ECOLOGICAL INTERACTIONS AND GEOLOGICAL IMPLICATIONS OF FORAMINIFERA AND ASSOCIATED MEIOFAUNA IN TEMPERATE SALT MARSHES OF EASTERN CANADA

by

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This is for you, Dave.
Without you, I would have never discovered
the treasures in the mud.

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ABSTRACT

Salt marshes are among the world's most productive and valuable ecosystems, where most primary production terminates in detritus that supports abundant foraminifera. Salt marsh foraminifera are indicators of modern wetland health and used for sea-level analysis in the geological record. However, few studies have examined these foraminifera as living communities, including their role with meiofauna ("small food web") in energy transfer to macrofauna. Better understanding would also aid in selection of foraminifera species for high-resolution paleo-sea-level and systems tract analyses. Biotic controls on the distribution and assemblages of foraminifera and meiofauna were studied for two cool-temperate salt marshes in Nova Scotia: mature, mesotidal Chezzetcook, and young, macrotidal Windsor. A laboratory mesocosm ran for two years and successfully represented Chezzetcook marsh, allowing year-round sampling. Foraminifera were more abundant than at comparable field sites, and vertical zones linked to tidal inundation accounted for the assemblage differences, with modulation from small-scale biotic interactions. Structural binary food webs constructed for each marsh had almost 300 taxa and 6000 feeding links in high-resolution webs. Low-resolution webs overemphasise the importance of vertebrates and undervalue the "small food web". Overall, taxonomic resolution is a primary factor in interpreting salt-marsh trophic structure, and analysis should discriminate between high–mid and low marsh–mudflat zones. Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) validated binary food web data and showed few significant differences in isotopic signatures and food-web properties between the marshes, despite large differences in their tidal range and geological age. The complexity of detritus-based food chains requires caution when using stable isotopes to interpret paleoenvironments by small isotope excursions. *In vivo* cultures and transmission electron microscopy of common agglutinated foraminifera confirm that these species are detritus-gathering, saprophagous bacterivores which outcompete co-occurring meiofauna in the middle–high marsh zones. Adhesion and cryptic mobility of these taxa may determine their value as precise sea level tracers and reduce post-mortem disturbance. Overall, the thesis results show that reworking of detritus in the "small food web" is a vital basic function of the ecosystem, supporting secondary productivity, biomass transfer, carbon storage, and confirming the value of agglutinated foraminifera as sensitive paleo-sea-level markers.

LIST OF ABBREVIATIONS AND SYMBOLS USED

ANOSIM	Analysis of similarity
ASL	Above sea level
C	Carbon
N	Nitrogen
CV	Coefficient of variation
DOM	Dissolved organic matter
LOI	Loss on ignition
MDS	Multidimensional scaling
MSL	Mean sea level
nMDS	Non-metric multidimensional scaling
NPP	Non-pollen palynomorph
OC	Organic carbon
OM	Organic matter
POM	Particulate organic matter
ppt	Parts per thousand
psu	Practical salinity unity
RSL	Relative sea level
SD	Standard deviation
SIA	Stable isotope analysis
SOM	Sediment organic matter
SST	Sea surface temperature
TEM	Transmission electron microscopy
‰	Parts per mil (stable isotopes)
° C	Degrees Celsius
$\delta^{13}C$	Delta Carbon-13
$\delta^{15}N$	Delta Nitrogen-15
μm	Micrometre

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Post-script: To all of those who have asked (even though you were not supposed to ask), "*have you finished your thesis*?" well, here you go. Happy reading!

CHAPTER 1: INTRODUCTION

1.1 General Introduction

Tidal salt marshes play a vital role in global carbon cycling, protection of shoreline erosion, and in sustaining a spectrum of wildlife that depends on high productivity of the interface between land and ocean for their survival (Mitsch and Gosselink, 1993, 2008; Bridgham et al. 2006; Doody, 2007; Costanza et al., 2011; Shepard et al., 2011; Kelleway et al., 2017). These marshes are low-lying, low-energy intertidal areas largely covered by halophytic grasses and succulent herbs or shrubs that are submerged by sea water regularly and may receive variable amounts of freshwater from rivers entering drowned valley systems (Adam, 2002; Scott et al., 2014). Despite the importance of these ecological powerhouses, there is still little knowledge about the ecological and biological interactions of the protozoan foraminifera and invertebrate meiofauna that dominate the sediments (Chandler, 1989; Schratzberger and Ingels, 2017). These faunal groups are often overlooked in ecological studies of modern salt marshes, despite dependence on foraminiferal fossil assemblages as records of paleoenvironments such as paleo-sea-levels (e.g., Scott and Medioli, 1980a; Kemp et al., 2013) and paleoearthquakes (e.g., Shennan et al., 1999; Hawkes et al., 2010; Hayward et al., 2015). Furthermore, past studies of salt marsh ecology have focused largely on warmer region USA and west European marshes (e.g., Teal, 1962; Pomeroy and Wiegert, 1981; Adam, 1993) rather than cool temperate salt marshes such as those of New England (Bertness, 1991), and in Atlantic Canada where seminal studies (Scott and Medioli, 1980a,b) were made of salt marsh foraminifera as ultra-sensitive markers of relative sea level change (RSL).

