are all indicative of a hostile chemical environment in both the sediments and water column (Schmidt et al. 2012). In addition, lower oxygen concentrations have been documented in *Ulva lactuca* mats relative to eelgrass during the daytime in late summer, which likely led to night time hypoxic events in Prince Edward Island (Schein et al. 2012). However, more direct assessment of the physico-chemical environment is necessary to identify the causes of change and the mechanisms that may be driving the differences between provinces.

4.4.1. Primary Consumers

The increase in phytoplankton is likely what stimulated the increase in epiphytic filter feeders like the bryozoans and hydroids as well as small infaunal bivalves at eutrophied sites in both provinces and the American oyster *Crassostrea virginica* in New Brunswick. Such a general increase in filter feeders with eutrophication has also been observed on rocky shores (Worm and Lotze 2006). Whereas the increase in the small gastropod *Bittium alternatum* and amphipods is likely due to the increase in opportunistic algae such as *Ulothrix speciosa* in New Brunswick and *Ulva lactuca* in Prince Edward Island. Both *B. alternatum* and amphipods have been shown to have a positive association with finely branched algae (Schneider and Mann 1991) and epifaunal amphipods are known to reach high densities in the presence of macroalgal mats because they provide a food source and refuge from predation (Price and Hylleberg 1982; Hodder 1986; Norkko et al. 2000). Schein et al. (2012) also observed higher densities of gammarid amphipods in mats of *Ulva lactuca* relative to eelgrass. Amphipods were also among the remaining invertebrates at highly eutrophied sites in Waquoit Bay (Valiela et al. 1992). According to Pearson and Rosenberg (1978) the increase in infaunal filter feeders is indicative of intermediate enrichment since they can take advantage of the increased food availability and are able to withstand lower oxygen and higher sulphide concentrations (Cardoso et al. 2004). Filter feeders epiphytic on eelgrass, such as bryozoans, hydroids and tunicates, are also tolerant to periods of anoxia: they are known to occur on intertidal algae (Williams 1996) and are raised above the sediment-water interface where chemical gradients are steepest (Raffaelli et al. 1998; Gray et al. 2002). The decrease in abundance of the epiphytic sponge *Amphilectus lobatus* and disappearance of the hydroid *Sertularia pumila* on eelgrass with eutrophication despite the increase in food availability indicates their sensitivity to the adverse chemical conditions at the eutrophied sites in Prince Edward Island (Fig. 4-8).

Both littorinid snail species and the only infaunal gastropod decreased in abundance with increasing eutrophication. This is surprising since *Littorina littorea* is known to graze on eelgrass periphyton (Hootsmans and Vermaat 1985). Also, *Littorina littorea* has a dietary preference for *Ulva lactuca* (Watson and Norton 1985) and has been previously observed at high densities in macroalgal mats (Hodder 1986). Although molluscs are

known to have a high tolerance for hypoxia (Pearson and Rosenberg 1978; Gray et al. 2002), an increase in hydrogen sulphide can decrease tolerance for low oxygen conditions (Gray et al. 2002) and may have stimulated the snails to migrate away, despite the increase in food availability. Isopods also declined with increasing eutrophication which was more pronounced in Prince Edward Island. Isopods are omnivores but have a preference for filamentous algae (Orav-Kotta and Kotta 2004) and are also more sensitive to hypoxia and hydrogen sulphide than molluscs (Gray et al. 2002), which is likely why the decline was not as severe in New Brunswick. In addition, the thinning of the eelgrass canopy with eutrophication would increase the distance between blades and may have increased the vulnerability of isopods to predation (Orav-Kotta and Kotta 2004). As such, the increase in small predatory fishes in both provinces may have contributed to the isopod decline (Tober et al. 2000), especially in Prince Edward Island where their dorsoventrally flattened shape is not as well adapted to take refuge in the alternative algal mat habitat relative to the thin eelgrass blades (Orav-Kotta and Kotta 2004).

4.4.2. *Deposit Feeders and Higher Order Consumers*

The mud snail *Nassarius obsoletus* is primarily a deposit feeder feeding on organic detritus and benthic microalgae but it will on occasion scavenge dead organisms (Scheltema 1964). Interestingly, the mud snail decreased in abundance in New Brunswick despite the increase in organic matter from settling phytoplankton which was likely due to the concomitant increase in hermit crabs, which are known gastropod predators (Hazlett 1981). The mud snail increased in Prince Edward Island which may be linked to the increase in algal detritus and the absence of predatory hermit crabs. Interestingly, there was no change in the abundance of polychaetes with eutrophication or between provinces, but the composition of the assemblage did differ with a decrease in the abundance of more sensitive species (e.g. *Eteone* spp.) and an increase in more tolerant predators (e.g. *Nereis* spp.) (Pearson and Rosenberg 1978), possibly fuelled by the increase in infaunal bivalves. The decline in the deposit feeding bamboo worm *C. torquata* in both provinces is contrary to previous studies that found that increased organic enrichment favours deposit feeders (Bachelet et al. 2000; Cardoso et al. 2004). However, these studies exhibited severe cases of organic enrichment with complete loss of seagrass from the study sites,

which contrasts with our study and supports the conclusion that our sites are experiencing intermediate levels of eutrophication. Sediment hypoxia and increasing hydrogen sulphide are known to restrict infauna to the upper few centimetres of sediment and to cause infauna to stretch their tubes further above the sediment surface to reach higher into the microgradients of oxygen, making them more vulnerable to predation (Diaz and Rosenberg 1995; Rosenberg et al. 2001; Sagasti et al. 2001). The disappearance of the bamboo worm at highly eutrophied sites in New Brunswick is likely due to the increase in predation pressure from the higher abundances of mud (*Dyspanopeus sayi*) and rock (*Cancer irroratus*) crabs (Stehlik 1993; Sagasti et al. 2001). Both crab species also prey on infaunal bivalves, gastropods, small crustaceans and polychaete worms, many of which have increased in abundance in response to higher nutrient loading in New Brunswick. However, crustaceans are more sensitive to hypoxia than polychaetes and molluscs (Sagasti et al. 2001), which would explain their near absence and thus the presence of bamboo worms at highly eutrophied sites in Prince Edward Island. The sensitivity of crustaceans to hypoxia may have also caused the decline in the sand shrimp *Crangon septemspinosa* despite the increase in their primary food source, organic debris of plant origin as well as infaunal bivalves on which they are also known to prey (Wilcox and Jeffries 1974). Overall, the decrease in crustaceans at the highly eutrophied sites in Prince Edward Island is consistent with the effects of increased hypoxia and anoxia (Pihl et al. 1991; Diaz and Rosenberg 1995; Fox et al. 2009).

We found that the eutrophied sites that had an abundance of filamentous epiphytic or benthic mat-forming algae in addition to the remnant eelgrass canopy to be more suitable habitat for the adults and juveniles of small sized fishes and crustaceans than simply an eelgrass canopy. Schein et al. (2012) also found that areas dominated by *Ulva lactuca* had a higher number of adults and juveniles of the mummichog *Fundulus heteroclitus* and juveniles of the threespine stickleback *Gasterosteus aculeatus* in the late summer indicating that, although they spawn in eelgrass habitats early in the summer, the juveniles migrate into the sea lettuce habitat after hatching. The increases in the Atlantic silverside *Menidia menidia*, sticklebacks *G. aculeatus* and *Apeltes quadracus*, and mummichog *F. heteroclitus* are likely related to the increase in both prey and shelter from predation. Amphipods were found to be the largest component of the diet of *F. heteroclitus* (Schein

2009) and *A. quadracus* (Lubbers et al. 1990), which increased along with other diet items such as snails and bivalves. Both *M. menidia* and *F. heteroclitus* were the most abundant fish in Waquoit Bay (Tober et al. 2000) and, as in our study, mummichog abundance increased with nutrient loading. In contrast, the Atlantic silverside was ubiquitous which may be linked to the homogeneous distribution of their primary prey, zooplankton (Tober et al. 2000). However, in Atlantic Canada the diet of *M. menidia* is dominated by amphipods as well as the sand shrimp *Crangon septemspinosa* and polychaetes (Gilmurray and Daborn 1981), which likely contributed to their increase at eutrophied sites.

The increased habitat complexity created by the filamentous eelgrass epiphytes and the folding habit of the sheets of sea lettuce at the eutrophied sites may have decreased the predation efficiency of crustaceans, fishes and birds (Sogard and Able 1991b; Isaksson et al. 1994; Raffaelli et al. 1998), thereby providing a refuge, which combined with increased food availability, allowed some benthic invertebrates and small fishes to increase in abundance. In addition, these highly mobile predators are capable of migrating away from adverse conditions or moving higher in the water column to escape a hostile chemical environment, thereby allowing them to take advantage of the abundant food and shelter resources until it becomes metabolically too costly (Pihl et al. 1991; Raffaelli et al. 1998). However, these algal refugia are highly seasonal and contribute large amounts of organic material and nutrients to the sediment creating a negative feedback which further degrades the physico-chemical environment (Raffaelli et al. 1998).

4.4.3. *Community Structure*

In contrast to previous studies (Dolbeth et al. 2003; Cardoso et al. 2004; Schein et al. 2012), the overall abundance of fishes, mobile and sessile invertebrates and infauna increased with eutrophication at our study sites. However, the species richness of the mobile and pelagic and benthic fauna decreased, highlighting the loss of sensitive species, which is consistent with previous studies (Hughes et al. 2002; Schein et al. 2012). Yet, unlike previous works (Bachelet et al. 2000; Cardoso et al. 2004), we found no change in the richness of the sessile fauna and infauna, although we did use larger taxonomic groupings for the infauna that may have masked changes in species richness. We note

that in all studies that documented declines in abundance and richness, seagrass was lost at the most affected sites, indicating that they were likely more eutrophied than our high sites that still had an eelgrass canopy (Schmidt et al. 2012). Furthermore, the loss of seagrasses would mean the decline or disappearance of invertebrates associated with the shoots and leaves, such as sessile epiphytes and isopods (Deegan et al. 2002), as well as eliminate any of the benefits of the roots and rhizomes, such as protection from predation and oxygenation to the infauna (Borum et al. 2006; Heck and Orth 2006). Overall, the more severe declines in abundance and richness shown at more eutrophied sites may serve as a guide of what may happen in Atlantic Canada if eutrophication continues.

Overall, we observed an increase in the prevalence of herbivory which was driven by the large increases in herbivorous snails, amphipods and filter feeders. Despite their increase in abundance, grazers were not able to control the blooms of opportunistic algae. This suggests that grazers cannot keep up with increasing algal productivity, as shown in laboratory and field studies (Lotze and Worm 2002; Worm and Lotze 2006), or a possible trophic cascade driven by the increase in small predatory fishes following the decline of larger predatory fishes (Jackson et al. 2001; Heck and Orth 2006; Moksnes et al. 2008). Many large species, like Atlantic cod *Gadus morhua* and American eel *Anguilla rostrata* are known to use eelgrass beds as nurseries and foraging grounds (Sogard and Able 1991b; Tupper and Boutilier 1995; Gillanders 2006), but these species were rare to absent during our study. Overall, the species and functional group composition of the faunal assemblage changed with eutrophication, which has led to the degradation and simplification of eelgrass food webs in the region making them less resilient and more vulnerable to further species extinctions (Coll et al. 2011).

4.5. Conclusions

Our research clearly shows a shift in the faunal assemblage that is linked to the different foraging and sheltering opportunities resulting from changes in primary producers as well as tolerance of a more hostile chemical environment with less oxygen and more hydrogen sulphide (Fig. 4-8). The predicted increase in nutrient loading to coastal waters with further human population growth (Millennium Ecosystem Assessment 2005) will

only exacerbate these changes and eventually lead to a species depauperate habitat with degraded ecosystem functions and services as observed in highly eutrophied estuaries around the world (Lotze et al. 2006; Hughes et al. 2009; Waycott et al. 2009). Recovery from such a degraded state is possible, as seen in the Mondego Estuary, Portugal and Tampa Bay, Florida (Waycott et al. 2009). However, it is a long, labour intensive and costly process to re-establish eelgrass beds once they have disappeared (Fishman et al. 2004), which requires system-wide management strategies and the removal of key stressors (Walker et al. 2006; Lotze et al. 2011). Although eelgrass is not officially protected in Canada, it has been listed as an ecologically significant species (Fisheries and Oceans Canada 2009) which is a step in the right direction. However, since we still have existing eelgrass beds in what are considered some of the most eutrophied sites in Atlantic Canada, we should already be looking to invest in a management strategy to conserve existing eelgrass beds and their associated services rather than travelling the more ecologically and economically costly path of trying to re-establish them once they have been lost.

Table 4-1. Minimum length at maturity data for species observed in eelgrass beds in Atlantic Canada. If data on an observed species was not available, we used a closely related species (source species) instead.

Species	Source species	Size (cm)	Source
<i>Alosa pseudoharengus</i>		25	Scott and Scott (1988)
<i>Anguilla rostrata</i>		35.5	Fishbase
<i>Apeltes quadracus</i>		3.3	Scott and Scott (1988)
<i>Clupea harengus harengus</i>		24.5	Scott and Scott (1988)
<i>Gasterosteus aculeatus</i>		3.6	Fishbase
<i>Fundulus heteroclitus</i>		3.5	Fishbase
<i>Menidia menidia</i>		7.8	Scott and Scott (1988)
<i>Pseudopleuronectes americanus</i>		25	Fishbase
<i>Syngnathus fuscus</i>	<i>S. rostellatus</i>	10	Fishbase
<i>Cancer irroratus</i>		5	Fisheries and Oceans Canada (2000a)
<i>Dyspanopeus sayi</i>		0.8	Swartz (1978)

Fishbase: A global information system on fishes www.fishbase.org

Table 4-2. Species presence (+) or absence (blank), their common name and functional group (FG) in eelgrass beds experiencing low (L) and high (H) levels of eutrophication in the provinces of New Brunswick (NB) and Prince Edward Island (PEI) in Atlantic Canada. P = predator, H = herbivore, D = detritivore, F = filter feeder. Data are separated into assemblage components (mobile and pelagic, benthic, sessile and infauna).

Species	Common Name	FG	NB		PEI	
			L	H	L	H
Mobile and pelagic fauna						
<i>Alosa pseudoharengus</i>	Alewife	P				+
<i>Anguilla rostrata</i>	American eel	P	+		+	+
<i>Aurelia aurita</i>	Moon jelly	P				+
<i>Cerebratulus lacteus</i>	Milky ribbon worm	P			+	
<i>Clupea harengus harengus</i>	Atlantic herring	P			+	
<i>Cyanea capillata</i>	Lion's mane jelly	P	+	+	+	
<i>Gasterosteus aculeatus</i>	Threespine stickleback	P	+	+	+	+
<i>Menidia menidia</i>	Atlantic silverside	P	+	+	+	+
<i>Pseudopleuronectes americanus</i>	Winter flounder	P	+			
<i>Syngnathus fuscus</i>	Northern pipefish	P			+	+
<i>Tautoglabrus adspersus</i>	Cunner	P		+		
<i>Urosalpinx cinerea</i>	American oyster drill	P			+	
Benthic fauna						
<i>Apeltes quadracus</i>	Fourspine stickleback	P	+	+	+	+
<i>Asterias forbesii</i>	Forbes seastar	P	+		+	+
<i>Asterias vulgaris</i>	Northern seastar	P	+	+		
<i>Bittium alternatum</i>	Horn snail	H	+	+	+	+
<i>Cancer irroratus</i>	Rock crab	P	+		+	
<i>Crangon septemspinosa</i>	Sand shrimp	D	+	+	+	+
<i>Crassostrea virginica</i>	American oyster	F		+	+	+
<i>Dyspanopeus sayi</i>	Mud crab	D	+	+		
<i>Fundulus heteroclitus</i>	Mummichog	P		+	+	+
<i>Idotea</i> sp.	Isopod	H	+	+	+	+
<i>Littorina littorea</i>	Common periwinkle	H		+		+
<i>Littorina saxatillis</i>	Rough periwinkle	H	+	+	+	+
<i>Mysis stenolepis</i>	Mysid shrimp	H	+	+	+	
<i>Mytilus</i> sp.	Mussel	H			+	
<i>Nassarius obsoletus</i>	Mud whelk	D	+	+	+	+
<i>Pagurus acadensis</i>	Acadian hermit crab	D	+	+	+	
<i>Palaemonetes</i> sp.	Grass shrimp	H		+	+	
Predatory polychaete	Bristle worm	P				+
<i>Turbonilla</i> sp.	Pyramid shell	H		+		
Sessile Fauna						
<i>Amphilectus lobatus</i>	Egg sponge	F			+	+
<i>Botryllus schlosseri</i>	Gold star tunicate	F				+
<i>Cliona celata</i>	Red boring sponge	F		+	+	
<i>Electra pilosa</i>	Hairy sea mat	F				+
<i>Halichondria panicea</i>	Breadcrumb sponge	F			+	

Species	Common Name	FG	NB		PEI	
			L	H	L	H
<i>Microciona prolifera</i>	Red beard sponge	F		+	+	
Other Hydroids	Hydroids	F		+	+	+
<i>Sertularia pumila</i>	Garland hydroid	F			+	
<i>Tegella unicornus</i>	Lacy crust bryozoan	F				+
Infauna						
Amphipod	Scuds	H		+		+
<i>Clymenella torquata</i>	Bamboo worm	D	+		+	+
Deposit feeding polychaetes	Bristle worms	D	+		+	
<i>Ensis directus</i>	Atlantic jackknife clam	F				+
<i>Eteone</i> spp.	Paddle worm	D			+	
Gastropod	Snail	H	+		+	+
<i>Glycera</i> spp.	Bloodworm	D	+	+	+	+
<i>Nereis</i> spp.	Clam worms	P			+	+
<i>Petricola pholadiformis</i>	False angel wing	F		+		+
Other bivalves	Clams	F	+	+	+	+
Other predatory polychaetes	Bristle worms	P	+	+	+	+

Table 4-3. Univariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on the total abundance as well as the multivariate results for the functional group (FG) and species (SPP) composition of benthic fauna. Protected univariate PERMANOVA on the abundance of individual functional groups are shown below the dark line. Residual and total degrees of freedom (df) = 128 and 131, respectively. Significant effects ($p \leq 0.05$) are in bold and non-significant effects in italics represent the term in the model that explains the most variance after the residual.

	SOURCE	PR	EUTRO	PR X EUTRO
	DF	1	1	1
Total	<i>pseudo-F</i>	46.9	1.27	6.84
	<i>p</i>	0.001	0.27	0.005
FG	<i>pseudo-F</i>	7.72	12.4	3.0
	<i>p</i>	0.001	0.001	0.035
SPP	<i>pseudo-F</i>	28.0	12.9	5.93
	<i>p</i>	0.001	0.001	0.001
Detritivores (D)	<i>pseudo-F</i>	3.27	6.25	9.76
	<i>p</i>	0.056	0.014	0.003
Filter Feeders (F)	<i>pseudo-F</i>	0.39	2.33	3.29
	<i>P</i>	0.54	0.16	<i>0.064</i>
Predators (P)	<i>pseudo-F</i>	37.8	0.22	0.03
	<i>P</i>	0.001	0.76	0.97
Herbivores (H)	<i>pseudo-F</i>	2.53	14.3	1.85
	<i>P</i>	0.078	0.001	0.14

Table 4-4. Protected univariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on the abundance of benthic fauna species identified by SIMPER analysis as consistently contributing to difference between provinces or levels of eutrophication. Residual and total degrees of freedom (df) = 128 and 131, respectively. Significant effects ($p \leq 0.05$) are in bold and non-significant effects in italics represent the term in the model that explains the most variance after the residual.

	SOURCE	PR	EUTRO	PR X EUTRO
	DF	1	1	1
<i>Nassarius obsoletus</i> (No)	<i>pseudo-F</i>	3.12	1.69	2.32
	<i>P</i>	0.07	0.18	0.12
<i>Littorina saxatilis</i> (Ls)	<i>pseudo-F</i>	4.25	3.50	8.12
	<i>P</i>	0.025	0.066	0.005
<i>Littorina littorea</i> (Ll)	<i>pseudo-F</i>	4.22	11.8	4.11
	<i>P</i>	0.04	0.001	0.024
<i>Bittium alternatum</i> (Ba)	<i>pseudo-F</i>	41.0	16.1	4.0
	<i>P</i>	0.001	0.001	0.03
<i>Crangon septemspinosa</i> (Cs)	<i>pseudo-F</i>	5.78	30.0	8.38
	<i>P</i>	0.014	0.001	0.001
<i>Idotea</i> spp. (I)	<i>pseudo-F</i>	2.90	33.5	3.96
	<i>P</i>	0.072	0.001	0.028
<i>Pagurus acadiensis</i> (Pa)	<i>pseudo-F</i>	9.06	9.06	11.1
	<i>P</i>	0.002	0.002	0.001
<i>Mysis stenolepis</i> (Ms)	<i>pseudo-F</i>	8.10	2.39	2.95
	<i>P</i>	0.001	0.11	0.043
<i>Asterias forbesii</i> (Af)	<i>pseudo-F</i>	31.8	0.47	0.47
	<i>P</i>	0.001	0.52	0.54
<i>Fundulus heteroclitus</i> (Fh)	<i>pseudo-F</i>	6.70	6.70	10.8
	<i>P</i>	0.005	0.009	0.001
<i>Apeltes quadracus</i> (Aq)	<i>pseudo-F</i>	6.19	4.39	1.82
	<i>P</i>	0.012	0.03	0.17
<i>Crassostrea virginica</i>	<i>pseudo-F</i>	1.72	0.97	6.87
	<i>P</i>	0.18	0.33	0.007

Table 4-5. Univariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on the total sessile fauna abundance as well as the multivariate results for sessile species (SPP) composition. Protected univariate PERMANOVA on the abundance of individual species identified by SIMPER analysis as consistently contributing to difference between provinces or levels of eutrophication are shown below the dark line. Residual and total degrees of freedom (df) = 128 and 131, respectively. Significant effects ($p \leq 0.05$) are in bold and non-significant effects in italics represent the term in the model that explains the most variance after the residual.

	SOURCE	PR	EUTRO	PR X EUTRO
	DF	1	1	1
Total	<i>pseudo-F</i>	110.0	3.14	0.292
	<i>p</i>	0.001	0.081	0.60
SPP	<i>pseudo-F</i>	27.0	6.21	5.31
	<i>p</i>	0.001	0.001	0.002
<i>Cliona celata</i>	<i>pseudo-F</i>	0.50	0.50	<i>1.66</i>
	<i>p</i>	0.86	0.87	<i>0.16</i>
<i>Microciona prolifera</i>	<i>pseudo-F</i>	0.73	0.73	<i>3.18</i>
	<i>p</i>	0.41	0.41	<i>0.07</i>
<i>Amphilectus lobatus</i>	<i>pseudo-F</i>	30.0	9.82	9.82
	<i>p</i>	0.001	0.002	0.002
<i>Electra pilosa</i>	<i>pseudo-F</i>	12.6	12.6	12.6
	<i>p</i>	0.001	0.001	0.001
<i>Tegella unicornis</i>	<i>pseudo-F</i>	3.82	3.82	3.82
	<i>p</i>	0.043	0.042	0.040
<i>Botryllus schlosseri</i>	<i>pseudo-F</i>	4.15	4.15	4.15
	<i>p</i>	0.022	0.018	0.018
<i>Sertularia pumila</i>	<i>pseudo-F</i>	9.92	9.92	9.92
	<i>p</i>	0.001	0.001	0.001
Other hydroids	<i>pseudo-F</i>	20.1	5.02	2.26
	<i>p</i>	0.001	0.02	0.123

Table 4-6. Univariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on the total infauna abundance as well as the multivariate results for functional group (FG) and species (SPP) composition. Protected univariate PERMANOVA on the abundance of individual species identified by SIMPER analysis as consistently contributing to difference between provinces or levels of eutrophication are shown below the dark line. Residual and total degrees of freedom (df) = 31 and 34, respectively. Significant effects ($p \leq 0.05$) are in bold and non-significant effects in italics represent the term in the model that explains the most variance after the residual.

	SOURCE	PR	EUTRO	PR X EUTRO
	DF	1	1	1
Total	<i>pseudo-F</i>	2.57	1.28	0.080
	<i>P</i>	0.12	0.27	0.89
FG	<i>pseudo-F</i>	2.10	2.16	0.28
	<i>P</i>	0.081	0.086	0.92
SPP	<i>pseudo-F</i>	3.05	4.34	0.23
	<i>P</i>	0.008	0.001	0.97
Detritivores (D)	<i>pseudo-F</i>	5.15	0.48	0.36
	<i>P</i>	0.024	0.56	0.64
Filter Feeders (F)	<i>pseudo-F</i>	0.11	4.07	0.35
	<i>P</i>	0.90	0.039	0.68
Predators (P)	<i>pseudo-F</i>	1.93	0.39	0.019
	<i>P</i>	0.16	0.59	0.99
Herbivores (H)	<i>pseudo-F</i>	0.53	0.32	0.92
	<i>P</i>	0.64	0.84	0.41
Amphipods (A)	<i>pseudo-F</i>	0.12	3.30	0.12
	<i>P</i>	0.78	0.11	0.78
Gastropod (G)	<i>pseudo-F</i>	0.78	1.35	0.96
	<i>P</i>	0.57	0.25	0.45
<i>Eteone</i> spp. (E)	<i>pseudo-F</i>	3.68	3.68	3.68
	<i>P</i>	0.072	0.072	0.086
<i>Glycera</i> spp.	<i>pseudo-F</i>	1.52	7.68	0.10
	<i>P</i>	0.22	0.006	0.82
<i>Clymnella torquata</i> (Ct)	<i>pseudo-F</i>	5.99	3.07	0.073
	<i>P</i>	0.021	0.079	0.90
<i>Nereis</i> spp. (N)	<i>pseudo-F</i>	10.2	0.65	0.65
	<i>P</i>	0.002	0.45	0.42

	SOURCE	PR	EUTRO	PR x EUTRO
	DF	1	1	1
Predatory polychaetes (O)	<i>pseudo-F</i>	2.02	0.11	0.23
	<i>P</i>	0.19	0.88	0.75
<i>Petricola pholadiformis</i> (Pp)	<i>pseudo-F</i>	1.07	3.26	1.07
	<i>P</i>	0.32	0.06	0.33
Other Bivalves (B)	<i>pseudo-F</i>	0.13	3.54	0.42
	<i>P</i>	0.91	0.05	0.63

Table 4-7. Multivariate PERMANOVA results of the effect of province (PR) and eutrophication (EUTRO) on the abundance of adult and juvenile life stages of demersal fishes and decapod crustaceans sampled using quadrats. Protected univariate PERMANOVA on the abundance of individual species identified by SIMPER analysis as consistently contributing to difference between provinces or levels of eutrophication are shown below the dark line. Residual and total degrees of freedom (df) = 128 and 131, respectively. Significant effects ($p \leq 0.05$) are in bold and non-significant effects in italics represent the term in the model that explains the most variance after the residual.

	SOURCE	PR	EUTRO	PR X EUTRO
	DF	1	1	1
Adult	<i>pseudo-F</i>	2.24	2.09	3.02
	<i>p</i>	0.052	0.08	0.008
Juvenile	<i>pseudo-F</i>	8.42	6.87	4.09
	<i>p</i>	0.001	0.001	0.005
<hr/>				
Adult				
<i>Apeltes quadracus</i>	<i>pseudo-F</i>	0.203	0.203	0.203
	<i>p</i>	0.71	0.70	0.72
<i>Dyspanopeus sayi</i>	<i>pseudo-F</i>	6.13	6.13	6.13
	<i>p</i>	0.007	0.011	0.009
<i>Cancer irroratus</i>	<i>pseudo-F</i>	0.34	0.34	3.06
	<i>p</i>	0.60	0.63	0.14
Juvenile				
<i>Apeltes quadracus</i>	<i>pseudo-F</i>	6.59	6.59	2.34
	<i>p</i>	0.011	0.01	0.13
<i>Fundulus heteroclitus</i>	<i>pseudo-F</i>	9.20	5.37	5.37
	<i>p</i>	0.002	0.02	0.014

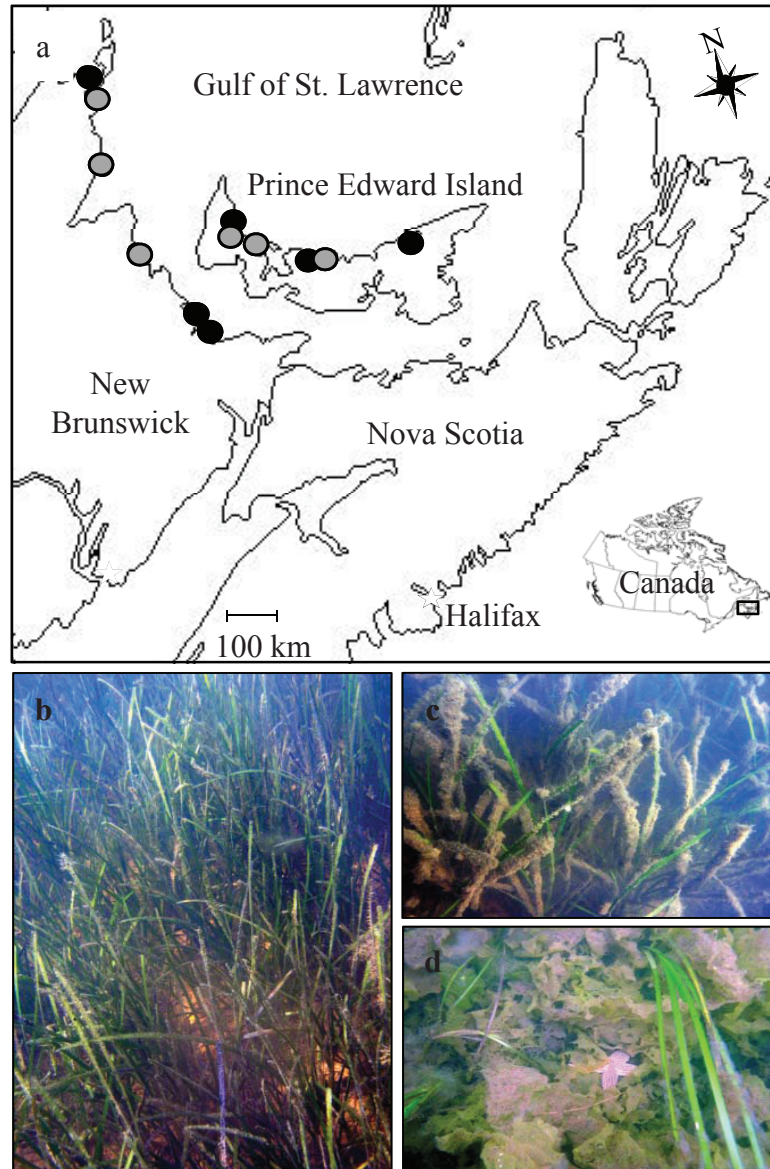


Figure 4-1. Map (a) and photos (b-d) of study sites with low (b; grey circle) and high (c-d; black circle) levels of eutrophication in the Provinces of New Brunswick (c) and Prince Edward Island (d) in Atlantic Canada. For more details on each site see Table 3-1). Fauna in the photos include: hydroids and small gastropods on eelgrass blades (b), a small gastropod among the epiphytic *Ulothrix speciosa* (c) and the seastar *Asterias vulgaris* on top of the thick mat of *Ulva lactuca* (d).

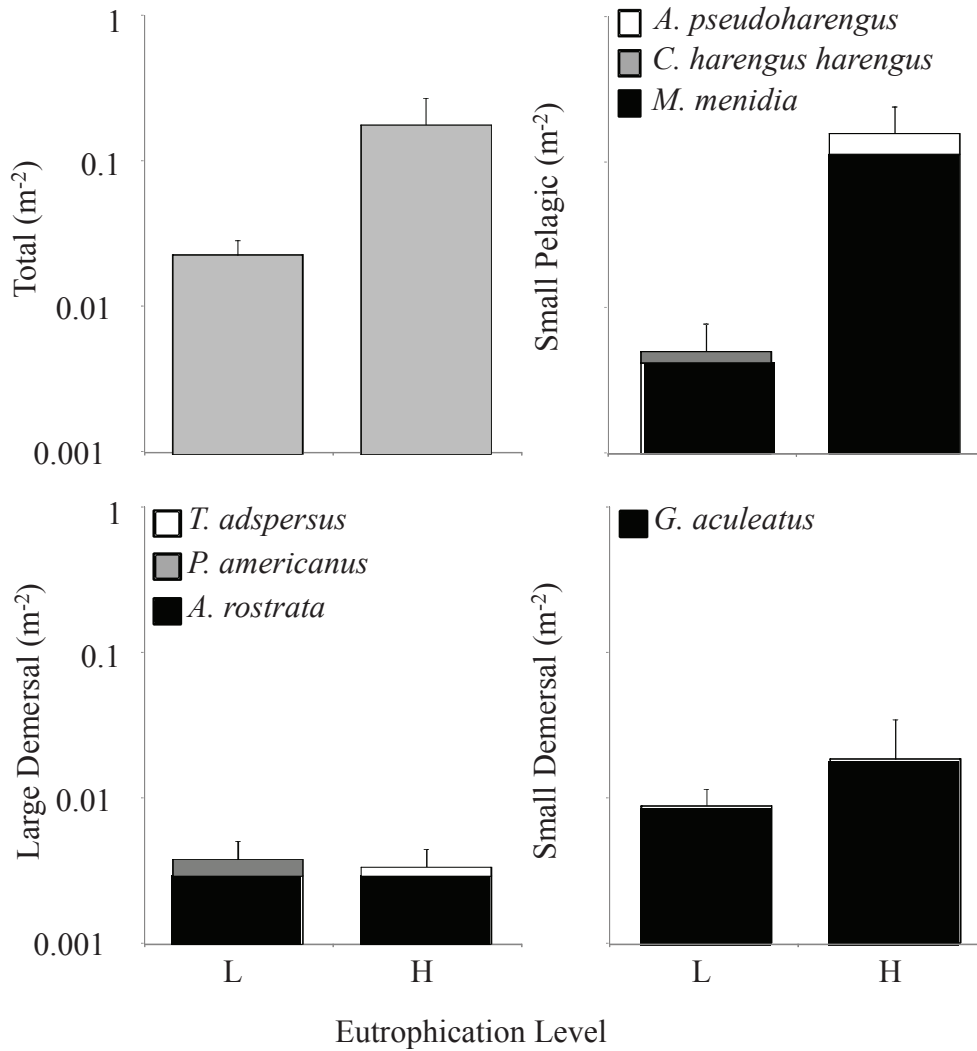


Figure 4-2. Abundance of mobile and pelagic fauna (m², mean +SE) at different levels of eutrophication (L = Low; H = High). Shown is the total abundance as well as small pelagics (*Menidia menidia*, *Clupea harengus harengus* and *Alosa pseudoharengus*), large demersals (*Anguilla rostrata*, *Pseudopleuronectes americanus* and *Tautogolabrus adspersus*) and small demersals (*Gasterosteus aculeatus*). The order of the species in the legends corresponds to the vertical order in the bars.

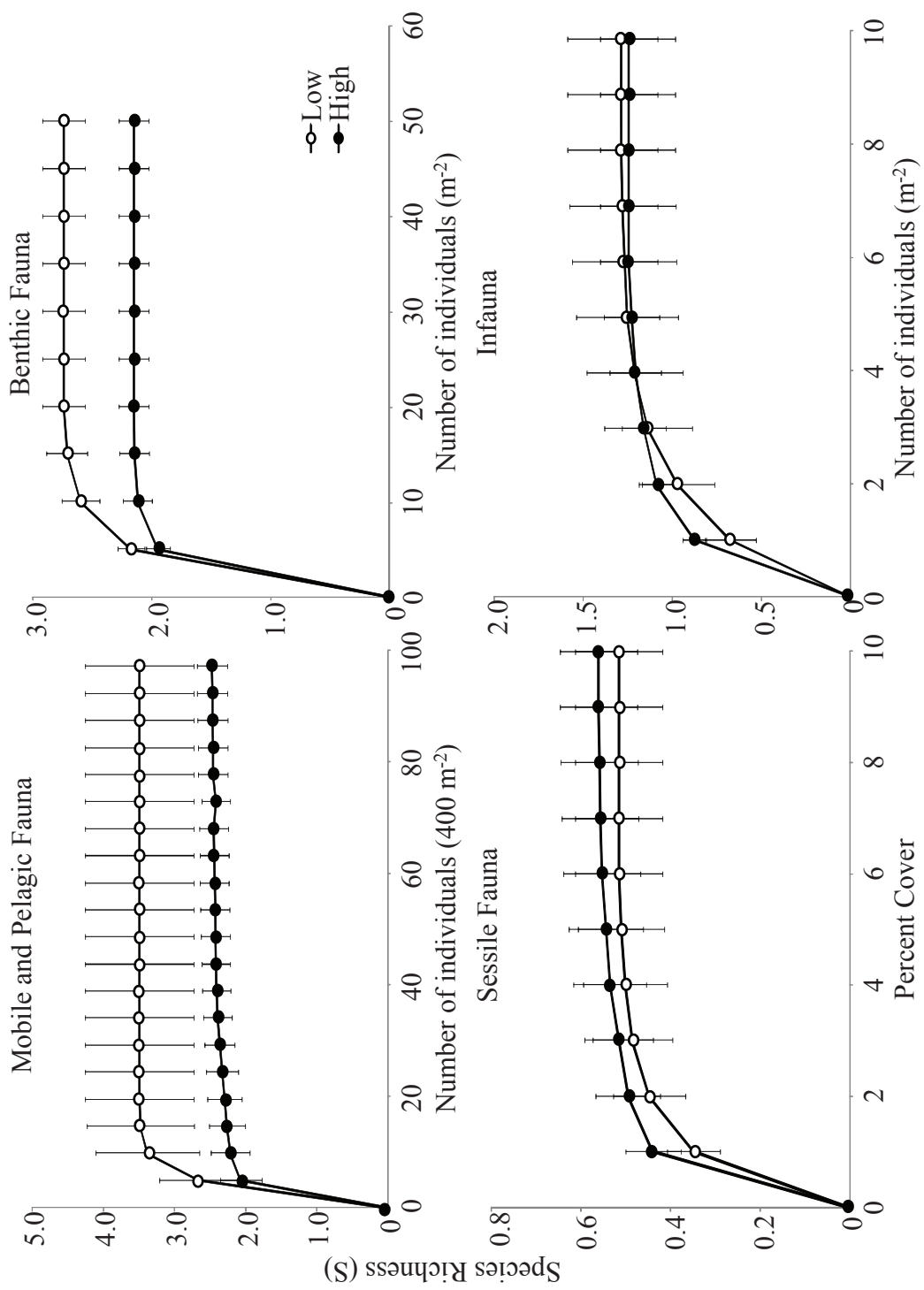


Figure 4-3. Rarefaction curve of mean (\pm SE) species richness with increasing number of individuals or percent cover sampled for mobile and pelagic, benthic and sessile fauna as well as infauna at low and high levels of eutrophication.

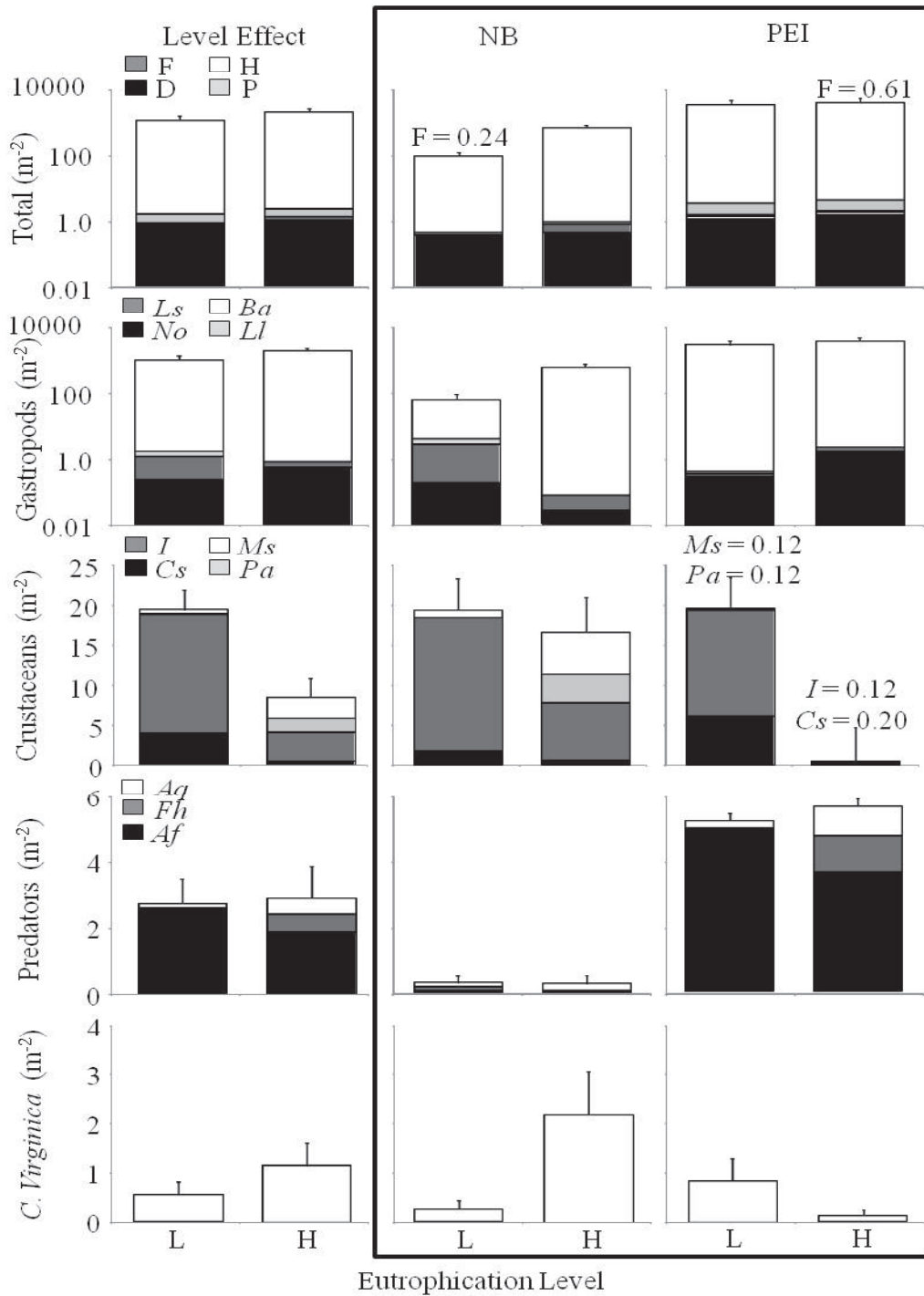


Figure 4-4. Abundance of benthic fauna (m^{-2} , mean +SE) broken down into functional groups (top row, F = Filter feeders, H = Herbivores, D = Detritivores, P = Predators) and those species identified by SIMPER analysis as consistently contributing to differences between levels of eutrophication (Level, L = Low; H = High) for New Brunswick (NB) and Prince Edward Island (PEI). Abbreviations for species names are shown in Table 4-4. Numbers above bars indicate the abundance of a functional group or species that is present but cannot be distinguished on the graph. The order of the species in the legends corresponds to the vertical order in the bars.