Salt marshes occupy the space between slightly lower than mean sea level (MSL) and mean higher high water (MHHW) (Chapman, 1960; Redfield, 1972; Scott et al., 2014). They characteristically display a vertical zonation controlled primarily by duration of tidal inundation (Scott et al., 2014). The zones are commonly site-specific depending on tidal range, climate, marsh maturity, and sedimentation rate, but regionally they are dominated by halophytic grass species, principally *Spartina* in non-polar, western-Atlantic regions, that tolerate a specific range of salinity, and water-logged, oxygen-poor soils (Roberts and Roberson, 1986; Pennings and Bertness, 2001; Scott et al., 2014). In general, the higher above MSL the area is (for example, middle and high zones of the marsh), the greater the number of species as there is a greater pool of species that are less tolerant of fully saline water. These differences in tolerance result in visible floral zones that range from microphytobenthos and filamentous algal biofilms in the mudflats to predominantly facultative halophytic terrestrial herbs and shrubs in the high marsh border (Chapman, 1960; Redfield, 1972; Mitsch and Gosselink, 1993; Scott et al., 2014). In terms of fauna, salt marshes are one of the few ecosystems that harbour terrestrial and marine animals (Pennings and Bertness, 2001; Silliman, 2014). Although latitude and climate influence salt marsh animal assemblages and the role of tall grasses, similar functional groups are found in all coastal wetlands.

More ecosystem services are provided by coastal wetlands than any other coastal ecosystem (Gedan et al., 2009; Chmura et al., 2012; Kelleway et al., 2017). Salt marshes are among the world's most productive and valuable ecosystems providing important fisheries, nursery grounds and refuges for birds and fishes, and protection for coastal infrastructure during ocean storms and tsunamis (Adam, 2002; Gedan et al., 2009;

Pennings, 2012). Although the importance of marshes for humans is commonly emphasized, there has been a recent paradigm shift towards their ecological importance (as stated in Gedan et al., 2009). For example, Costanza et al. (2017) argued that there is a greater need to shift to a "whole system" approach when examining ecosystem services.

In a recent study, more than 350,000 salt marshes were counted in 99 countries, totaling 5.5 million hectares, and in 2002, Canada had more than 10,000 salt marshes covering over 111,000 hectares (Mcowen et al., 2017). However, salt marshes are under threat, with 25 – 50% loss by area globally since the 1800s (Adam, 2002; Mcowen et al., 2017). Nova Scotia has lost 65% of its salt marshes since the 1600s, mainly due to European settlement on the Bay of Fundy where less than 150 km^2 remains of an estimated 400 km^2 (Hanson and Calkins, 1996). This high rate of loss in the understudied cool-temperate climate region of Nova Scotia, where tides range from low-mesotidal on the Atlantic Coast to the world's highest in the Bay of Fundy, are additional incentives for future studies.

The loss of salt marsh results in reduction of important sites for carbon storage. A long-held paradigm is that salt marshes are major carbon exporters to adjacent estuarine communities (Teal, 1962), especially in terms of dissolved inorganic carbon (DIC; Wang et al., 2016). The statements by Teal (1962), who maintains 45% of grass production is immediately exported to nearshore communities before consumption, have been under scrutiny for decades (Haines, 1977; Nixon, 1980). It has been recently calculated that 70% of marsh net primary productivity (NPP) is directly respired, 20% NPP is exported as dissolved or particulate organic carbon, and 10% NPP is stored in the soil as "blue carbon" (Wang et al., 2016). Though 10% is fairly low, carbon stored in salt marshes is