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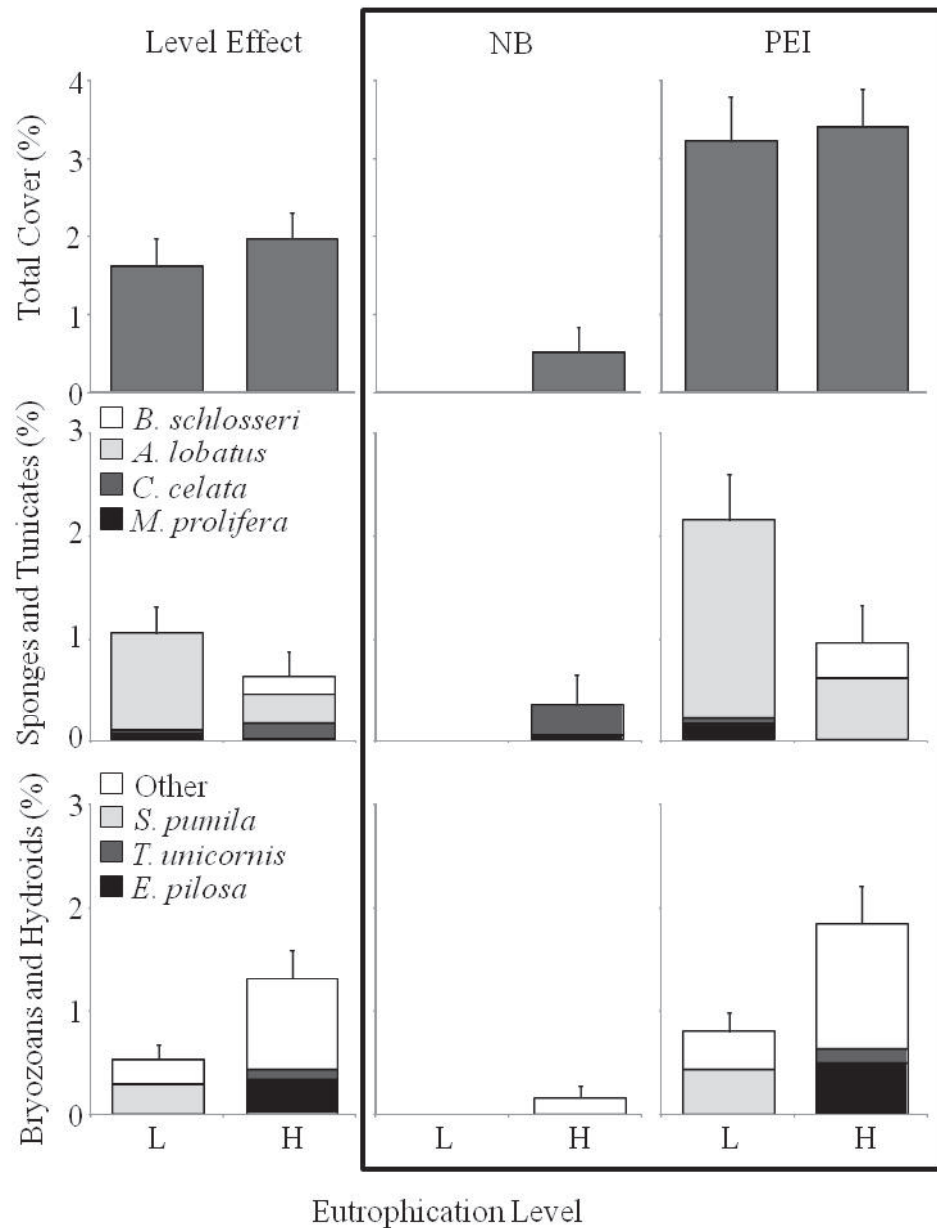


Figure 4-5. Abundance of sessile fauna (% cover, mean +SE) as total filter feeder cover (top row) and those species identified by SIMPER analysis as consistently contributing to differences between levels of eutrophication (L = Low; H = High) in New Brunswick (NB) and Prince Edward Island (PEI). Species names are in Table 4-5. The order of the species in the legends corresponds to the vertical order in the bars.

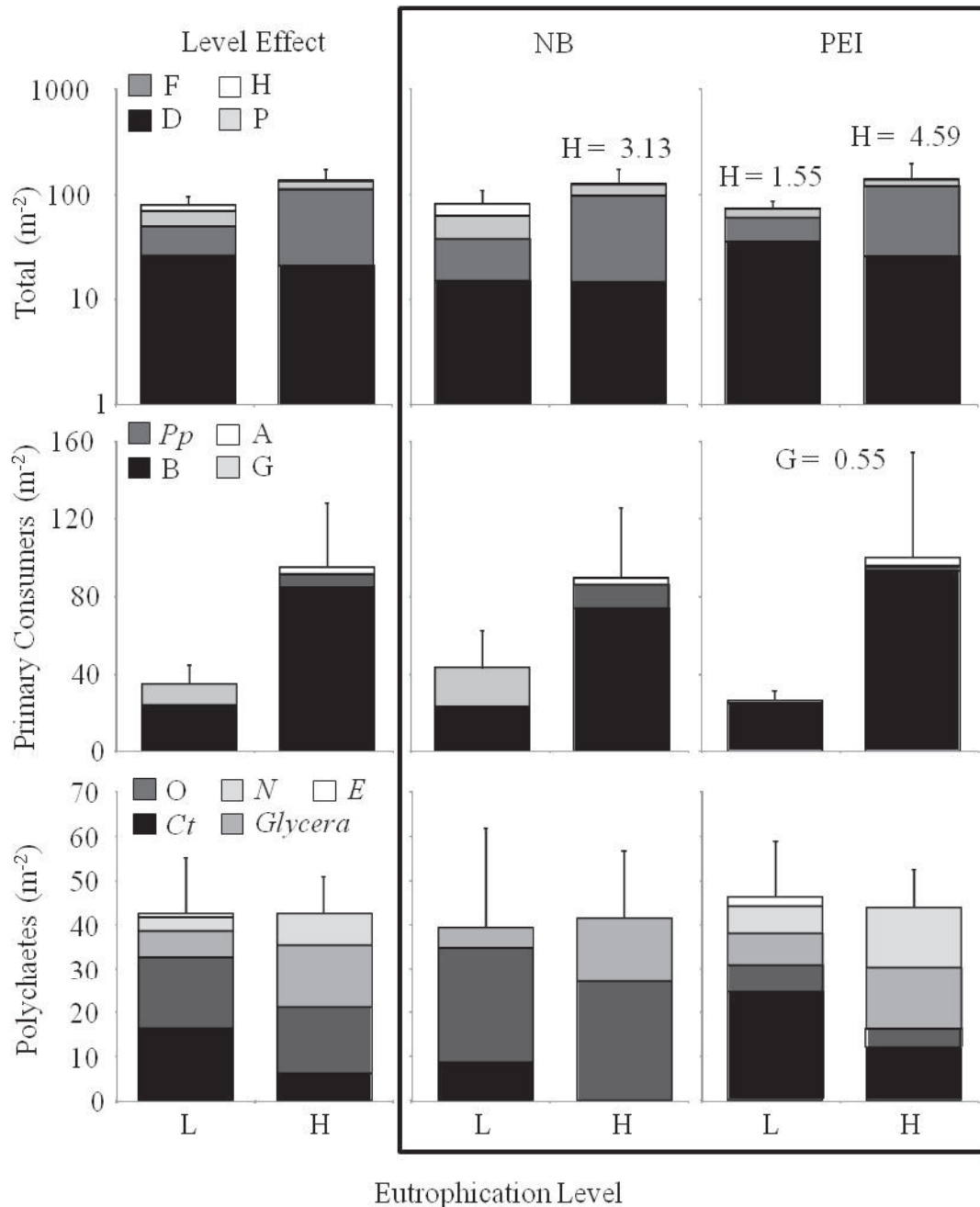


Figure 4-6. Abundance of infauna (m², mean +SE) broken down into functional groups (top panels) and those species identified by SIMPER analysis as consistently contributing to differences between levels of eutrophication (L = Low; H = High) in New Brunswick (NB and Prince Edward Island (PEI). Species names are in Table 4-6. Numbers above the bars indicate the numerical abundance values for a functional group or species that cannot be easily distinguished in the graph. The order of the species in the legends corresponds to the vertical order in the bars.

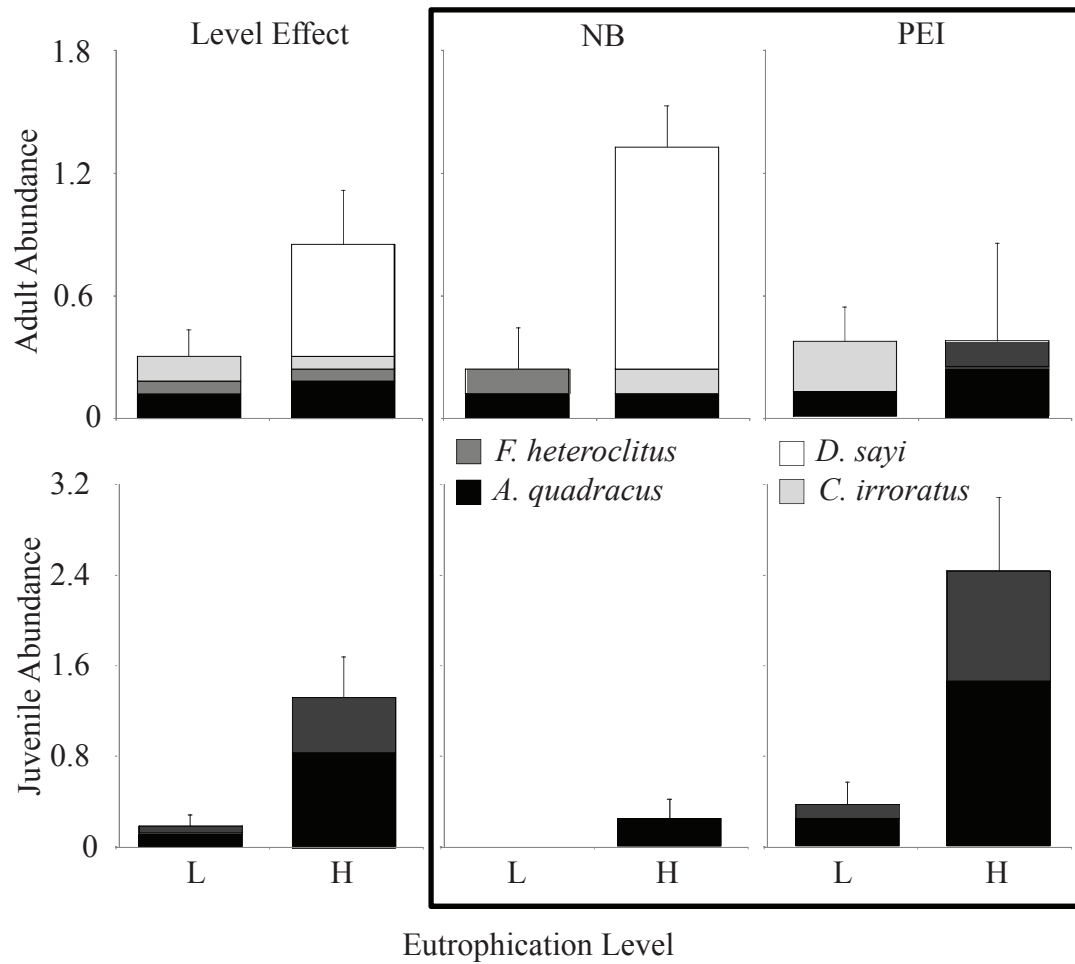


Figure 4-7. Adult and juvenile benthic fauna abundance (m⁻²) at low (L) and high (H) levels of eutrophication in New Brunswick (NB) and Prince Edward Island (PEI), Canada.

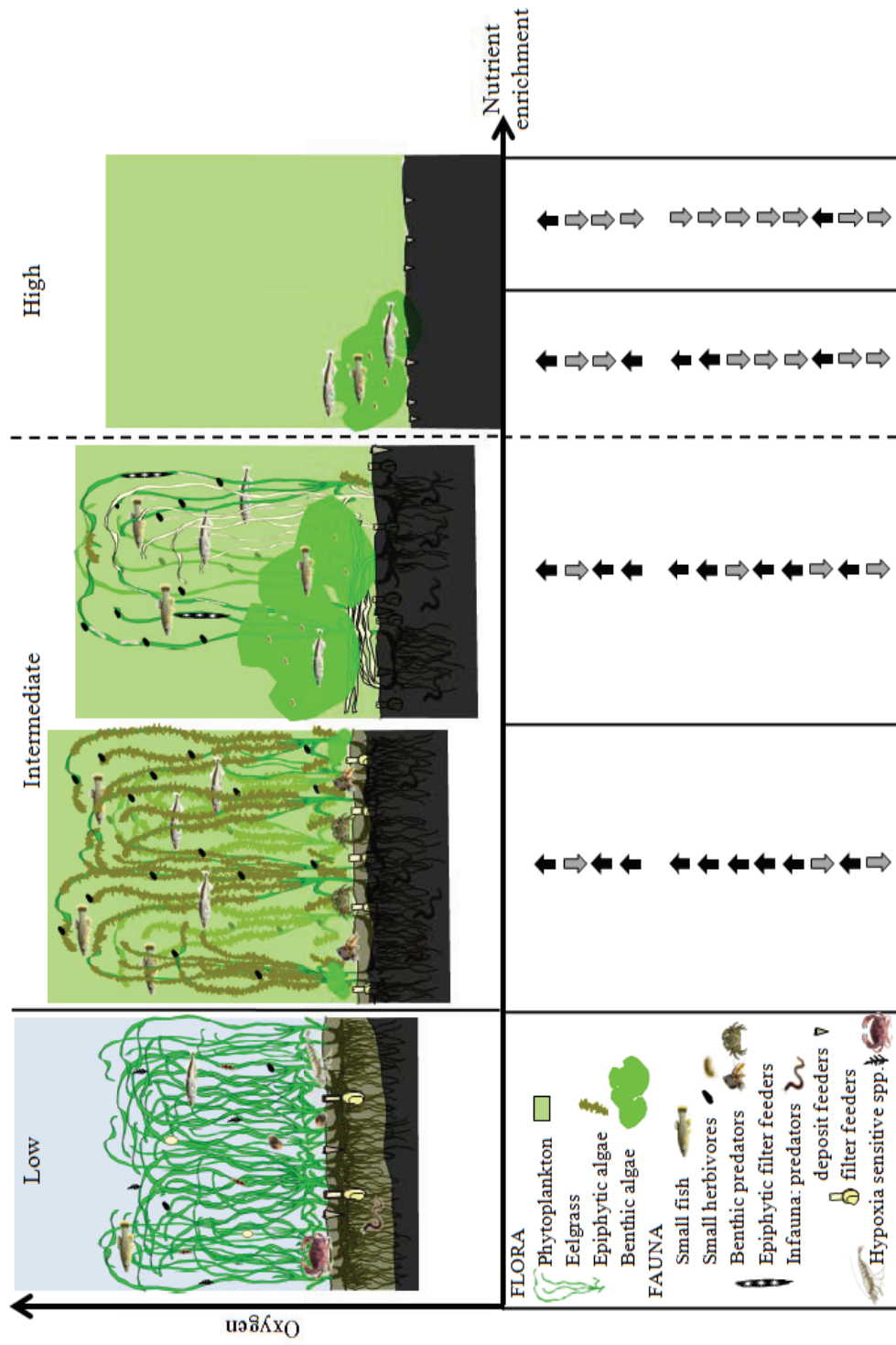


Figure 4-8. Diagrammatic representation of the changes in flora, fauna and sediment structure associated with a gradient of oxygen and nutrient enrichment in temperate seagrass beds. To the left of the dashed line generalizes our findings for the low and two intermediate enrichment conditions and to the right represents information on highly eutrophic conditions summarized from the literature cited throughout. All of the arrows show the changes relative to the low nutrient enrichment conditions.

CHAPTER 5

Ecosystem Services of Marine Macrophytes: their Relative Contribution to Primary Production, Carbon and Nitrogen Storage and Habitat Provision

5.1. Introduction

Fringing the ocean along the continental margins are estuarine and coastal ecosystems such as mangroves, seagrass meadows, salt marshes and macroalgal beds that have two things in common: they are dominated by highly productive vegetation adapted to endure harsh environments and are among the most impacted ecosystems in the world (Adam 2002; Alongi 2002; Duarte 2002; Steneck et al. 2002a; Lotze et al. 2006; Orth et al. 2006; Waycott et al. 2009). Some of the most critical, tangible and impacted services supported by these ecosystems include the support of viable fisheries, the provision of nursery habitats for a wide range of marine species and the filtration and detoxification of coastal waters (Worm et al. 2006). Increasingly, the importance of another service, carbon storage and sequestration within the vegetation and underlying sediments, also termed “blue carbon”, is becoming more apparent (Nellemann et al. 2009; McLeod et al. 2011). Understanding the relative contribution of the different marine vegetated ecosystems in providing essential habitat and other services is a key for the proper management and protection of the coastal ocean.

Current research into blue carbon sinks have focussed on vegetation dominating soft-sediments, such as mangroves, seagrasses and salt marshes, because they can sequester carbon over long time scales (millennial) within the underlying sediments through the burial of non-living biomass, in addition to the short-term sequestration in their living above- and belowground tissues (Duarte et al. 2005; Lo Iacono et al. 2008; Kennedy et al. 2010). However, there are vast tracts of rocky shorelines around the world that are dominated by canopy forming perennial seaweeds, such as kelp forests and furoid beds (Steneck et al. 2002a; Kerswell 2006), that contribute to short-term carbon sequestration (Reed and Brzezinski 2009; Schmidt et al. 2011). They also export on average 44% of their production (Duarte and Cebrián 1996) to adjacent habitats where it is either consumed or buried (Vetter and Dayton 1999; Krumhansl and Scheibling 2011; Kelly et al. 2012). Thus, not including macroalgae as a blue carbon sink underestimates the role of the coastal ocean in binding, storing and even sequestering carbon and other tissue bound nutrients. This review therefore estimates the role of macroalgae as a carbon sink and compares it to other marine and terrestrial ecosystems on a global scale.

There is abundant research on the habitat services provided by macrophyte ecosystems examining their role as breeding, nursery, sheltering and foraging grounds (e.g. Rangeley and Kramer 1998; Heck et al. 2003). However, comparisons between different ecosystem types have focussed on a specific faunal species such as Atlantic cod (*Gadus morhua*; Tupper and Boutilier 1995) and cunner (*Tautoglabrus adspersus*; Tupper and Boutilier 1997) or limited to a couple of habitats on a local scale (e.g. Guidetti 2000; Lazzari and Tupper 2002). So far, a global synthesis of the relative importance of all macrophyte ecosystems to a range of species groups has been missing.

Coastal habitats have been important to people throughout history for fishing, harvesting other resources and being sheltered from open waters (Jackson et al. 2001; Lotze and Milewski 2004). In turn, human activities have influenced coastal habitats and four of the most pressing issues include overfishing, habitat alteration, pollution and climate change (Jackson et al. 2001; Lotze et al. 2006; Worm et al. 2006; Halpern et al. 2008). Historical losses of mangroves, seagrasses and salt marshes in addition to their continued decline severely limits their ability to provide ecosystem services essential for human well-being (Lotze et al. 2006; Waycott et al. 2009; Barbier et al. 2010; Deegan et

al. 2012). Although there are no global estimates quantifying the decline in macroalgal beds, losses have been reported from Australia and Tasmania (Wernberg et al. 2011) and throughout Europe (Airoldi and Beck 2007). Predicted future changes in ocean temperature and acidity with increasing carbon dioxide emissions in addition to other pressures (e.g. disease, eutrophication, fishing) may put marginal populations and species at risk of further decline and potential extinction (Jackson et al. 2001; Lafferty et al. 2004; Millennium Ecosystem Assessment 2005; Wernberg et al. 2011).

Despite increasing understanding of the importance, historical losses and current threats to marine vegetated ecosystems, an assessment of their relative importance on a global scale is lacking. Such an assessment, however, would be valuable for management and conservation to set priorities and curb further losses, to identify research needs, and to increase public awareness on the value of these coastal ecosystems. Therefore, the objective of this review is to compare the relative contribution of different vegetated habitats found around the world in producing biomass, binding carbon and nitrogen and providing essential adult and juvenile habitat to a range of associated species. First, we will provide an overview of each macrophyte dominated ecosystem, including seagrass meadows, mangroves, salt marshes and macroalgal beds, evaluating their global distribution and extent. We will then compare the carbon and nitrogen binding services by reviewing estimates of global productivity, burial and standing stock biomass with its tissue carbon and nitrogen content. The global carbon stock estimates will then be compared to those of other terrestrial and marine biomes. We will also examine the habitat services of each ecosystem by comparing habitat characteristics and how they influence the species richness and abundance of adult and juvenile marine fishes and invertebrates. To complement our review, we will examine current and future threats to vegetated marine ecosystems, as well as their IUCN Red List of Threatened Species status.

5.2. Methods

For each component of Table 5-1 we used values from the most recent review papers containing data on the extent, production, export, burial, biomass and tissue carbon and nitrogen content. When the information was not found in the review paper, we worked

backwards through their references as well as supplemented with literature searches for material after the publication date of the review using Web of Science and Google scholar. Since very little information about carbon and nitrogen storage has been reviewed for macroalgae, we collated the data for each component of Table 5-1 from the published primary literature for at least 3 kelp and furoid species in the group and took the average. We then used the data from Table 5-1 to compare the global area and carbon stock of coastal vegetated ecosystems with those of major terrestrial and oceanic biomes as reported in the literature (Table 5-2).

To estimate the importance of each macrophyte ecosystem as habitat and nursery, we searched for field studies that contained species richness, total or juvenile abundance (mean density, total number, number per sample or catch per unit effort (CPUE)) for marine fishes, decapods and infauna inside the vegetation as well as in nearby unvegetated areas (Table B-1). However, we limited our examination of the effect of macrophytes on juvenile abundance to fishes because there was only one study for decapods that met our criteria and none for infauna. We excluded any studies with experimental manipulations unless they had both un-manipulated vegetated and unvegetated controls which we could use. In many cases, studies only reported the total abundance or richness over the entire study which included many sites or seasons or both. However, if they reported seasonal patterns, diurnal patterns or data across sites, we took the average over seasons, time of day or sites. Studies that compared collection methods were included by taking the average of the collection methods only if all methods were used in both vegetated and unvegetated areas. In addition, all studies needed to have concurrent sampling of the vegetated and adjacent unvegetated areas. We therefore excluded studies that collected data before and after the loss or recovery of a macrophyte ecosystem. After careful selection, a total of 75 studies were included, 66 and 73 studies reported the abundance or species richness, respectively, of at least one species group and only 18 studies reported the abundance of juvenile fishes.

The effect size of the presence of a macrophyte canopy was measured as the log ratio of the abundance or species richness inside and outside of the vegetation for each species group. We used the response ratio because it has clear biological meaning whereby a response ratio that is significantly greater than zero indicates an enhancement

effect of the macrophyte canopy whereas less than zero means that the canopy had a negative effect on the abundance or species richness. Response ratios can also summarize the effect without requiring a measure of variance (Adams et al. 1997) in addition to showing the least bias of several meta-analytical metrics and its sampling distribution is approximately normal (Hedges et al. 1999). Residual variation in meta-analysis is composed of both within and between study variation and the contribution of each to the residual can be estimated (Hedges et al. 1999). Similar to Shurin et al. (2002) and Edwards et al. (2010), many of our studies did not report measures of variance so we could not estimate the components of the residual variance nor could we use the standard error to weight our effect sizes. Eliminating these studies would have drastically reduced our sample size and possibly introduced bias into our data set (Englund et al. 1999). Using unweighted estimates of the response ratio increases the Type II error rate of parametric statistical tests (Gurevitch and Hedges 1999) so we used the sample size to construct weights as in Adams et al. (1997). We then used two-tailed t-tests to compare weighted and unweighted means of faunal abundance ($t_{28} = 0.003$, $p = 0.99$), juvenile fish abundance ($t_6 = 0.36$, $p = 0.73$) and faunal richness ($t_{28} = -0.63$, $p = 0.54$) separately. We found no significant differences and therefore use the unweighted data for our analyses. We used t-tests to examine significant differences in the response of the abundance or richness of the different species groups from zero. We did not statistically compare the enhancement effect of different macrophytes because of the small sample sizes ($n < 10$) in some of the ecosystems.

Finally, to examine the global and annual losses of coastal macrophyte ecosystems and the loss drivers, we used values reported in Boström et al. (2011), modified their Table 1 to include macroalgae and supplemented with the most recent information with the same temporal baseline from the primary literature where needed.

5.3. Marine Vegetated Habitats

5.3.1. Seagrasses

Seagrasses are a mixed group of angiosperms that are restricted to growing in shallow marine and estuarine environments where they typically form extensive beds or meadows (Fig. 5-1a,b; Duarte 2002; Green and Short 2003). Currently, there are 72 distinct species found around the world (Short et al. 2011) that are distributed within six bioregions except the Southern Ocean (Short et al. 2007). The Temperate North Atlantic bioregion has the lowest diversity with only five seagrass species and beds are typically monospecific, whereas the Tropical Indo-Pacific has the highest diversity with 24 species and as many as 14 species growing together in one bed (Short et al. 2007). All seagrass species are clonal plants with an extensive system of roots and rhizomes in addition to shoots and leaves (Kuo and Hartog 2006) that form complex three dimensional habitats mainly in soft sediments with a few species on rocky substrates (Green and Short 2003).

Estimates of the global extent of seagrasses range from 177,000 to 600,000 km² because of major gaps in information for regions such as South America, Africa, Indonesia and the Pacific archipelagos (Spalding et al. 2003; Duarte et al. 2005) in addition to the continuing loss of seagrass area (Orth et al. 2006; Waycott et al. 2009). Interestingly, when evaluating the global net loss of seagrass extent, the lower estimate of the total seagrass area was used (Waycott et al. 2009) whereas when estimating their role in the oceanic carbon cycle estimates of 300,000 to 600,000 km² were used (Duarte et al. 2005; Duarte et al. 2010; Fourqurean et al. 2012). Spalding et al. (2003) argue that the upper estimate of 600,000 km² is an overestimate because it is derived from productivity from an unspecified source and that a simple model based on the depth range of seagrasses and turbidity of coastal waters estimates a maximum area of 500,000 km². Due to the size of the areas with little to no information on seagrass extent and the likelihood for the existence of extensive beds in those areas (Spalding et al. 2003), we will use and report values for the intermediate estimate of 300,000 km² as reported in Duarte et al. (2005) (Table 5-1).

5.3.2. *Mangroves*

Mangrove trees and shrubs are the only woody halophytes that have forged an intertidal living along tropical and subtropical coastlines worldwide (Alongi 2002). Mangroves colonize low energy sedimentary habitats that enable them to establish their complex and unique aerial root system (Fig. 5-1c). Along with other morphological and physiological adaptations, the root system allows them to inhabit extreme conditions of high temperatures and salinity, strong winds and anaerobic soils (Kathiresan and Bingham 2001; Hogarth 2007). Mangrove forests are highly productive but typically less complex and speciose compared to rainforests because they often lack understory; however, the submerged roots, trunks and branches create a complex three-dimensional marine habitat that is rich with associated flora and fauna (Kathiresan and Bingham 2001; Alongi 2002).

There are 70 species of mangroves worldwide (Polidoro et al. 2010). However, about 30 species dominate global mangrove communities and of these, 25 belong to only two families, the Avicenniaceae and Rhizophoraceae (Hogarth 2007). Mangroves are limited in their distribution by the winter 20° isotherm, with species richness decreasing as this threshold is approached (Hogarth 2007). The most diverse biogeographical regions are in the Indo-Pacific (Alongi 2002). Mangrove area has been estimated since the early 1980s ranging from 124,291 to 198,818 km² (Wilkie and Fortuna 2003). The most current estimate covers 137,760 km² with 42% found in Asia and 75% in only 15 countries (Giri et al. 2011). Although this is the most current estimate, it represents the extent at the turn of the century and mangroves are being lost at a rate of 2.1% per year (Valiela et al. 2001; Nellemann et al. 2009) which if held constant would mean a decrease in area of 30,974 km² over 12 years for a total area of 106,786 km² in 2012. Despite this discrepancy, the most commonly used value in recent literature as the global extent of mangroves is 160,000 km² (Bouillon et al. 2008; Bouillon et al. 2009) which is also what we will use (Table 5-1).

5.3.3. *Salt Marshes*

Salt marshes are intertidal habitats that are characterized by an assemblage of herbaceous vascular plants (Fig. 5-1d) whose upper limit of occurrence is that of the highest

astronomical tide and the lower limit is mean high water neap tide level (Adam 2002). Many marshes are estuarine but they can also be found fringing any soft-sediment coast exposed to the full range of tidal regimes from micro- to macrotidal as well as seasonal water level fluctuations but do require relatively low wave energy (Hodgkin and Hamilton 1998; Allen 2000; Adam 2002). Colloquially, mangroves are viewed as the tropical equivalent of salt marshes which are predominantly found along temperate coastlines (Greenberg et al. 2006; Chmura 2011). However, there can be extensive salt marshes found adjacent to mangroves and therefore have a global distribution with the exception of Antarctica (Adam 2002). Contrary to the latitudinal patterns exhibited by most biomes, plant species richness is lowest near the equator and increases with latitude, peaking at high temperate latitudes (Adam 1990; Greenberg et al. 2006).

As of 2011, there was no global inventory on the extent of salt marshes (McLeod et al. 2011) despite being easily delineated on remotely-sensed images (Adam 2002). Estimates of 22,000 – 45,000 km² can be found in the literature but exclude large areas such as the Arctic or are limited to Canada, United States of America, Europe and South Africa (Chmura et al. 2003; Greenberg et al. 2006). Duarte et al. (2005) used a salt marsh area estimate of 400,000 km² from 1973 to examine the role of marine vegetation in the carbon cycle. The original estimate of 380,000 km² from Woodwell et al. (1973) included both marshes and mangroves. However, when we compare Figure 1 from Woodwell et al. (1973) to Figure 16b from Nellemann et al. (2009) many of the areas where marshes are known to occur were not included and other areas with unknown salt marsh extent (e.g. Northern and Eastern Russia) were included in the 1973 estimate because of their crude method. The most recent estimate by Duarte et al. (2008) puts the global extent of salt marshes at 1,400,000 km²; however, there is no mention of how this was estimated or if it represents current extent or maximum historical coverage. The latter is unlikely since the areal extent of other vegetated habitats in Duarte et al. (2008) fall within the range of values reported in the Seagrasses and Mangroves sections above. Given that salt marshes are globally distributed, we therefore use 380,000 km² from Woodwell et al. (1973) (Table 5-1).

5.3.4. *Macroalgal Beds*

Globally, there are 1500 species of marine green algae and 6200 red and 1800 brown algae, most of which are marine (Guiry 2012). By far the most conspicuous are the canopy forming brown algae such as rockweeds (Fucales, Fig. 5-1f) and kelps (Laminariales, Fig. 5-1e) that form intertidal and subtidal macroalgal beds or forests along rocky temperate coasts worldwide (Raffaelli and Hawkins 1996; Steneck et al. 2002a; Huovinen and Gómez 2012). Macroalgae are also present in tropical marine systems but when occurring in a healthy coral reef system they are not the main habitat providers and therefore have a fundamentally different role from the extensive beds found in temperate regions (Mejia et al. 2012). However, this is changing as reef ecosystems are degraded by pollution, disease outbreaks, bleaching events and overfishing which in many cases leads to the dominance of macroalgae (Bellwood et al. 2004). In addition, the recently discovered deep water kelp beds in the tropics have similar roles in providing habitat and nursery services (Graham et al. 2007a) but these services have yet to be quantified. Therefore, deep water tropical kelp beds are only included in Tables 5-1 and 5-2.

Fucoid species dominate intertidal zones in both hemispheres as well as the shallow subtidal down to 25 m in the southern hemisphere (Schiel and Foster 1986; Raffaelli and Hawkins 1996). Kelps have a low photosynthesis to biomass ratio which constrains them to well illuminated zones which in temperate areas is <45 m with beds forming in waters <30 m (Schiel and Foster 1986; Vadas and Steneck 1988). However, in clear tropical waters extensive deep water beds can be found between 30-200 m where cooler water and upwelling can support kelp growth (Graham et al. 2007a). Fucoids and laminarians have diverse morphologies from branched floating (e.g. *Ascophyllum nodosum*, *Macrocystis pyrifera*) to strap like stipated (e.g. *Durvillaea antarctica*, *Saccharina latisima*) canopies ranging from 10 cm to 45 m in height creating complex three-dimensional habitats that support diverse communities of associated flora and fauna (Abbott and Hollenberg 1976; Steneck et al. 2002a; Schmidt et al. 2011).

The global extent of kelps estimated by De Vooy (1979) from a coastal landforms map and coastal lengths of countries assumes that 30,000 km of coastline have significant kelp beds. To estimate the global area of kelp coverage we assumed an average

bed width of 40 m (Mann 1972b; Choat and Schiel 1982) therefore the area covered would equal 1,200,000 km². In addition, we would need to account for the deep tropical beds that are estimated to cover ~ 23,500 km² (Graham et al. 2007a) for a total kelp coverage of 1,223,500 km² (Table 5-1). No coastal length data was available for rockweeds but fucoids have the same geographical distribution as kelps so, they too would cover 30,000 km of coastline (De Vooy 1979). We assumed an average bed width of 15 m (Mann 1972b; Choat and Schiel 1982) for a total rockweed extent of 450,000 km². This however, would not take into account the extensive beds in the Baltic Sea where there are few kelps (Wallentinus 1991). These crude estimates are greater than that of seagrass extent which seems reasonable since although laminarian and fucoid species are limited in their distribution by temperature, laminarians occur at deeper depths than seagrasses in both temperate and tropical waters (den Hartog 1970; Vadas and Steneck 1988; Graham et al. 2007a) and both can occur along rocky shorelines adjacent to subtidal seagrasses (Wernberg et al. 2006). The only other estimate in the literature is 3.5 times higher than our estimate because it represents the total area of world ocean available to benthic algae based on the depth of the photic zone (Charpy-Roubaud and Sournia 1990) but it does not take into consideration bottom type or taxon.

5.4. Carbon and Nitrogen Storage Services

In order to estimate carbon and nitrogen storage services of a habitat, we need to consider the amount of primary production, local burial and export as well as the burial of exported material and the remaining standing stock. Estimates of productivity of coastal macrophyte systems has a long history with some of the earliest work in the early 1900s (e.g. Harper 1918) and expanded to all coastal habitats in the 1960s-70s (e.g. Golley et al. 1962; Mann 1972a; Penhale 1977). It continues to this day refining methods as well as expanding our knowledge of other important compartments, like below ground production (Mateo et al. 2006; Komiyama et al. 2008). The most productive coastal habitats are macroalgal beds with 14% more production than mangroves and double that of seagrasses and salt marshes (Table 5-1) because of their rapid turnover (Smith 1981) and high detritus production (Krumhansl 2012) relative to the other macrophytes.

In contrast, mangroves have the highest burial rate (Table 5-1) because of their high sediment accumulation rates (Kathiresan and Bingham 2001; Sanders et al. 2010). The most recent works that examine the importance of coastal macrophyte communities as carbon sinks focus on the productivity of seagrasses, salt marshes and mangroves and the fraction of their local production that is buried in underlying sediments (Table 5-1). They do not include macroalgae because they grow on rocky substrates and therefore do not bury carbon locally (Table 5-1; Duarte et al. 2005; Nellemann et al. 2009; McLeod et al. 2011). However, macroalgal systems do export the most primary production (Table 5-1) as detritus produced via erosion (Krumhansl 2012), breakage (Viejo and Åberg 2003; Filbee-Dexter and Scheibling 2012) or dislodgment (Wernberg et al. 2006; Graham et al. 2007b). Like other marine macrophytes, some of the detritus ends up as beach wrack (Williams and Feagin 2010; Dugan et al. 2011) or as drift in other low energy coastal habitats (Wernberg et al. 2006; Krumhansl and Scheibling 2011) and deep waters (Harrold et al. 1998; Dierssen et al. 2009; Filbee-Dexter and Scheibling 2012) 10s of meters to 1000s of kilometers away (Edgar 1987; Ólafsson et al. 2001; Thiel and Gutow 2005; Biber 2007). Much of the macrophyte detritus acts as a subsidy in the receiving habitats (Harrold et al. 1998; Rossi and Underwood 2002; Heck et al. 2008; Williams and Feagin 2010; Kelly et al. 2012) but no work has been done on the potential for carbon and nitrogen storage via the burial of the exported detrital material in these low energy habitats. Typically, less than 10% of the terrigenous and phytoplankton based organic matter reaching the ocean floor is ultimately preserved in marine sediments (Hedges and Keil 1995). If we apply this same percentage to the material exported by marine macrophyte ecosystems, macroalgal systems bury more exported material than any other macrophyte system but reach only one third of the total burial of other macrophyte ecosystems (Table 5-1). Regardless, this amounts to a burial rate of $39,500 \text{ kg C km}^{-2} \text{ yr}^{-1}$ and $3,961 \text{ kg N km}^{-2} \text{ yr}^{-1}$. Although these estimates are crude, it does show that macroalgae are not inconsequential and do play a role in carbon and nitrogen storage and potentially even sequestration.

Interestingly, work on terrestrial carbon budgets take the standing stock of plant biomass into consideration (Trumper et al. 2009), whereas this is neglected for macrophytes in coastal habitats (e.g. Nellemann et al. 2009; McLeod et al. 2011), likely because

they are viewed as ephemeral, with the exception of mangroves, relative to many terrestrial habitats. We would like to challenge this idea and propose that the global standing stocks of marine vegetated habitats are at least as important a reservoir of carbon and nutrients as their terrestrial counterparts. Considering that coastal vegetated habitats occupy 0.7% of the total ocean area, together they account for 12% of oceanic carbon stock and store more carbon (6.9 PgC) than all other ecosystems except phytoplankton, savanna and tropical forest (Table 5-2) making these marine ecosystems important players in the global carbon and nitrogen cycles.

Salt marshes had the highest tissue carbon content followed by mangroves (Table 5-1), yet salt marshes had a lower carbon standing stock per unit area than mangroves because of their smaller biomass. Seagrasses stored the least amount of carbon and nitrogen even with moderate tissue content because of their low standing biomass (Table 5-1). The global macroalgal carbon stock stores 40-98% more carbon than any other marine habitat, except phytoplankton, and 52-64% more than grasslands, temperate coniferous forests and tundra despite being only one third to one sixth of the area of these terrestrial habitats (Table 5-2). Macroalgae also had the highest average tissue nitrogen content and nitrogen standing stock (Table 5-1). Interestingly, mangroves had the lowest tissue nitrogen content but the second highest nitrogen standing stock because of their immense biomass (Table 5-1). Since major plant nutrients are assimilated along with carbon (Pedersen et al. 2004) patterns in global nitrogen stocks will likely be similar to carbon. The substantial carbon production and nutrient uptake by marine macrophytes provides a significant carbon and nutrient sink through the accumulation of biomass and detritus (Smith 1981; Pedersen et al. 2004).

Like many terrestrial forests mangroves can live up to 80-90 years (Jimenez et al. 1985; Fromard et al. 1998; Luysaert et al. 2007) which is not surprising since it is a coastal forest. What is surprising is that some beds of the seagrass *Posidonia oceanica* have been dated to 3385 years before present (BP), others estimated at 6000-7000 years BP (Mateo et al. 1997) and individual clones of *Zostera marina* in the Baltic Sea up to 4000 years BP (Reusch et al. 1999). Similarly, salt marshes can take decades to centuries to form and mature marshes can be stable for centuries (Alongi 2002). The majority of large canopy forming macroalgae are perennial, some kelp species can live up to 25 years

(Steneck and Dethier 1994) and some rockweeds have been estimated to live longer than 120 years (Åberg 1992). The longevity of these coastal habitats, except kelps, rivals or exceeds the stand age (45-121 years) of many existing forest biomes around the world (Luyssaert et al. 2007). Although the longevity of individual macroalgal species may be low, a macroalgal bed may persist in an area for centuries (Tegner and Dayton 2000; Steneck et al. 2004). It is the persistence of the biomass in each of these coastal habitats over centuries to millennia that make them important for coastal carbon and nitrogen storage and justifies their inclusion in the global carbon budget.

5.5. Habitat and Nursery Services

Seagrass meadows, mangroves, salt marshes and macroalgal beds create very distinct three-dimensional habitats that provide unique opportunities for settlement, refuge, and foraging for a wide range of species (Heck et al. 2003; Minello et al. 2003; Hogarth 2007; Schmidt et al. 2011). Across the reviewed studies, the presence of macrophytes had a positive effect on associated fauna compared to unvegetated habitats, since the average response ratio for both abundance and richness was above zero for all ecosystems and species groups (Fig. 5-2). However, only seagrasses, mangroves and salt marshes significantly enhanced the abundance or species richness of the total faunal assemblage (Fig. 5-2). The enhancement effect of a macrophyte canopy was significant for all species groups with the highest enhancement for decapod abundance and both decapod and fish species richness (Fig. 5-2). The range of morphologies within a macrophyte type also influences the distribution of mobile fauna since the choice of location within and between habitat types is influenced by the abundance and distribution of prey and predation refuge (Edgar 1990; Denno et al. 2005). This is likely one factor contributing to the large within habitat variability in the response of species richness and abundance in all habitats except seagrass when pooled across species groups (Fig. 5-2) as well as when broken down into individual species groups (Fig. 5-3). The small sample size (≤ 10) of many of the data points is also likely playing a role in the large confidence intervals, and prevented us from statistically analyzing the effect of macrophyte type on individual species groups. We will therefore focus on the patterns observed in average response ratios.

Seagrasses had the highest enhancement effect on total abundance with 1.7 times greater enhancement than mangroves and salt marshes and 6 times greater than macroalgae (Fig. 5-2). The presence of seagrasses also doubled species richness relative to mangroves and enhanced richness by 1.6 and 5 times relative to macroalgae and salt marshes, respectively (Fig. 5-2). For individual species groups, seagrasses always had the highest enhancement effect on abundance and species richness except for decapod abundance which was highest in salt marshes (Fig. 5-3). Seagrasses increased the richness of decapods, fishes and infauna by 1.6, 7 and 3.6 times, respectively (Fig. 5-3). A good example of the greater effect on fishes can be seen in Guatemala where decapod species richness increased from three species in unvegetated areas to 14 species inside *Thalassia testudinum* beds whereas fish species richness increased from one to 16 species inside the seagrass beds (Appendix 1; Arrivillaga and Baltz 1999). In Australia, the number of infauna species doubled (74 to 160) with the presence of a canopy of *Nanozostera muelleri capricorni* (Appendix 1; Barnes and Barnes 2012).

Although mangroves had the highest average enhancement effect on juvenile fishes, the large variability precluded any significant results (Fig. 5-3). Seagrasses, on the other hand, significantly enhanced the abundance of juvenile fishes, such as Atlantic cod (*Gadus morhua*; Lazzari and Stone 2006) and the large-mouth goby (*Redigobius macrostoma*; Gray et al. 1998) by 2.5 and 3 times more than salt marshes and macroalgae, respectively. Like all marine macrophytes, seagrasses are ecosystem engineers in that they modify the physical environment via their physical structure thereby modulating resource availability and maintaining a habitat (Jones et al. 1994). The increased aboveground complexity provided by the seagrass blades increases sedimentation of organic matter (Hasegawa et al. 2008; Herkül and Kotta 2009) and the highly complex structure of roots, rhizomes and associated rhizosphere increases sediment oxygenation (Penhale and Wetzel 1983; Herkül and Kotta 2009) thereby increasing the food and oxygen availability to infaunal communities. In addition, the higher habitat complexity has been shown to decrease predator foraging efficiency (Edgar 1990; Heck and Orth 2006) and prevent resuspension and transport of infauna (Orth 1977) thereby decreasing the risk of predation on juvenile fishes while increasing infaunal food availability to those same juveniles. Interestingly, seagrasses also had the highest enhancement effect on fish abun-

dance (Fig. 5-3). However, the dominant species inside the seagrass beds in more 70% of the studies were either small (<20 cm max length) like the small-mouth hardyhead (*Atherinosoma microstoma*; Connolly 1994), Port Jackson perchlet (*Ambassis jacksoniensis*; Gray et al. 1996) and three-spine stickleback (*Gasterosteus aculeatus*; Joseph et al. 2006), or highly specialized (e.g. pipefishes; Edgar and Shaw 1995a; Franco et al. 2006; Schmidt et al. 2011) and likely taking advantage of the same resources and cover as the juveniles.

Despite the small sample size, mangroves showed the second highest enhancement effect on the infauna abundance and richness (Fig. 5-3), likely due to the high sediment organic content and sedimentation rates (Kathiresan and Bingham 2001; Nagelkerken et al. 2008). Mangroves are highly complex and host a range of habitats from the aerial roots, trunks, pneumatophores, creeks and even permanent water holes across a range of physico-chemical environments (Hindell and Jenkins 2004; Hogarth 2007). Mangroves also significantly enhanced fish species richness and abundance while the effect on decapods was variable (Fig. 5-3). In one study, there was even a negative effect of the mangrove habitat on decapods (Appendix 1; Bloomfield and Gillanders 2005). This is likely an artifact of the sampling methods. The majority of decapod species do not migrate with the tides but rather remain in burrows at high tide to avoid predation and emerge at low tide to forage (Hogarth 2007) and are therefore not being captured by the high-tide seining or passive trapping techniques (Rozas and Minello 1997).

Salt marshes enhanced decapods abundance by 1.3-14 times more than any of the other macrophyte ecosystems (Fig. 5-3). Salt marshes exhibit sharp zonation of plant species from low to high marsh, offering a range of habitat complexity and high productivity (Barbier et al. 2010) which likely contributed to high abundances of primary consumers, such as gastropods (Shervette and Gelwick 2008). In addition, salt marshes also accumulate large amounts of detritus that would increase food availability to detritivorous crabs and shrimps, like the mud shore crab *Helograpsus haswellianus* (Bloomfield and Gillanders 2005) and brown shrimp *Farfantepenaeus aztecus* (Minello 1999). The high productivity and increased number of small prey items would also attract omnivorous decapods like the blue crab *Callinectes sapidus* which is reflected in their higher abun-

dances in salt marshes relative to unvegetated areas (Minello 1999; Shervette and Gelwick 2008).

Overall, macroalgae had the lowest total abundance enhancement (Fig. 5-2) because of the opposing effects of the decapods and fishes (Fig. 5-3), but also a very low numbers of studies. The canopy of highly branched macroalgae can be very dense which limits maneuverability and predation efficiency effectively deterring and maybe even excluding large individuals from entering the canopy (Denno et al. 2005). In kelp beds, wave surge produces a sweeping motion of strap-like blades that scours the bottom excluding many sessile organisms (Connell 2003) and deterring predators (Velimirov and Griffiths 1979). In addition, the closest equivalent to infauna on the rocky shore is holdfast fauna which were not included in our estimates of the enhancement of richness and abundance because of the literature bias towards the highly complex kelp holdfasts. This omission led us to underestimate the total enhancement effect of macroalgae relative to unvegetated rocky substrates. For example, a kelp holdfast can host on average 600 individuals (Tuya et al. 2011) and more than 8 species or faunal groups (Schmidt and Scheibling 2006; Włodarska-Kowalczyk et al. 2009; Tuya et al. 2011).

One notable omission in this review was the sessile benthic and epiphytic fauna as well as non-canopy forming algae and mobile invertebrates that were not decapods. The main reason for omitting these groups was because of the limited number of studies examining the richness and abundance of these groups as a whole in each of the habitats. However, mangroves are known to host a diverse sessile epiphyte community on their areal roots, trunks and pneumatophores (Kathiresan and Bingham 2001) as do seagrasses (Borowitzka et al. 2006) and macroalgae (Schmidt and Scheibling 2006; Schmidt et al. 2011) leading us to underestimate the habitat service of these ecosystems. Since only mangroves and salt marshes have an aerial component, we opted to omit the terrestrial inhabitants in the estimates of richness and abundance enhancement. However, the terrestrial inhabitants of mangroves and salt marshes (e.g. insects, frogs, birds) as well as seabirds, shorebirds and opportunistic mammals (e.g. mink, deer) in seagrasses and macroalgae are known to play an essential role in the transfer of marine production to terrestrial biomes (Heck et al. 2008).

In addition, the dispersal and migration of species between coastal ecosystems connects them on both a local (10-100s m) and broad scale (10-100s of km; Polis et al. 1997). For example, many highly mobile and migratory fish species (e.g. pollock *Pollachius pollachius*, herring *Clupea harengus*) use a variety of coastal habitats during their movements thereby influencing the local food web as predators or prey and in so doing transport production in the form of nutrients across ecosystem boundaries (Polis et al. 1997). Salt marshes, mangroves and some macroalgal beds are intertidal and therefore adjacent subtidal seagrasses and macroalgae likely host adults and juveniles of migrant species at low tide. Some species also have habitat specific ontogenic shifts that transition through all lifestages only when the required habitats are in close proximity to each other (Nagelkerken et al. 2001; Pittman and McAlpine 2003). It is only then that they are able to provide sufficient food resources and predator refugia for this life history transition (Nagelkerken et al. 2001; Pittman and McAlpine 2003) further emphasizing the importance of maintaining habitat diversity on local and regional scales.

5.6. Threats to Ecosystem Services

Coastal marine vegetated habitats exist in a narrow band around the continents and, for their limited size, play a disproportionate role in climate regulation and nutrient cycling (Table 5-1, 5-2). In addition, they provide essential habitat and nursery services to a range of fauna (Fig. 5-2, 5-3) as well as a number of other services such as flood protection, raw materials, recreation and food production to name a few (Steneck et al. 2002a; Boström et al. 2011). However, it is this narrow existence that makes them the most vulnerable habitats to the anthropogenic impacts of the 3.1 billion people living within 150 km of the coast and the eight largest coastal megacities (>8 million inhabitants; Halpern et al. 2007; Halpern et al. 2008; United Nations 2012). Historical losses in the extent of seagrass meadows, salt marshes and mangroves exceed 25% with no data available on the global loss of macroalgae beds (Table 5-3). Of the four ecosystems, macroalgal habitats (rocky reefs and intertidal) have been ranked among the most vulnerable (Halpern et al. 2007) and they are the systems we know the least about with respect to their ecosystem services.

Climate change, either through increasing water temperature or sea level rise is currently affecting coastal habitats (Table 5-3); a threat that will continue at least into the next century (Short and Neckles 1999; Adam 2002; Gilman et al. 2008; Wernberg et al. 2011). Increasing water temperature causes alteration to growth rates and physiological functions as well as poleward range shifts due to temperature stress and changes in reproduction. This poleward migration for cold adapted species will lead to an eventual range contraction as they reach their water temperature limits and can no longer shift north or south (Short and Neckles 1999; Adam 2002; Gilman et al. 2008; Wernberg et al. 2011). Range shifts have already been documented in a number marine and terrestrial species in accordance with their physiological constraints (Root et al. 2003; Bercibar et al. 2009; Wernberg et al. 2011). In addition, the nature of salt marsh and mangrove species may inhibit rapid expansion as would winter air temperature since many southern species are frost sensitive (Adam 2002; Gilman et al. 2008). However, as the climate warms the number of extreme cold weather events and frost days will decrease and will become less critical in limiting range expansion (Gilman et al. 2008).

Sea level rise may be the biggest climate change related threat to intertidal ecosystems. Sea-level rise is already happening with a 12-22 cm increase in the 20th century and is projected to accelerate over the coming decades (Solomon et al. 2007). If the rate of change in elevation in salt marshes and mangroves cannot keep pace with the changing sea-level, landward migration is the only option to maintain their preferred hydroperiod (Adam 2002; Gilman et al. 2008). Macroalgal habitats will likely also move landward to maintain adequate light levels as the water gets deeper. However, extensive coastal development (e.g. roads, seawalls, cities) provide effective barriers to this landward migration which may lead to a reduction in area or local extirpation of the ecosystem (Gilman et al. 2008). Currently, mangroves are keeping pace with sea level and salt marshes in the Wadden Sea have been estimated to tolerate between 5-10 mm rise per year (Adam 2002; Gilman et al. 2008). However, the processes controlling increases in sediment surface are extremely site specific (Adam 2002; Gilman et al. 2008) and may change as sea level rise accelerates (Solomon et al. 2007). In addition, the health of mangroves and salt marshes and their ability to keep pace is seriously threatened when sea-level rise is coupled with the predicted increased frequency and intensity of storms and extreme weather events

(Adam 2002; Gilman et al. 2008). The increased storm activity will also cause increased physical disturbance to macroalgal canopies which interact with and compound the negative effects of increased ocean temperature; reducing the canopy's ability to withstand and recover from disturbance and if chronically disturbed may lead to species poor assemblages (Wernberg et al. 2011).

Throughout history humans have preferred settling in coastal areas for easy access to resources, transportation and defence (United Nations 2011). Currently, coastal ecosystems around the world contain four times greater urban population than any other ecosystem. Human coastal settlements in developing countries are growing rapidly and this growth is expected to remain high due to high fertility rates and the ongoing migration of people from inland to coastal areas (United Nations 2011). Currently, pressures from human populations are negatively affecting coastal ecosystems through nutrient pollution from agricultural run-off and sewage, increased demand for wood products and food resources, and land use changes for agriculture, mariculture and coastal urbanization (Table 5-3). The cumulative effects of these multiple uses are reflected in the high to very high impact rating of all of the heavily populated coasts (Halpern et al. 2008). Of the coastal vegetated ecosystems, rocky reefs have the highest cumulative impact score with more than 50% of the reefs experiencing medium high to very high impacts (Halpern et al. 2008). Similarly, half of the mangroves around the world are experiencing medium high to very high cumulative impacts whereas most seagrasses are experiencing medium to medium high effects (Halpern et al. 2008). Unfortunately, salt marshes were not included in this cumulative impact analysis but their vulnerability to anthropogenic stressors is similar to mangroves (Halpern et al. 2007) and they are therefore likely experiencing similarly high levels of cumulative impacts. Anthropogenic pressures and their cumulative effects are only expected to increase with coastal human population growth (Millennium Ecosystem Assessment 2005; United Nations 2011).

In addition, human population expansion has a long history of intentional and unintentional introductions of alien species into ecosystems (Preston et al. 2004) that is only increasing in this era of globalization (Hulme 2009). Some of these species have become invasive, profoundly altering native ecosystems (Gurevitch and Padilla 2004). Only 6% of all taxa listed as threatened on the IUCN Red List of Threatened Species

(<http://www.iucnredlist.org/>) can be linked to direct or indirect effects of alien species but 33% of species in the database are threatened by habitat loss or alteration (Gurevitch and Padilla 2004). Therefore, if invaders change the structure of the habitat they may have profound effects on the associated community, trophic structure and ecosystem services. Evidence of this can already be seen in macroalgae beds with the invasion of the macroalgae *Codium fragile* ssp. *tomentosoides* (Schmidt and Scheibling 2007), salt marshes with the invasion of the marsh plant *Phragmites australis* (Robertson and Weis 2005), mangroves with the invasion of the wood boring isopod *Spaeroma terebrans* (Carlton 2001) and seagrass beds with the invasion of the European green crab *Carcinus maenas* (Garbary et al. 2004).

The consequences of centuries of human pressures on coastal vegetated ecosystems are reflected in their historical and continued global declines (Table 5-3) and IUCN red list status. Of the 70 mangrove species, 16% were assigned to a threatened category as well as 14% of the 72 species of seagrass (Polidoro et al. 2010; Short et al. 2011). Two mangrove species were listed as critically endangered and may disappear within the next decade if conservation measures are not put in place (Polidoro et al. 2010). Although seagrasses have more species in the threatened category, when combined with the near threatened category, they have a lower proportion of species in those categories (21%) relative to mangroves (26%), which may be indicative of the greater human pressures exerted by the widespread clearing of mangroves. Human activities were also identified as affecting 93% of all the seagrass species (Short et al. 2011). The majority of species listed as least concern are wide-ranging, fast-growing species with large distributions, many of which have also suffered population declines and may be locally threatened. However, their global population declines were below the threshold required for assignment to a threatened category (Polidoro et al. 2010; Short et al. 2011) but may be listed in the future if current trends continue.

Thus far assessment efforts in salt marshes and macroalgal beds have been on individual species and a comprehensive review of the status of salt marshes and macroalgae as a group is so far lacking. Currently, only 12 salt marsh vegetation species are on the IUCN red list, three of which are seagrasses (*Ruppia cirrhosa*, *R. maritima* and *Zostera capensis*). Although seagrasses do occur in salt marshes, they are not emergent salt marsh

vegetation. Many salt marsh species such as those from the genus *Spartina* and *Sarcocornia* among many others have not yet been assessed. Of the remaining nine salt marsh species in the IUCN database, five are listed as threatened and four are either of least concern or data deficient. Of the 43 species of plants and protists listed in the IUCN database for the rocky intertidal and macroalgal habitats, the only fucoid, *Sargassum galapense*, was listed as data deficient and no kelp species at all were assessed. Considering the important role of salt marshes and macroalgal ecosystems in providing essential services and the increasing human pressure in the coastal zone, there is an urgent need to assess the status of the constituent species and identify key knowledge gaps that need to be filled to adequately address the status of these ecosystems as a whole.

5.7. Conclusions

There are clear differences in the carbon and nitrogen storage and habitat and nursery services between coastal vegetated habitats (Table 5-1, 5-2; Fig. 5-2, 5-3). Each ecosystem had a unique strength, macroalgae had the highest C and N standing stock, mangroves had the highest C and N burial, salt marshes had the highest decapod abundance enhancement whereas seagrasses had the highest overall enhancement on total fauna abundance and richness as well as significantly enhanced juvenile fish abundance; emphasizing that one macrophyte cannot replace the other but that they are all key players in the provision of ecosystem services. In addition, the export of detrital material and the dispersal and migration of flora and fauna connects these habitats in an interdependent coastal mosaic.

Currently, our lack of good estimates of global extent of marine macrophytes, especially for salt marshes and macroalgae, limits our understanding of the magnitude of the ecosystem services they provide. The development of a rapid assessment method of estimating the global extent of all marine macrophyte ecosystems would allow us to get a more complete map of their current status but also monitor changes over time. However, the most important knowledge gap lies with macroalgae, where very little research exists into their carbon and nitrogen storage services despite their enormous biomass and global distribution. In addition, we only focused on laminarians and fucoids, more work needs to

be done on other algal species or groups to understand the role they play in providing important ecosystem services. It is imperative that we have more studies comparing the abundance of juvenile and adult fishes, crustaceans, gastropods, infauna, holdfast fauna and other mobile invertebrates as groups inside relative to outside vegetation to get a clearer picture of the habitat and nursery services of coastal vegetated systems for all mobile species.

The continued loss of these highly valuable ecosystems jeopardizes the functioning of the coastal ocean and its ability to provide services essential for human well being (Millennium Ecosystem Assessment 2005; Gilman et al. 2008; Short et al. 2011). We can no longer view these ecosystems in isolation and the application of landscape ecology to the coastal seascape offers a spatially-explicit perspective to resource management, conservation and restoration planning (Boström et al. 2011). Increasing habitat connectivity in marine reserves has been shown to increase their performance by maintaining ecological processes thereby increasing the resilience and trophic exchange among protected habitats as well as in adjacent aquatic and terrestrial habitats (Olds et al. 2012). If we are to truly protect the ecosystem services provided by the coastal ocean, it is essential that we consider the mosaic of ecosystems and their connectivity in the planning, implementation and management of protected areas as well as remediation and restoration projects.

Table 5-1. Global estimates of the spatial extent, production, export, burial and standing biomass as well as tissue content (%) and standing stock of carbon (C) and nitrogen (N) for four coastal vegetated habitats. Where possible measures for both above (Abg) and below (Blg) ground components are listed and their sum (Total) or mean (Mean) calculated. Standing stock was estimated by multiplying the biomass of each component with their respective % tissue C or N. – indicates that no data were available and that there is no below ground component for macroalgae. See text for discussion and references of extent

		Seagrass	Mangrove	Salt marsh	Macroalgae
Extent (10 ⁵ km ²)		3.0	1.6	3.8	16.7
Production (10 ⁵ g DW km ⁻² day ⁻¹)	Abg	38.4 ¹	54.2 ⁶	33.6 ⁹	100.2 ¹³
	Blg	12.1 ¹	32.2 ⁶	18.3 ⁹	-
	Total	50.5	86.4	51.9	100.2
Export (10 ⁵ g DW km ⁻² day ⁻¹)	Total	12.3 ³	3.87 ³	12.2 ³	43.6 ³
Burial (10 ⁵ g DW km ⁻² day ⁻¹)	Production	11.3 ²	14.7 ²	13.2 ²	-
	Export	1.2	0.4	1.2	4.4
	Total	12.5	15.1	14.4	4.4
Biomass (10 ⁶ DWg km ⁻²)	Abg	239.4 ¹	17188.0 ⁷	792.4 ¹⁰	8168.0 ¹⁴
	Blg	235.6 ¹	12211.0 ⁷	7662.0 ¹⁰	-
	Total	475.0	29399.0	8454.4	8168.0
% tissue C	Abg	33.6 ⁴	42.0 ⁶	43.5 ¹¹	24.8 ¹⁵
	Blg	25.5 ⁵	44.0 ⁶	47.1 ¹²	-
	Mean	29.6	43.0	45.3	24.8
% tissue N	Abg	1.8 ⁴	-	1.4 ⁸	2.3 ⁸
	Blg	0.6 ⁵	-	0.8 ¹²	-
	Mean	1.2	0.4 ⁸	1.1	2.3
C standing stock (10 ⁶ g DW km ⁻²)	Abg	80.5	7219.0	344.7	2025.7
	Blg	60.1	5372.8	3608.8	-
	Total	140.5	12591.8	3953.5	2025.7
N standing stock (10 ⁶ g DW km ⁻²)	Abg	4.36	-	11.1	187.9
	Blg	1.51	-	61.3	-
	Total	5.9	105.8	72.4	187.9

¹Duarte and Chiscano (1999), ²McLeod et al. (2011), ³Duarte and Cebrián (1996), ⁴Duarte (1990), ⁵Schmidt et al. (2012), ⁶Bouillon et al. (2008), ⁷Komiyama et al. (2008), ⁸Cebrian (1999), ⁹Chmura (2009) and Woodwell et al. (1973), ¹⁰Gallagher et al. (1980), Groenendijk and Vink-Lievaart (1987), Clarke and Jacoby (1994), Caçador et al. (2004) and Neves et al. (2007), ¹¹Curtis et al. (1989), ¹²Curtis et al. (1990), ¹³Charpy-Roubaud and Sournia (1990), ¹⁴Mann (1972b), Vadas et al. (2004), Reed and Brzezinski (2009) and Schmidt et al. (2011), ¹⁵Duarte (1992).

Table 5-2. Comparison of global estimates of area and standing biomass based carbon (C) stocks for the vegetation component of the major terrestrial biomes from Del Grosso et al. (2008), phytoplankton from Chavez et al. (2011), calcium carbonate production in corals from Smith and Gattuso (2009) and seagrasses, mangroves, salt marshes and macroalgae by multiplying the standing biomass by the average tissue carbon and area from Table 5-1. Pg = petagram = 10^{15} g

Ecosystem	Area (10^6 ha)	C stock (Pg C)
Terrestrial		46.0
Tundra	1030	1.2
Boreal forest	1900	6.0
Temperate deciduous forest	1206	6.6
Temperate coniferous forest	246	1.2
Grasslands	968	1.6
Savanna	3197	12.1
Tropical forest	1747	15.2
Desert	2607	1.0
Wetlands/Ice	227	1.1
Marine		57.0
Phytoplankton	36302	50.0
Coral reefs	60	0.08
Seagrasses	30	0.04
Mangroves	16	2.1
Salt marshes	38	1.5
Macroalgae	167	3.4

Table 5-3. Global areal losses since the 1940s, current annual areal loss rates, IUCN red list status and the main drivers of the loss of coastal vegetated habitats. The IUCN red list status represents the percentage of species under elevated threat of extinction. Loss drivers are not listed in order of importance. Table modified from Boström et al. (2011). - indicates no data. Urbanization refers to increases in coastal development and pollution. Removal refers to the mechanical damage to seagrasses through dredging, mooring or other shallow water development such as aquaculture.

	Seagrasses ¹⁻²	Mangroves ³	Salt Marshes ⁴⁻⁷	Macroalgae ⁸⁻¹⁰
Global loss (%)	33	34	25	-
Annual loss rate (%)	7	3.3	2.1	-
IUCN (%)	14	16	-	-
Loss drivers	Warming Sea level rise	Sea level rise Urbanization	Sea level rise Urbanization	Warming Urbanization
	Eutrophication Removal	Mariculture Forestry	Eutrophication Invasions	Fisheries Invasions

¹Waycott et al. (2009), ²Short et al. (2011), ³Polidoro et al. (2010), ⁴Boström et al. (2011), ⁵Duarte et al. (2008), ⁶Valiela et al. (2009), ⁷Deegan et al. (2012), ⁸Wernberg et al. (2011), ⁸Coleman et al. (2008), ⁹Steneck et al. (2002a). Nellemann et al. (2009) was used for global losses and annual loss rates and Halpern et al. (2007) was used for all habitats.

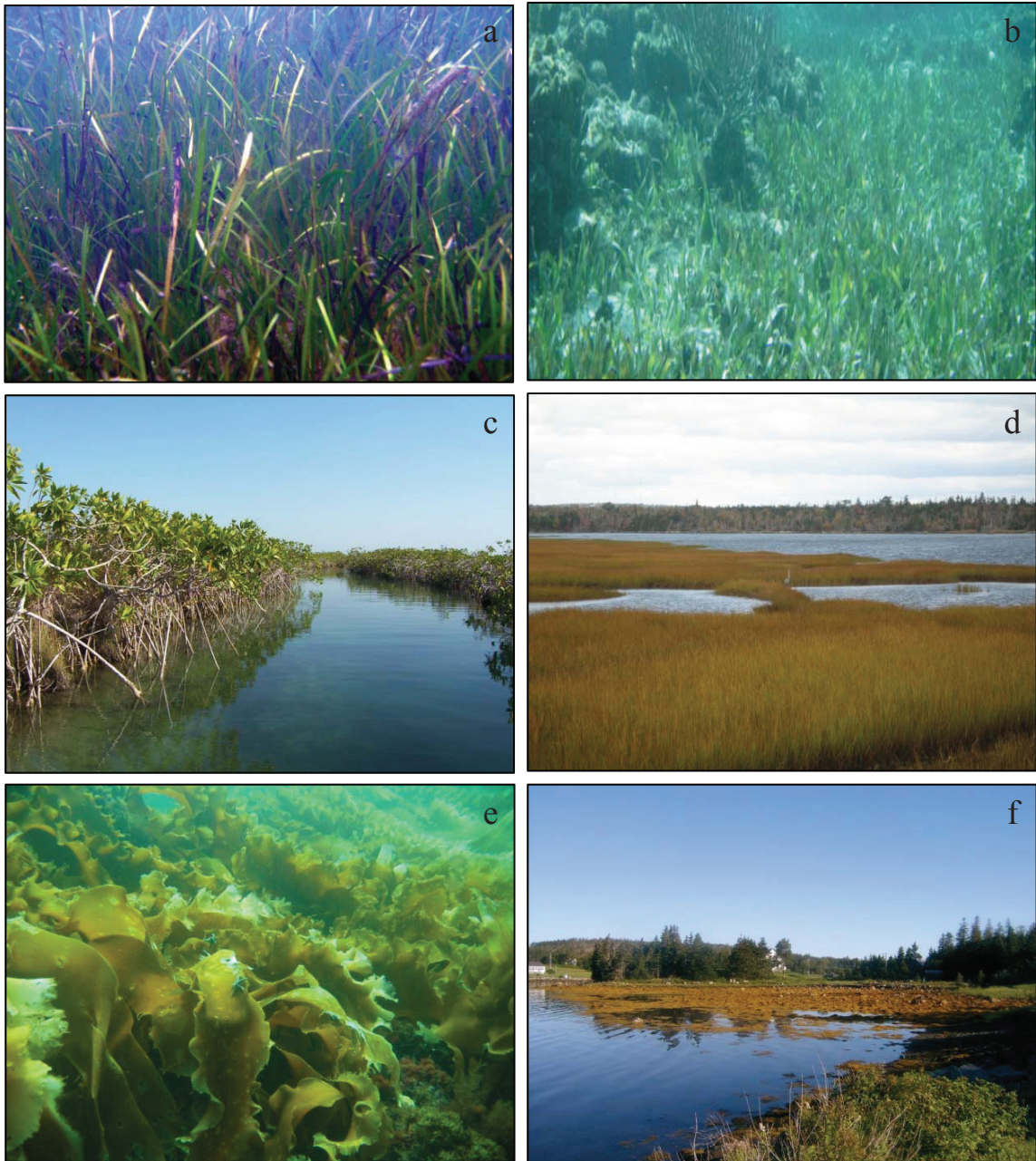


Figure 5-1. Coastal vegetated ecosystems: a) temperate seagrass bed in New Brunswick, Canada, b) tropical seagrass bed and c) mangrove in Quintana Roo, Mexico as well as a d) temperate salt marsh, e) kelp bed and f) rockweed bed in Nova Scotia, Canada. Photos b) and e) courtesy of Louise Schmidt and Robert Scheibling, respectively.

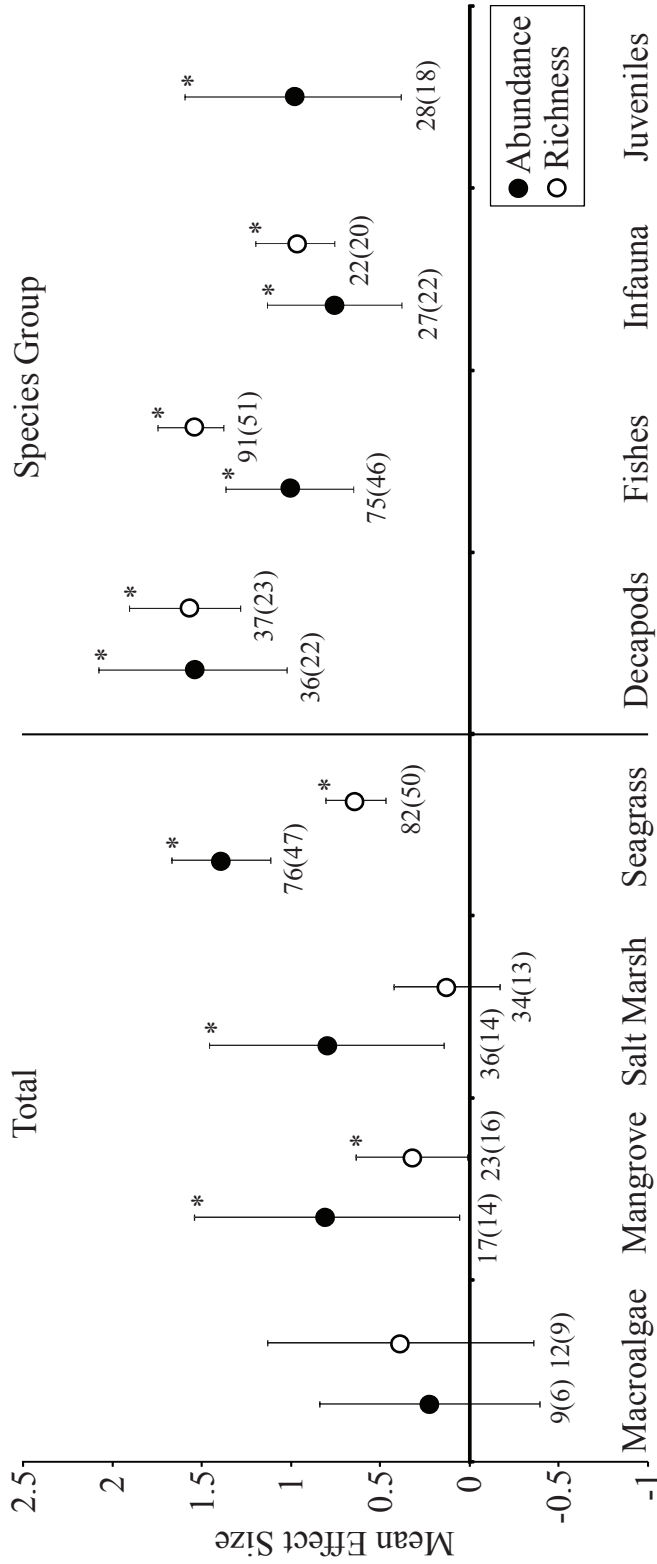


Figure 5-2. Average response ratios (ln(vegetated/unvegetated)) and 95% confidence intervals of abundance and species richness responses of the total faunal assemblage (pooled across species groups, excluding juvenile fishes) to the presence of four vegetation types and species groups and juvenile fishes (abundance only) to the presence of vegetation (pooled across the four types). The value below the error bars represents the number of results included in the analysis and, in the parentheses, is the number of articles from which those results were extracted. Values that differ significantly from zero ($p \leq 0.05$) are noted with an asterisk.

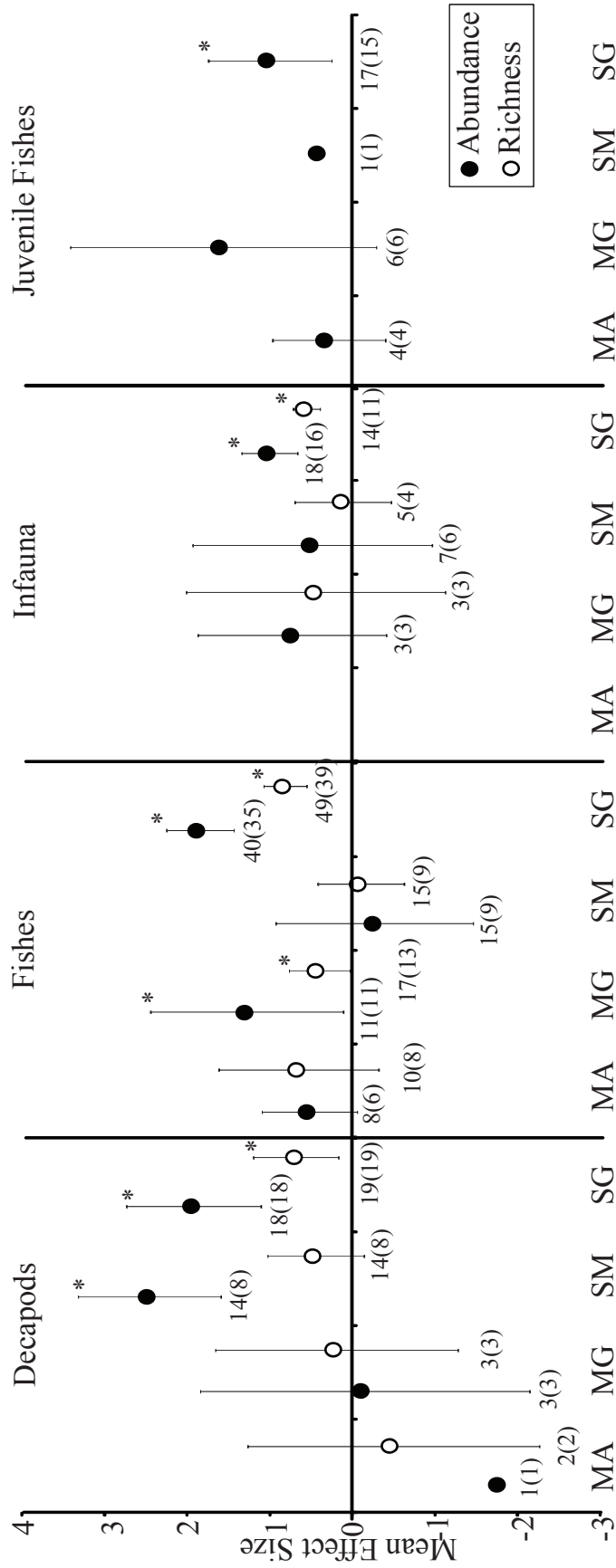


Figure 5-3. Average response ratios (ln(vegetated/unvegetated)) and 95% confidence intervals of abundance and species richness responses of different species groups and juvenile fishes (abundance only) to the presence of macroalgae (MA), mangrove (MG), salt marsh (SM) and seagrass (SG) vegetation. The value below the error bars represents the number of results included in the analysis and, in the parentheses, is the number of articles from which those results were extracted. Values that differ significantly from zero ($p \leq 0.05$) are noted with an asterisk.

CHAPTER 6

General Discussion

6.1. Summary

Overall, my work demonstrated that the extent to which marine vegetation provide important habitat as well as nitrogen and carbon storage services depends on the foundation species, and that these services are negatively affected by eutrophication. The comparison of rockweed (*Ascophyllum nodosum*) and eelgrass (*Zostera marina*) ecosystems in Chapter 1 clearly showed that the much greater biomass in rockweed beds can store significantly more carbon and nitrogen than eelgrass but that sediments in eelgrass beds have a large storage capacity because of the high local burial rates. Both habitats significantly enhanced the abundance and diversity of associated species compared to unvegetated habitats, including some commercially important species. However, there was also within and between ecosystem variation in the habitat and nursery services as a function of the 3-dimensional complexity of the ecosystem that influenced the identity and spatial distribution of the associated flora and fauna. Lastly, both rockweed and eelgrass food webs were more vulnerable to simulated species loss, especially when including primary producers, compared to other marine food webs, underscoring their vulnerability to disturbances affecting the functionally dominant primary producers.

One of the main impacts of eutrophication in terrestrial, freshwater and marine ecosystems is a shift in the composition of the primary producer assemblage (Smith et al. 1999). This shift was evident at a regional scale in eelgrass beds of the Canadian Maritimes, as demonstrated in Chapter 2. The dominance of perennial eelgrass shifted to increasing abundance of phytoplankton and opportunistic macroalgae under intermediate levels of eutrophication and, as a result, decreased the carbon storage services of the ecosystem. While each primary producer component showed its own response to eutrophica-

tion, often influenced by local environmental conditions, I showed that a combined index incorporating all three components provided the best quantitative signal of eutrophication across a regional gradient of nutrient loading. The shift in dominance also changed the complexity of the habitat and food availability to filter feeders, herbivores and detritivores. These changes, coupled with the increasingly hostile chemical environment of the sediments and water column, led to the increase in pollution tolerant species, the loss of sensitive species and an overall decline in the species richness of fishes and invertebrates, as demonstrated in Chapter 3. Thus, chapters two and three together indicate the specific and wide-ranging consequences of eutrophication on coastal ecosystem structure, functions and services.

Coastal vegetated habitats such as mangroves, salt marshes, seagrasses and macroalgae play an important role in oceanic carbon and nitrogen storage. As I show in Chapter 4, together these ecosystems make up 12% of the oceanic carbon stock (PgC) and their contribution to the global carbon stock is only exceeded by phytoplankton, savanna and tropical forests. In addition, all of these ecosystems play key roles in providing habitat and nursery services to many commercially and non-commercially important species at a local scale, enhancing their abundance and diversity compared to unvegetated habitats. This local enhancement will have regional effects through highly migratory fish and invertebrate stocks with eventual global economic impacts. Overall, my review showed that each of the investigated ecosystems has its strength, either in carbon storage and sequestration or with respect to habitat and nursery services indicating that one ecosystem cannot replace the other. This emphasizes the importance of all coastal vegetated ecosystems in providing the full complement of essential services.

6.2. Management Implications

Despite their importance in providing ecosystem services essential for humans the conservation, management and restoration of coastal vegetated ecosystems lags behind terrestrial biomes such as tropical rainforests (Duarte et al. 2008). Part of the imbalance can be attributed to the lack of public awareness of the global declines in the extent of

coastal ecosystems and their underlying causes as well as the societal value of these ecosystems. Such public awareness is necessary to set in motion effective management, protection or restoration strategies (Lotze et al. 2011). However, public awareness is only part of the equation. Having a national legislative framework that can be used to create effective policies and management plans in response to public pressure is an essential piece of the puzzle (Lotze et al. 2011). However, underlying the policy there needs to be sound independent science that managers can rely on to make effective decisions about economic activities and the protection of the environment and natural resources (Government of Canada 2002). Yet, current research efforts do not reflect the areal extent or the potential economic value of services provided by coastal ecosystems (Duarte et al. 2008). This lack of supporting research needed to inform the management process may lead to inaction. Thus, one overarching goal of my thesis was to provide quantitative scientific information on the ecosystem services coastal vegetated habitats provide and how they are affected by anthropogenic nutrient loading.

Recently, eelgrass (*Zostera marina*) was designated an Ecologically Significant Species (ESS) because of its habitat and nursery services (Fisheries and Oceans Canada 2009). Although this designation does not afford the species any legal protection, it is an official recognition of its importance and a step in the right direction. This was followed by a review of the human activities that may constitute a Harmful Alteration, Disruption or Destruction (HADD) of habitat provided by eelgrass (Fisheries and Oceans Canada 2012b). Both the process of designating eelgrass as ESS as well as the HADD review required very detailed information about habitat usage, tolerances and thresholds that in many cases just don't exist in the literature even for this relatively well-studied species. Many academics are currently undertaking research that could contribute to the management process but have no clear idea of what information is actually needed. We need increased communication between managers and scientists to bridge this gap so that scientists can tailor their work to satisfy their research interests while also providing useful information to management process. I was fortunate that my research on eelgrass beds could already contribute to the process of designating eelgrass as ESS and reviewing its HADD in Atlantic Canada. So far, however, no such process has been started for rock-

weed (or other marine habitat-providing plants) despite its similarly high importance in providing ecosystem services.

6.3. Future Directions

Most coastal ecosystems are not just being affected by one human activity; rather, they are a modern representation of multiple past and present perturbations (Lotze et al. 2006) and understanding how ecosystems are affected by these activities is essential for managers. Aquaculture is growing rapidly in Atlantic Canada and is viewed by federal and provincial governments as an economic opportunity to revitalize rural economics (Fisheries and Oceans Canada 2012a) that are declining because of dwindling wild fisheries. In Prince Edward Island alone, the mussel industry has seen growth from 100,000 pounds in 1980 to 44 million pounds in 2010 (www.gov.pe.ca). In New Brunswick, bivalve aquaculture is being promoted as a “green” industry that “improves the quality of coastal marine ecosystems” (www.gnb.ca). However, researchers have found ecosystem level effects of bivalve aquaculture because of the strong control of dense bivalve populations on phyto- and zooplankton dynamics, the diversion of suspended material to benthic food webs and the alteration of coastal nutrient dynamics (Cranford et al. 2003). What is not known are the consequences of the interaction between the effects of bivalve aquaculture on the plankton assemblage and increased nutrient loading on the functions and services of coastal vegetated ecosystems. All of my study sites in New Brunswick and Prince Edward Island, except one, had bivalve aquaculture within the estuary but I was unable to tease apart these interactions. Further investigation into the plankton species assemblage and size structure would enable us to understand the mechanisms of change and wider implications of both of these activities on the receiving ecosystems and their food-webs.

Salmon aquaculture is also on the rise with production increasing from 78 tonnes in 1986 to 32,000 tonnes in 2010 (Fisheries and Oceans Canada 2012a). Salmon farms are a significant local source of nutrient pollution in coastal estuaries and embayments (Wu 1995) that are typically located adjacent to the shore thereby affecting the nearby ecosys-

tems. We now know that eutrophication has profound impacts on eelgrass ecosystems (e.g. this thesis, Hauxwell et al. 2001; Deegan et al. 2002; Hughes et al. 2002) and rocky shores (e.g. Worm and Lotze 2006), but these effects remain to be examined in local macroalgal ecosystems such as rockweed and kelp beds. In addition, many rockweed beds are also being harvested with unknown consequences of the harvest or the interaction between the harvest and eutrophication on the structure and services of rockweed ecosystems.

6.4. Conclusions

What we do know is that the loss in eelgrass irrespective of the mechanism will have profound effects on associated species and the trophic transfer of these ecosystems. This was demonstrated by the high rate of secondary extinctions that I observed with the simulated removal of primary producers in the food web models (Chapter 1). Rockweed food web models showed that they are even more vulnerable to the loss of the foundation species thereby emphasizing the need to take the precautionary approach when managing activities that affect the structure of rockweed ecosystems. The simple binary network models I used were able to detect fundamental changes in the food web structure. The next step would be to model the food webs using more complex mass-balanced techniques (Coll et al. 2008) to examine changes in ecosystem functions in the face of eutrophication, harvesting and their interaction.

Although there are many other pieces of the puzzle that we still need to understand the full extent of the services provided by coastal vegetated ecosystems, we now know enough to warrant the protection and careful management of activities that could lead to their decline.

APPENDIX A

Supplementary Information for Chapter 2

The comparison of the effect of different transect lengths and widths on our analysis of the abundance of mobile transect and quadrat macrofauna (A1) as well as information on sources for length at maturity data (A2), trophic groups and diet references (A3) and the species present at our study sites (A4 to A5).

Because we did not replicate transects within a location we could not directly test for the interaction between site and location to examine the effect of the different transect dimensions on the highly mobile macrofauna. Both Sale and Sharp (1983) and Cheal and Thompson (1997) found significantly higher fish densities in 1 m vs. 2 m wide transects for many species on coral reefs. However, Horinuchi et al. (2005) demonstrated that there were no differences in species richness and density between transect widths for fishes grouped based on their microhabitat preferences within seagrass beds and swimming abilities. Moreover, Mapstone and Ayling (1998) found that for highly mobile fishes and benthic organisms of relatively low abundance 20 and 60 m long transects were not statistically distinguishable. Based on these studies and the lack of significant differences in any factor (PERMANOVA: $p > 0.075$), we assumed that changes in length and width did not affect the number of species observed or their abundances.

When compared to the results of the analyses on the quadrat macrofauna, sessile benthic and epiphytic species abundance data using the original transect lengths, the overall results of the PERMANOVA analyses of the shorter transects remained the same; both had a significant site nested within canopy by location interactions (ORIGINAL: Table 2-4; SHORT: Macrofauna: pseudo- $F_{10,84} = 3.1$, $p = 0.001$; Sessile Benthic: $F_{10,84} = 7.2$, $p = 0.001$; Epiphytic: $F_{10,84} = 4.4$, $p = 0.001$). Only 13 of the 81 (16%) site-by-site within a canopy type and location post-hoc comparisons showed a different result when using the

shortened compared to the original transects (S5). Since the transects only differed by a maximum of one quadrat, this indicates that the differences were most likely between sites and not the number of quadrats used to collect the data. In turn, almost all comparisons between sites with transects that differed by three, five, or six quadrats revealed the same results when analyzing all or shortened transects. The only exception was a significant difference in the epiphyte community between standard (11 quadrats) and short (five quadrats) transects inside the rockweed habitat (PDI, TGI; S5). This difference was no longer significant once both transects were of equally short length. However, this short transect (TGI) was not different from any of the other standard transects (EJI, NTI) inside a rockweed habitat, suggesting that the significant effect is a difference between sites and not the difference in length.

Table A-1. Results of PERMANOVA post hoc comparisons between each site nested within canopy by location (see Table 2-1 for site and location abbreviations) when using the original (ALL; 5–11 quadrats) and the randomly shortened (SHORT; five quadrats) transect abundance data for the mobile macrofauna, sessile benthic and epiphytic species to examine the effect of the number of quadrats on the outcome. The difference in the number of quadrats (#Q) between the transects being compared applies only to the original data; all the shortened data had five quadrats. The longest transect is listed first in the site comparison. The shortest transect in both canopy types is in bold. – indicates no significant difference between transects, all other comparisons list the species identified by SIMPER analysis that consistently contribute (in decreasing order) to the differences and the direction (</>) between transects. Lt = *Littorina* sp., Lv = *Lacuna vincta*; P = *Pagurus* sp.; Cr = *Crangon septemspinosa*; C = *Carcinus maenas*; Cl = *Cladophora rupestris*; Ch = *Chondrus crispus*; Co = *Corallina officinalis*; M = *Membranipora membranacea*; S = *Spirorbis* sp. and F = *Fucus vesiculosus*.

Site & Location Comparison	#Q	Mobile Macrofauna		Sessile Benthic		Epiphytic	
		All	Short	All	Short	All	Short
Eelgrass							
FPI, THI	3	-	-	-	-	M >	M >
FPI, MHI	0	Lt >; Lv <; P >	Lt >; Lv <; P >	-	-	M >	S <
MHI, THI	3	Lt >; Lv <	Lt >; Lv <	-	-	-	-
FPE, THE	1	Lv >; P <	-	-	-	M <	M <
FPE, MHE	0	Lt <; Lv, P >	Lt <; Lv >; C <	-	-	S <	-
MHE, THE	1	Lt >; Lv, P <	Lt >; P, Lv <; C >	-	-	S <	M <
FPO, THO	0	P <	-	-	-	-	-
FPO, MHO	0	Cr, Lt <	Cr, Lt <	-	-	-	-
MHO, THO	0	Cr, Lt >	Cr, Lt <; P >	-	-	-	-
Rockweed							
EJI, NTI	1	-	-	-	-	-	-
PDI, NTI	1	Lt <	Lt <	-	-	-	-
NTI, TGI	5	-	-	-	-	-	-
EJI, PDI	0	Lt >	-	-	-	-	-
EJI, TGI	6	-	-	-	-	-	-
PDI, TGI	6	-	-	-	-	F >	-
NTE, EJE	1	-	-	Cl >	Cl, Ch >	S >	S >
NTE, PDE	0	Lt >	-	Ch <	Ch, Co <	S >	S, M >
NTE, TGE	0	Lt <	-	Cl >; Ch <	-	S >	-
PDE, EJE	1	-	-	Cl <; Ch >	Cl <; Ch, Co >	S <	S <
TGE, EJE	1	-	-	Cl <	Cl, Ch <	M, S <	S <
PDE, TGE	0	Lt <	-	-	-	-	-
NTO, EJO	0	-	-	-	-	-	-
NTO, PDO	1	P, Lt <	P, Lt <	-	-	-	-
NTO, TGO	0	Cr >	-	-	-	-	-
EJO, PDO	1	P, Lt <	P, Lt <	-	-	-	-
EJO, TGO	0	-	-	-	-	-	-
TGO, PDO	1	P, Lt <	P, Lt <	-	-	-	-

Table A-2. Minimum length at maturity data for species observed in rockweed and eelgrass habitats in Nova Scotia, Canada. If data on an observed species was not available, we used a closely related species (source species) instead.

Observed Species	Source Species	Size (cm)	Source
<i>Anguilla rostrata</i>		35.5	Fishbase
<i>Cancer borealis</i>		8.5	Fisheries and Oceans Canada (2000b)
<i>Cancer irroratus</i>		5	Fisheries and Oceans Canada (2000a)
<i>Carcinus maenas</i>		3.4	Berrill (1982)
<i>Gadus morhua</i>		32.1	Fishbase
<i>Gasterosteus aculeatus</i>		3.6	Fishbase
<i>Homarus americanus</i>		5.5	Cobb and Phillips (1980)
<i>Microgadus tomcod</i>	<i>Trisopterus minutus</i>	11	Fishbase
<i>Myoxocephalus octodecemspinosus</i>	<i>M. scorpius</i>	14	Fishbase
<i>Myoxocephalus scorpius</i>		14	Fishbase
<i>Pholis gunnellus</i>	<i>P. nebulosa</i>	14	Fishbase
<i>Pseudopleuronectes americanus</i>		25	Fishbase
<i>Scomber scombrus</i>		26.2	Fishbase
<i>Syngnathus fuscus</i>	<i>S. rostellatus</i>	10	Fishbase
<i>Tautoglabrus adspersus</i>	<i>Tautoga onitis</i>	18	Fishbase

Fishbase: A global information system on fishes www.fishbase.org

Table A-3. Trophic groups and associated diet reference(s) for rockweed *Ascophyllum nodosum* (A) and eelgrass *Zostera marina* (Z) network models. The number indicates the trophic groups included in each model with 60 and 50 groups, respectively.

Groups	A	Z	Diet References
Fishes			
<i>Anguilla rostrata</i>	32		Facey DE, Labar GW (1981) Biology of American eels in Lake Champlain, Vermont. Tran Amer Fish Soc 110:396-402.
<i>Gadus morhua</i>	34		Hacunda JS (1981) Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. Fish Bull 79:775-788.
<i>Gasterosteus aculeatus</i>	27	24	Bowman RE, Stillwell CE, Michaels WL, Grosslein MD (2000) Food of northwest Atlantic fishes and two common species of squid. NOAA Tech. Memo. NMFS-NE 155, 138 p.
<i>Microgadus tomcod</i>	33		Grabe SA (1978) Food and feeding habits of juvenile Atlantic tomcod, <i>Microgadus tomcod</i> , from Haverstraw Bay, Hudson River. Fish Bull 76:89-94.
<i>Myoxocephalus octodecemspinosus</i>	30		Bowman RE, Stillwell CE, Michaels WL, Grosslein MD (2000) Food of northwest Atlantic fishes and two common species of squid. NOAA Tech. Memo. NMFS-NE 155, 138 p.
<i>Myoxocephalus scorpius</i>		25	Ibid
<i>Syngnathus fuscus</i>	28		Ibid
<i>Pholis gunnelus</i>	31		Wosnitza CV (1975) Die Nahrung von Fischbrut in der westlichen Ostsee. Berichte der deutschen wissenschaftlichen Kommission fuer Meeresforschung 24:79-92.
<i>Pseudopleuronectes americanus</i>	35	26	Bowman RE, Stillwell CE, Michaels WL, Grosslein MD (2000) Food of northwest Atlantic fishes and two common species of squid. NOAA Tech. Memo. NMFS-NE 155, 138 p.
<i>Scomber scombrus</i>	36		Ibid
<i>Tautoglabrus adspersus</i>	29		Ibid
Other fish species	37	27	Ibid
Invertebrates			
<i>Asterias forbesii</i>	13	11	Menge BA (1979) Coexistence between the seastars <i>Asterias vulgaris</i> and <i>A. forbesii</i> in a Heterogeneous Environment: a non-equilibrium explanation. Oecologia 41: 245-272.
<i>Asteria vulgaris</i>		12	Ibid
<i>Cancer borealis</i>	14		Stehlik L (1993) Diets of the Brachyuran crabs <i>Cancer irroratus</i> , <i>C. borealis</i> and <i>Ovalipes ocellatus</i> in the New York Bight. J Crust Biol 23:723-735.
<i>Cancer irroratus</i>	15	13	Ibid
<i>Carcinus maenas</i>	16	14	Hadlock RP (1980) Alarm response of the intertidal snail <i>Littorina littorea</i> (L.) to predation by the crab <i>Carcinus maenas</i> (L.). Biol Bull 159:269-279
			Moksnes PO, Pihl L, van Montfrans J (1998) Predation on postlarvae and juveniles of the shore crab <i>Carcinus maenas</i> : importance of shelter, size and cannibalism. Mar Ecol Prog Ser 166: 211-225

Groups	A	Z	Diet References
<i>Carcinus maenas</i>			Miron G, Audet D, Landry T, Moriyasu M (2005) Predation potential of the invasive green crab (<i>Carcinus maenas</i>) and other common predators on commercial bivalve species found on Prince Edward Island. J Shell Res 24:579-586.
<i>Crangon septemspinosa</i>	18	15	Wilcox R, Jeffries HP (1974) Feeding habits of the sand shrimp <i>Crangon septemspinosa</i> . Biol Bull 146:424-434.
<i>Homarus americanus</i>	17		Ojeda FP, Dearborn JH (1991) Feeding ecology of benthic mobile predators: experimental analyses of their influence in rocky subtidal communities of the Gulf of Maine. J Exp Mar Biol Ecol 149:13-44.
<i>Idotea</i> sp.	8		Svensson PA, Malm T, Engkvist R (2004) Distribution and host plant preference of <i>Idotea baltica</i> (Pallas) (Crustacea: Isopoda) on shallow rocky shores in the central Baltic Sea', Sarsia 89:1 – 7.
<i>Lacuna vincta</i>	17		Chavanich S, Harris LG (2002) The influence of macroalgae on seasonal abundance and feeding preference of a subtidal snail, <i>Lacuna vincta</i> (montagu) (littorinidae) in the Gulf of Maine. J Moll Stud 68:73-78.
Limpet spp.	24	20	Stephenson RL, Tan FC, Mann KH (1986) Use of stable carbon isotope ratios to compare plant material and potential consumers in a seagrass bed and kelp bed in Nova Scotia, Canada. Mar Ecol Prog Ser 30:1-7.
<i>Littorina</i> sp.	21	19	Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar Biol 68:299-319.
			Barker KM, Chapman ARO (1990) Feeding preferences of periwinkles among four species of <i>Fucus</i> . Mar Biol 106: 113-118.
			Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar Biol 68: 299-319.
			Wingand C, Churchill AC (1988) Laboratory studies on eelgrass seed and seedling predation. Estuaries 11(3): 180-183.
<i>Mytilus</i> sp.	22		Graham A (1933) Molluscan diets. Proceedings of the Malacological Society.
<i>Pagurus</i> sp.	19	16	Hazlett BA (1981) The Behavioral Ecology of Hermit Crabs. An Rev Ecol Syst 12: 1-22.
<i>Semibalanus balanoides</i>	23		Rainbow PS (1984) An introduction to the biology of British littoral barnacles. Field Stud 6:1-51
Ascidians	11		Boyd HC, Brown SK, Harp JA, Weissman IL. (1986) Growth and sexual maturation of laboratory cultured monterrey <i>Botryllus Schlosseri</i> . Biol Bull 170: 91-109.
Gastropods	20	18	Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar Biol 68: 299-319.
Polychaetes	10	10	Fauchald KP, Jumars A (1979) The diet of worms: a study of polychaete feeding guilds. Ocean Mar Biol An Rev 17: 193-284.
Porifera	12		Reiswig HIM (1971) Particulate feeding in natural populations of three marine demosponges. Biol Bull 141: 568-591.

Groups	A	Z	Diet References
Suprabenthos	9	9	Gorokhova E, Hansson S (2000) Elemental composition of <i>Mysis mixta</i> (Crustacea, Mysidacea) and energy costs of reproduction and embryogenesis under laboratory conditions. J Exp Mar Biol Ecol 246:103-123 Robertson AL, Mann KH (1980) The role of isopods and amphipods in the initial fragmentation of eelgrass detritus in Nova Scotia, Canada. J Mar Biol 59 (1): 63-69.
Other infauna	21		Fauchald KP, Jumars A (1979) The diet of worms: a study of polychaete feeding guilds. Ocean Mar Biol An Rev 17: 193-284.
Other benthic invertebrates	25	22	Shumway SE, Cucci TL, Newell RC, Yentsch CM (1985) Particle selection, ingestion, and absorption in filter-feeding bivalves. J Exp Mar Biol Ecol 91: 77-92. We used the same references as all the above benthic invertebrates that are not included in the infauna or suprabenthos groups.
Epiphytic fauna	26	23	Best MA, Thorpe JP (1986) Feeding-current interactions and competition for food among the bryozoan epiphytes of <i>Fucus serratus</i> . Mar Biol 93(3): 371-375.
Zooplankton	8	7	Schnetzer A, Steinberg DK (2002) Natural diets of vertically migrating zooplankton in the Sargasso Sea. Mar Biol 141:89-99.
Birds			
<i>Anas crecca</i>	38	28	Olney PJS (1963) The food and feeding habitats of teal <i>Anas crecca crecca</i> L. Proc Zoo Soc Lon. 140:169-210.
<i>Anas rubripes</i>	39	29	Jorde DG, Owen Jr, RB (1990). Food of black ducks, <i>Anas rubripes</i> , wintering in marine habitats of Maine. Can Field Nat 104:300-302. Lynch JT (1939) Marine algae in food of Rhode Island waterfowl. The Auk 56:374-380
<i>Ardea herodias</i>	40	30	Butler RW (1995) The patient predator: foraging and population ecology of the Great Blue heron <i>Ardea herodias</i> in British Columbia. Canadian Wildlife Service, Occasional Paper #CW69-1/86E
<i>Branta bernicla</i>	41	31	Cottam C, Lynch JT, Nelson AL (1944) Food habits and management of American sea brant. J Wild Man 8:36-56
<i>Branta canadensis</i>	42	32	Martell AM (1997) Canada goose ecology in winter at Port Joli, Nova Scotia, 1967-69. In: Erskine, AJ (ed) Canada goose studies in the Maritime Provinces 1950-1992. Environment Canada, Atlantic Region, Sackville, New Brunswick, Canada, pp 26-38
<i>Cephus grylle</i>	43	33	Ewins PJ (1990) The diet of black gilletmots <i>Cephus grylle</i> in Shetland. Hol Ecol 13: 90-97
<i>Ceryle alcyon</i>	44	34	White HC (1953) The Eastern belted kingfisher in the Maritime Provinces. Fisheries Research Bulletin #97
<i>Haliaeetus leucophalus</i>	45	35	Cash KJ, Austin-Smith PJ, Banks D, Harris D, Smith PC (1985) Food remains from bald eagle nest sites on Cape Breton Island, Nova Scotia. J Wild Man 49:223-225
<i>Larus argentatus</i>	46	36	Harris MP (1965) The food of some <i>Larus</i> gulls. Ibis 107:43-53
<i>Larus marinus</i>	47	37	Ellis JC, Chen W, O'Keefe B, Shulman MJ, Witman JD (2005) Predation by gulls on crabs in rocky intertidal and shallow subtidal zones of the Gulf of Maine. J Exp Mar Biol Ecol 324:31-43
<i>Mergus serrator</i>	48	38	White HC (1957) Food and natural history of Merganzers on Salmon waters in the Maritime Provinces of Canada. Can Fish Res Board Bull #116

Groups	A	Z	Diet References
<i>Pandion haliaetus</i>	49	39	Greene E, Greene A, Freedman B (1983) Foraging behaviour and prey selection by Ospreys in coastal habitats in Nova Scotia, Canada. In Bird DM, Seymour, NR and Gerrard JM (eds) Biology and Management of Bald Eagles and Ospreys. Harpell Press, Ste. Anne de Bellevue, Quebec
<i>Phalacrocorax auritus</i>	50	40	Scattergood LW (1950) Observations on the food habits of the double-crested cormorant, <i>Phalacrocorax a. auritus</i> . The Auk 67:506-508
<i>Phalacrocorax carbo</i>	51	41	Lorensten S-H, Grémillet D, Nymoën GH (2004) Annual variation in diet of breeding great cormorants: Does it reflect varying recruitment of gadoids? Waterbirds 27: 161-169
<i>Somateria mollissima</i>	52	42	Cantin M, Bédard J, Milne H (1974) The food and feeding of common eiders in the St. Lawrence estuary in summer. Can J Zoo 52:319-334
<i>Sterna hirundo</i>	53	43	Mills DH (1957) Herring Gulls and Common Terns as possible predators of lobster larvae. J Fish Res Board Can 14: 729-730
Mammals			
<i>Halichoerus grypus</i>	54	44	Hammil MO, Stenson GB (2000) Estimated prey consumption by harp seals (<i>Phoca groenlandica</i>), hooded seals (<i>Cystophora cristata</i>), grey seals (<i>Halichoerus grypus</i>) and harbour seals (<i>Phoca vitulina</i>) in Atlantic Canada. J Northwest Atl Fish Sci 26:1-23
<i>Lutra canadensis</i>	55	45	Larsen DN (1984) Feeding habits of river otters in coastal Southeastern Alaska. J Wildl Man 48: 1446-1452
<i>Mustela vison</i>	56	46	Burness GP, Morris RD 1993 Direct and indirect consequences of mink presence in a common tern colony. The Condor 95:708-711
			Dunstone N, Birks JDS (1987) The feeding ecology of the mink (<i>Mustela vison</i>) in coastal habitat. J Zool (Lond) 212: 69-83
			Sargeant AB, Swanson A, Doty HA (1979) Selective predation by mink, <i>Mustela vison</i> , on waterfowl. Amer Midland Nat 89:208-214
<i>Phoca vitulina</i>	57	47	Hammil MO, Stenson GB (2000) Estimated prey consumption by harp seals (<i>Phoca groenlandica</i>), hooded seals (<i>Cystophora cristata</i>), grey seals (<i>Halichoerus grypus</i>) and harbour seals (<i>Phoca vitulina</i>) in Atlantic Canada. J Northwest Atl Fish Sci 26:1-23
<i>Phocoena phocoena</i>	58	48	Smith GJ, Gaskin DE (1974) The diet of harbour porpoises (<i>Phocoena phocoena</i> (L.)) in coastal waters of eastern Canada, with special reference to the Bay of Fundy. Can J Zoo 52:777-782
Primary Producers			
<i>Ascophyllum nodosum</i>	1		
<i>Chondrus crispus</i>	2		
<i>Fucus vesiculosus</i>	3	2	
<i>Zostera marina</i>		1	
Other macroalgae	4	3	
Epiphytic flora	5	4	

Groups	A	Z	Diet References
Microalgae	6	5	
Phytoplankton	7	6	
Detritus and Imports	59	49	
Imports to the system	60	50	

Table A-4. Mean abundance (\pm SE; 1000 m⁻²) of transect macrofauna observed during the day- or night-time high tide inside, along the edge and outside of rockweed (n = 3) and eelgrass (day n = 3; night n = 1) beds. * indicates species that are the target of a current or historical commercial fishery in Atlantic Canada.

	Rockweed				Eelgrass				
	In	Day Edge	Out	Night Edge	In	Day Edge	Out	Night Edge	
Crustaceans									
<i>Cancer borealis</i> *	0	0	0	0	0	0	0	0	0.05 (0)
<i>Cancer irroratus</i> *	0	0	0	0	0	0.035 (0.035)	0	0	0
<i>Carcinus maenas</i>	0.36 (0.15)	0.18 (0.068)	0.0063 (0.0063)	0.24 (0.19)	0.082 (0.082)	0.0089 (0.0087)	0.017 (0.017)	0.23 (0)	0.025 (0)
<i>Homarus americanus</i> *	0	0	0	0.0065 (0.0065)	0	0	0	0	0
<i>Mysis stenolepis</i>	3.1 (3.1)	2.0 (2.0)	0	1.1 (0.68)	21 (21)	0.21 (0.21)	0	0.26 (0)	0.25 (0)
Fishes									
<i>Anguilla rostrata</i> *	0.0065 (0.0065)	0	0	0.039 (0.017)	0	0	0	0	0
<i>Gadus morhua</i> *	0	0	0	0.019 (0.013)	0	0	0	0	0
<i>Gasterosteus aculeatus</i>	0.031 (0.031)	0	0	0.0063 (0.0063)	0.041 (0.041)	0	0	0.1 (0)	0.5 (0)
<i>Microgadus tomcod</i>	0	0	0	0.02 (0.012)	0	0	0	0	0
<i>Scomber scombrus</i> *	0.46 (0.46)	1.3 (0.91)	0	0.02 (0.02)	0.62 (0.62)	0	0	0.052 (0)	0.0075 (0)
<i>Syngnathus fuscus</i>	0	0.02 (0.02)	0	0.0065 (0.0065)	0	0	0	0.026 (0)	0
<i>Tautoglabrus adspersus</i>	0	0.013 (0.013)	0	0.0065 (0.0065)	0	0	0	0	0

Table A-5. Species composition: percent of total abundance (mean \pm SE) of each species within the transect and quadrat macrofauna, sessile benthic and epiphytic species inside (IN), along the edge (EDGE), and outside (OUT) the rockweed and eelgrass canopies. In bold is the total abundance (mean \pm SE) for the transect and quadrat macrofauna (individuals m⁻²) and sessile benthic and epiphytic species (%). * indicates species only observed at night.

	Rockweed			Eelgrass		
	IN	EDGE	OUT	IN	EDGE	OUT
TRANSECT MACROFAUNA (m⁻²)	0.38 (0.26)	0.64 (0.40)	0	1.34 (1.25)	0.05 (0.05)	0
CRUSTACEA						
<i>Homarus americanus</i> *	0	16.6 (16.6)	0	0	0	0
<i>Mysis stenolepsis</i>	37.3 (23.7)	30.5 (20.8)	0	33.3 (33.3)	28.7 (28.7)	0
MAMMALIA						
<i>Halichoreus grypus</i>	0	0	0	33.3 (33.3)	0	0
OSTEICHTHYES						
<i>Anguilla rostrata</i>	0.35 (0.35)	0	0	0	0	0
<i>Gadus morhua</i> *	0	0.49 (0.49)	0	0	2.29 (2.29)	0
<i>Gasterosteus aculeatus</i>	0.25 (0.25)	0	0	2.08 (2.08)	0	0
<i>Microgadus tomcod</i> *	0	0.14 (0.14)	0	0	2.29 (2.29)	0
<i>Pholis gunnellus</i>	12.5 (12.5)	0	0	0	0	0
<i>Scomber scombrus</i>	24.6 (24.6)	47.2 (24.8)	0	31.3 (31.3)	0	0
<i>Syngnathus fuscus</i>	0	0.22 (0.22)	0	0	0	0
<i>Tautoglabrus adpersus</i>	0	4.90 (4.90)	0	0	0	0
QUADRAT MACROFAUNA (m⁻²)	22.7 (5.28)	31.3 (7.74)	6.40 (2.58)	52.0 (10.0)	46.6 (8.16)	6.17 (3.48)
CRUSTACEA						
<i>Cancer borealis</i>	0	0	0.13 (0.13)	0	0	0
<i>Cancer irroratus</i>	0.23 (0.23)	0.33 (0.33)	1.02 (1.02)	0.08 (0.08)	0	3.03 (1.51)
<i>Carcinus maenas</i>	0.96 (0.56)	1.97 (0.93)	5.99 (2.45)	0.81 (0.64)	0.30 (0.17)	0
<i>Crangon septemspinosa</i>	0	0	17.7 (6.64)	0.60 (0.60)	1.52 (1.38)	12.5 (9.66)
<i>Idotea</i> sp.	0	0	0	0.80 (0.80)	0.11 (0.11)	0
<i>Pagurus</i> sp.	0	0.95 (0.57)	4.70 (3.34)	0.65 (0.51)	13.8 (7.55)	6.86 (4.78)
<i>Semibalanus balanoides</i>	17.9 (7.44)	5.99 (4.71)	0	0	0	0
ECHINODERMATA						
<i>Asterias forbesii</i>	0.05 (0.05)	0.76 (0.44)	0.85 (0.54)	0	0.50 (0.50)	0.34 (0.34)
<i>Asterias vulgaris</i>	0	0	0	0	0.04 (0.04)	0
MOLLUSCA						
<i>Crepidula fornicata</i>	0	0.22 (0.22)	0	0	0	0
<i>Lacuna vineta</i>	0	0	0	71.7 (26.1)	56.9 (8.81)	0
<i>Littorina</i> spp.	75.4 (8.69)	86.6 (5.59)	52.2 (12.4)	25.4 (24.4)	21.2 (18.5)	45.3 (22.7)
<i>Mytilus</i> sp.	5.37 (2.54)	2.65 (2.16)	2.27 (2.27)	0	0	0
<i>Nassarius trivittatus</i>	0	0	0	0	2.53 (1.34)	5.56 (5.56)
<i>Notoacmaea testudinalis</i>	0	0.38 (0.38)	0.75 (0.75)	0	0	0.28 (0.28)
OSTEICHTHYES						
<i>Myoxocephalus octodecemspinus</i>	0	0	2.27 (2.27)	0	0	0

	Rockweed			Eelgrass		
	IN	EDGE	OUT	IN	EDGE	OUT
<i>Myoxocephalus scorpius</i>	0	0	0	0	0.05 (0.05)	0
<i>Pseudopleuronectes americanus</i>	0	0.19 (0.19)	0.68 (0.24)	0	0	1.85 (1.38)
SESSILE BENTHIC SPECIES (%)	0.16 (0.05)	15.5 (10.0)	0.68 (0.44)	0.03 (0.03)	0.17 (0.17)	0
PORIFERA						
<i>Halichondria panacea</i>	0	0.47 (0.33)	0	0	0	0
PLANTAE						
CHLOROPHYTA						
<i>Cladophora rupestris</i>	2.50 (2.50)	31.7 (18.4)	2.27 (2.27)	0	0	0
PHAEOPHYTA						
<i>Pilayella littoralis</i>	0	4.55 (4.55)	0	0	0	0
<i>Sphacelaria arctica</i>	0	0.75 (0.75)	0	0	0	0
RHODOPHYTA						
<i>Ahnfeltia plicata</i>	0	0	0	0	3.33 (3.33)	0
<i>Chondrus crispus</i>	12.0 (4.6)	24.2 (11.7)	0	0	0	0
<i>Corallina officinalis</i>	0	11.0 (7.9)	0	5.56 (5.56)	0	0
<i>Polysiphonia fucoids</i>	0	0	2.27 (2.27)	0	0	0
EPIPHYTIC SPECIES (%)	0.80 (0.59)	9.0 (5.3)	0	3.8 (2.4)	6.0 (4.5)	0
BRYOZOA						
<i>Membranipora membranacea</i>	1.89 (1.89)	8.20 (4.39)	0	25.9 (25.9)	29.5 (15.9)	0
POLYCHAETA						
<i>Spirorbis</i> sp.	2.08 (2.08)	36.9 (16.0)	0	25.9 (13.4)	36.3 (21.0)	0
UROCHORDATA						
<i>Botryllus schlosseri</i>	0	4.17 (4.17)	0	0	0	0
PLANTAE						
PHAEOPHYTA						
<i>Ascophyllum nodosum</i>	0	2.27 (2.27)	0	0	0	0
<i>Ectocarpus siliculosus</i>	0	3.27 (3.27)	0	0	0	0
<i>Fucus vesiculosus</i>	14.9 (10.7)	2.27 (2.27)	0	5.56 (5.56)	0	0
RHODOPHYTA						
<i>Erythrotrichia carnea</i>	0	2.01 (2.01)	0	0	0	0
<i>Polysiphonia fucoids</i>	0	0	0	5.56 (5.56)	0	0

APPENDIX B

Supplementary Information for Chapter 5

Table B-1: Species richness (S) and juvenile and total abundance for decapods (D), fishes (F) and infauna (I) in seagrass, salt marsh, mangrove and macroalgal ecosystems and nearby unvegetated areas. Units are as follows: Haul = total number per haul; aHaul = average per haul; Total = total number; Trawl = average per beam trawl; Sample = total number per sample; m^{-2} or $x(c)m^{-x}$ = average per m^{-2} or $x(c)m^{-x}$; Net = average per gillnet; Core = average number per core; Site = average number per site; Freq = Frequency of occurrence; CPUJE = catch per unit effort.

Ecosystem	Fauna	Units	Vegetated			Unvegetated			Reference
			S	Juvenile	Total	S	Juvenile	Total	
Seagrasses	F	Site	17.51	81.43	197.14	8.62	37.14	81.43	Connolly (1994)
	F	aHaul	8.00	79.33		3.17	13.50		Dennis (1992)
	F	$100 m^{-2}$	35.00		1.86	28.50		1.41	Franco et al. (2006)
	F	Total	49.00		41141.00	29.00		2251.00	Gray et al. (1996)
	F	Total	35.50	8610.00		18.00	2132.00		Gray et al. (1998)
	F	$40 m^{-2}$	20.50		2229.55	9.00		1840.91	Guidetti (2000)
	F	$1000 m^{-2}$	7.65	39.05	47.14	0.88	2.14	3.57	Gullström et al. (2008)
	F	$1000 m^{-2}$	2.06	9.76	12.62	0.88	2.14	3.57	Gullström et al. (2008)
	F	Haul	6.33		380.00	2.33		24.50	Heck et al. (1989)
	F	Trawl	6.44			2.40			Lazzari and Tupper (2002)
	F	CPUJE	10.00		7.95	5.00		0.75	Lazzari (2002)
	F	m^{-2}	13.00		1.18	4.00		0.04	Mattila et al. (1999)
	F	$100 m^{-2}$	17.00	42.30		5.00	0.80		Nagelkerken and Van Der Velde (2002)
	F	$100 m^{-2}$	11.00			3.00			Nagelkerken and Van Der Velde (2002)
	F	$100 m^{-2}$	21.00		46.00	8.00		1.70	Nagelkerken and Van Der Velde (2002)
	F	m^{-2}	8.57		50.00	14.29		90.00	Nagelkerken et al. (2000)
	F	m^{-2}	5.71	40.00		7.14	60.00		Nagelkerken et al. (2000)
F	$100 m^{-3}$		6913.45			5907.15		Olney and Boehlert (1988)	
F	$100 m^{-3}$		1140.75			5907.15		Olney and Boehlert (1988)	

Ecosystem	Fauna	Units	Vegetated			Unvegetated			Reference
			S	Juvenile	Total	S	Juvenile	Total	
Seagrasses	F	Haul	27.00		8238.00	11.00		303.00	Orth and Heck (1980)
	F	100 m ⁻²	9.00	6.17		7.00	1.21		Polte and Asmus (2006)
	F	Haul	58.50		53.72	19.00		10.54	Robertson and Duke (1987)
	F	m ⁻²	2.55		9.55	0.80		2.00	Rozas and Minello (1998)
	F	m ⁻²	1.72	0.18	1.50	0.03	0.13	0.25	Schmidt et al. (2011)
	F	Haul	58.00		29.80	46.00		26.70	Sedberry and Carter (1993)
	F	m ⁻²	14.00		4.38	11.00		2.54	Sheridan (1992)
	F	Total	37.00		1174.00	32.00		170.00	Shibuno et al. (2008)
	F	Total	4.00	115.83		2.00	4.73		Shibuno et al. (2008)
	F	Total	33.50		918.00	11.00		65.00	Travers and Potter (2002)
	F	Total	33.50		961.50	10.00		49.00	Travers and Potter (2002)
	F	Total	32.00		242.00	19.00		70.00	Travers and Potter (2002)
	F	Total	25.00		459.00	28.00		149.00	Travers and Potter (2002)
	F	100 m ⁻²	2.98		38.80	0.54		1.10	Tuya et al. (2005)
	F	500 m ⁻²	64.00		475.50	60.00		314.70	Valesini et al. (2004)
	F	Total	12.00		779.00	12.00		389.00	Sogard and Able (1991)
	F	Total	23.00		1470.00	23.00		940.00	Weng (1990)
	F	m ⁻²	73.00		13.99	84.00		10.05	Minello (1999)
	F	Total			578000.00			545000.00	Briggs and O'Connor (1971)
	F	Haul	32.00		108.65	21.00		11.92	Edgar and Shaw (1995)
	F	Haul	26.00		97.00	23.00		40.21	Edgar and Shaw (1995)
	F	Haul	25.00		74.81	23.00		54.09	Edgar and Shaw (1995)
	F	Haul	44.00		85.74	19.00		5.27	Edgar and Shaw (1995)
	F	m ⁻²		5.07			2.63		Edgar and Shaw (1995)
	F	Net			374			742	Edgar and Shaw (1995)
	F	Net			585			190	Edgar and Shaw (1995)
	F	Net			294			184	Edgar and Shaw (1995)
F	aHaul	28.00		45.08	20.00		5.49	Jenkins and Wheatley (1998)	
F	aHaul	30.00		51.83	17.00		20.46	Jenkins and Wheatley (1998)	
F	aHaul	30.25		119.18	22.75		51.59	Jenkins and Sutherland (1997)	
F	aHaul	27.67		123.81	23.67		30.26	Jenkins and Sutherland (1997)	
F	m ⁻²		3.25			1.00		Levin (1991)	
F	m ⁻²	16.00		4.34	1.00		0.20	Arrivillaga and Baltz (1999)	
F	Sample	15.00		591.00	14.00		377.00	Bloomfield and Gillanders (2005)	
F	Sample	18.00		1046.84	18.00		214.45	Joseph et al. (2006)	

Ecosystem	Fauna	Units	Vegetated			Unvegetated			Reference
			S	Juvenile	Total	S	Juvenile	Total	
Seagrasses	F	Total	21.00		1908.00	13.00		84.00	Kanouse et al. (2006)
	F	Freq	22.00		37.00	20.00		34.00	Maiao (2007)
	F	m ⁻²	23.00		11.84	13.00		2.98	Rozas et al. (2012)
	F	Haul	5.00		59.25	3.00		18.25	Summerson and Peterson (1984)
	F	CPUe	18.00	0.85		18.00	0.30		Lazzari and Stone (2006)
	F	CPUe		6.55			23.36		Lazzari (2008)
	F	CPUe		42.73			6.63		Lazzari et al. (2003)
	D	Haul	26.00		43.00	29.00		6.90	Lazzari et al. (2003)
	D	m ⁻²	12.00		775.88	1.50		634.38	Robertson and Duke (1987)
	D	m ⁻²	4.20		35.55	0.90		1.55	Rozas and Minello (1998)
	D	m ⁻²	44.00		50.22	50.00		5.45	Minello (1999)
	D	Haul	4.00		176.42	3.33		59.17	Heck et al. (1989)
	D	Trawl	4.00			3.60			Lazzari and Tupper (2002)
	D	CPUe	5.50		92.60	5.00		54.65	Lazzari (2002)
	D	Total	4.00		847.00	3.00		566.00	Mattila et al. (1999)
	D	m ⁻²	0.67		4.77	0.63		7.41	Schmidt et al. (2011)
	D	m ⁻²	22.00		100.08	16.00		32.46	Sheridan (1992)
	D	Total	6.00		3518.00	6.00		1078.00	Sogard and Able (1991)
	D	m ⁻²	14.00		4.99	3.00		0.72	Arrivillaga and Baltz (1999)
	D	Sample	10.00		735.00	9.00		107.00	Bloomfield and Gillanders (2005)
	D	Sample	4.00		374.39	4.00		344.48	Joseph et al. (2006)
	D	Total	4.00		549.00	4.00		43.00	Kanouse et al. (2006)
	D	Freq	7.00		34.67	9.00		28.00	Maiao (2007)
	D	m ⁻²	4.00		13.20	0.00		0.00	Nakamura and Sano (2005)
	D	m ⁻²	20.00		47.40	11.00		5.29	Rozas et al. (2012)
	D	Haul	3.00		98.50	2.00		26.75	Summerson and Peterson (1984)
	D	Haul	11.00		13032.00	9.00		115.00	Heck and Orth (1980)
I	m ⁻²	19.00		22402.00	11.00		10538.00	Nakamura and Sano (2005)	
I	m ⁻²	160.00		2628.00	74.00		1039.00	Barnes and Barnes (2012)	
I	m ⁻²	7.48		35731.80	4.60		11640.00	Boström and Bonsdorff (1997)	
I	m ⁻²			13000000.00			12100000.00	Fonseca et al. (2011)	
I	0.01 m ⁻²			775.56			832.22	Hosack et al. (2006)	
I	m ⁻²	80.00		16108.37	38.00		3990.15	Lewis and Stoner (1983)	
I	m ⁻²	12.00		2693.00	16.00		1486.00	Mattila et al. (1999)	
I	m ⁻²	30.00		50875.00	22.00		10425.00	Reise (1978)	
I	m ⁻²	39.33		3184.67	24.00		1754.00	Stoner (1980)	

Ecosystem	Fauna	Units	Vegetated		Unvegetated		Reference
			S	Juvenile	S	Juvenile	
Seagrasses	I	m ²	12.70	1924.79	6.40	530.58	Summerson and Peterson (1984)
	I	m ²	41.33	1039.00	28.56	156.00	Poore (1982)
	I	Total	300.00		185.00		Edgar et al. (1994)
	I	Sample		33.40		16.80	Edgar et al. (1994)
	I	0.016 m ²	18.00	2887.50	9.00	356.50	Edgar (1990)
	I	0.016 m ²	18.00	1799.50	9.00	356.50	Edgar (1990)
	I	0.016 m ²	15.00	850.00	8.00	494.00	Edgar (1990)
	I	m ²	17.50	2618.60	8.00	476.00	Orth (1977)
	I	m ²	2.05	16.00	1.00	2.30	Castellanos and Rozas (2001)
Salt Marshes	F	m ²	4.50	16.73	2.50	5.78	Rozas and Minello (2006)
	F	m ²	0.95	1.50	1.66	7.54	Rozas and Zimmerman (2000)
	F	m ²	1.45	5.40	1.66	7.54	Rozas and Zimmerman (2000)
	F	m ²	1.55	14.15	1.66	7.54	Rozas and Zimmerman (2000)
	F	m ²	1.60	1.80	2.56	24.13	Rozas and Zimmerman (2000)
	F	m ²	2.03	8.78	2.56	24.13	Rozas and Zimmerman (2000)
	F	m ²	2.90	9.95	0.80	2.00	Rozas and Minello (1998)
	F	Total	28.00	222.00	13.00	66.00	Shervette and Gelwick (2008)
	F	Total	6.00	5259.00	8.00	3532.0	Valiñas et al. (2010)
	F	Total		2300.00		639.00	Valiñas et al. (2012)
	F	m ²	82.00	7.71	84.00	10.05	Minello (1999)
	F	m ²	73.00	14.89	84.00	10.05	Minello (1999)
	F	m ²	47.00	3.54	84.00	10.05	Minello (1999)
	F	Sample	1.00	1.00	14.00	377.00	Bloomfield and Gillanders (2005)
	F	m ²	19.00	8.89	13.00	2.98	Rozas et al. (2012)
	F	Total	28.00	100.60	12.00	98.60	Shervette and Gelwick (2008)
	D	m ²	4.85	200.65	0.90	1.55	Rozas and Minello (1998)
	D	m ²	49.00	83.54	50.00	5.45	Minello (1999)
	D	m ²	39.00	36.04	50.00	5.45	Minello (1999)
	D	m ²	23.00	15.73	50.00	5.45	Minello (1999)
D	m ²	1.25	7.80	0.95	0.90	Castellanos and Rozas (2001)	
D	m ²	5.25	46.99	2.50	1.33	Rozas and Minello (2006)	
D	m ²	3.30	12.05	1.54	4.94	Rozas and Zimmerman (2000)	
D	m ²	3.75	32.85	1.54	4.94	Rozas and Zimmerman (2000)	
D	m ²	2.88	44.18	1.54	4.94	Rozas and Zimmerman (2000)	
D	m ²	6.10	61.65	2.04	6.23	Rozas and Zimmerman (2000)	

Ecosystem	Fauna	Units	Vegetated		Unvegetated		Reference		
			S	Juvenile	Total	S		Juvenile	Total
Salt Marshes	D	m ²	5.68		84.93	2.04		6.23	Rozas and Zimmerman (2000)
	D	Total	19.00		1383.00	11.00		86.00	Shervette and Gelwick (2008)
	D	Sample	1.00		28.00	9.00		107.00	Bloomfield and Gillanders (2005)
	D	m ²	19.00		25.59	11.00		5.29	Rozas et al. (2012)
	D	Total	19.00		200.00	14.00		199.90	Shervette and Gelwick (2008)
	I	Total	13.00		1824.00	10.00		272.00	Hedge and Kriwoken (2000)
	I	Total	16.00		1620.00	10.00		272.00	Hedge and Kriwoken (2000)
	I	Total	98.00		22929.00	76.00		5386.00	Lana and Guiss (1991)
	I	Core	7.50		183.33	17.50		216.67	Levin et al. (1998)
	I	0.02 m ²	17.00		17.54	36.00		26.50	Netto and Lana (1999)
	I	m ²			14255.56			107988.89	Valiñas et al. (2012)
	I	m ²			261200.00			1179000.00	Gregg and Fleeger (1998)
	Mangroves	F	aHaul		13.67		3.17	13.50	
F		Total	58.00	877.80	1540.00	39.00	1669.53	2929.00	Ikejima et al. (2003)
F		100 m ²	21.00	163.20		5.00	0.80		Nagelkerken and Van Der Velde (2002)
F		100 m ²	18.00			3.00			Nagelkerken and Van Der Velde (2002)
F		100 m ²	26.00		199.50	8.00		1.70	Nagelkerken and Van Der Velde (2002)
F		m ²	14.29		210.00	14.29		90.00	Nagelkerken et al. (2000)
F		m ²	8.57	190.00		7.14	60.00		Nagelkerken et al. (2000)
F		100 m ²	16.00	358.44		18.00	280.63		Nagelkerken et al. (2000)
F		Total	7.83		361.67	8.83		694.83	Ooi and Chong (2011)
F		Haul	38.00		269.50	19.00		10.54	Payne and Gillanders (2009)
F		Haul	73.00		135.80	46.00		26.70	Robertson and Duke (1987)
F		m ²	5.00		6.92	11.00		2.54	Sedberry and Carter (1993)
F		Total	58.00		900.00	32.00		170.00	Sheridan (1992)
F		Total	3.00	149.14		2.00	4.73		Shibuno et al. (2008)
F		100 m ²	18.00		1.58	13.00		2.22	Shibuno et al. (2008)
F		Total	20.00		1458.75	20.50		594.00	Xavier et al. (2012)
F		Sample	8.00		257.00	14.00		377.00	Hindell and Jenkins (2004)
D		Haul	6.25		529.30	1.50		634.38	Bloomfield and Gillanders (2005)
D		m ²	9.00		6.31	16.00		32.46	Robertson and Duke (1987)
D		Sample	6.00		423.00	9.00		107.00	Sheridan (1992)
I		6.61 cm ²	12.00		8.65	19.50		12.00	Bloomfield and Gillanders (2005)
I		m ²	9.00		2076.00	9.00		612.50	Dittmann (2001)
I		m ²	48.00		148.95	8.00		47.00	Schrijvers et al. (1995)
								Sasekumar (1974)	

Ecosystem	Fauna	Units	Vegetated		Unvegetated		Reference
			S	Juvenile	S	Juvenile	
Macroalgae	F	Site	13.89	153.29	13.64	153.29	Anderson and Millar (2004)
	F	40 m ⁻²	17.50	2250.00	9.00	1840.91	Guidetti (2000)
	F	Trawl	7.00		2.40		Lazzari and Tupper (2002)
	F	m ⁻²	3.03	1.65	0.05	0.37	Schmidt et al. (2011)
	F	aHaul	31.00	19.42	20.00	5.49	Jenkins and Wheatley (1998)
	F	aHaul	27.00	35.38	17.00	20.46	Jenkins and Wheatley (1998)
	F	CPUE	16.00	0.62	18.00	0.30	Lazzari and Stone (2006)
	F	CPUE		12.99		23.36	Lazzari (2008)
	F	CPUE	16.00	7.13	29.00	6.63	Lazzari et al. (2003)
	F	500 m ⁻²	7.20	18.12	11.00	40.55	Choat and Schiel (1982)
	F	500 m ⁻²	5.60	159.88	6.00	57.73	Choat and Schiel (1982)
	D	Trawl	5		3.6		Lazzari and Tupper (2002)
	D	m ⁻²	0.27	1.01	0.91	0.28	Schmidt et al. (2011)
				1.22		5.73	

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