of key importance (Chmura et al., 2003; Mcleod et al., 2011). Global estimates show that salt marsh carbon storage (<0.5 m depth) is approximately 430 Tg C, and there is a global rate of carbon sequestration of 210 ±2 g m^{-2} yr^{-1} (Chmura et al., 2003). Additionally, carbon turnover rate is slower than in terrestrial systems (hundreds to thousands of years, versus less than 100 years), thus further acting as a major buffer against anthropogenic increase in atmospheric CO_2 (Pendleton et al., 2012; Kelleway et al., 2017). Salt marshes sequester carbon at 4–5x greater rates than boreal wetlands (Mitsch et al., 2013) due to their faster vertical accretion and greater ability to trap sediments and carbon (Mcleod et al., 2011; Kelleway et al., 2017).

Salt marshes also hold high-resolution paleoenvironmental records of sea-level rise (Scott et al., 1980a; Kemp et al., 2013, 2017). The integrated records of relative sea-level rise in salt marsh sediments provide stronger, less "noisy" evidence of global warming than do sea-surface temperature instrumental records (Cheng et al., 2017). Another paleoenvironmental importance of salt marshes is that sediments record earthquake precursor events which are especially important for areas without seismic instrumentation (Hawkes et al., 2005; Scott et al., 2014 and references therein).

The importance of several second-order changes on salt marshes as productive biological and ecological communities, however, has received little attention (Gedan et al., 2009). In particular, little conclusive information is available concerning the important small-scale interactions in the sediments at lower trophic levels (Lipps and Valentine, 1970; Kuipers et al., 1981; Kneib, 1984; Cohen et al., 2003; Woodward et al., 2005; Schmid-Araya et al., 2016; Schratzberger and Ingels, 2017). These interactions are key to the post-mortem processing of grasses with their immense primary production:

after death, >90% of the grass enters a relatively unknown decompositional and detritivorous system in the salt marsh surface sediment (as initially outlined by Teal (1962); Figure 1.1).

My research addresses the unknowns on how cool temperate salt marshes function at the base of the food web, specifically, what are the detailed roles of foraminifera and meiofauna to this detritivorous system? Answers to these questions will assist in understanding energy flow from the highly productive grasses, which survive largely unconsumed directly in cool temperate regions, to the larger invertebrates, fishes and birds (Teal, 1962; Haines, 1977; Kuipers et al., 1981; Kreeger and Newell, 2000). The roles of the main primary food sources in the ecosystem (grasses vs. microphytobenthos and algae) have been under debate for many years (Haines, 1977; Galvan et al., 2008) and are not addressed here since both sources enter the detrital sediment web, regardless of individual contributions to productivity.

The organic detritus on and in the surface sediment in salt marshes is processed principally by bacteria and fungi, which convert the decaying plant matter into a form that can be assimilated by small invertebrate and protozoan detritivores, as well as larger deposit- and filter-feeders (Teal, 1962; Kuipers et al., 1981; Kreeger and Newell, 2000). Energy is thus transferred from micro- to macrofaunal levels of the food web, and tiny organisms play a vital role in the energy flow of a salt marsh, consuming up to 80% of all organic material available in a tidal flat of the Wadden Sea (the "small food web" of Kuipers et al., 1981). Because of their high densities in the sediment, the total meiofauna, which comprises marsh foraminifera and invertebrates in the 63 – 500 μm size range, may yield larger production numbers than microbenthic animals (e.g., Lipps, 1983;

Moodley et al., 2008). Meiofauna consume a wide spectrum of food sources (bacteria, detritus, microalgae, other metazoans), and can provide up to 80% of the diet of larger consumers, making them a vital link from the microbiota up the food chain (Lipps and Valentine, 1970; Buzas and Carle, 1979; Gooday et al., 1992; Moodley et al., 2008; Schratzberger and Ingels, 2017). Although the meiofaunal biomass may be less than 10% of macrofaunal biomass at any given time, the meiofauna account for over 1.5x the throughput and 2x the production of macrofauna (in mudflats, Leguerrier et al., 2003). However, as seen in Figure 1.1, meiofauna have rarely been defined in food-web studies and are grouped as "decomposers" or "detrital" entities, despite their significance for energy flow in the system and uncertainties regarding the relative importance of individual taxonomic groups, from foraminifera to flatworms. Exclusion of meiofauna biases interpretations of ecosystem energy flow and dynamics in stream systems, and can lead to erroneous interpretations of food web patterns (Schmid-Araya et al., 2002). Similar misinterpretations of connectance occur in salt marshes.

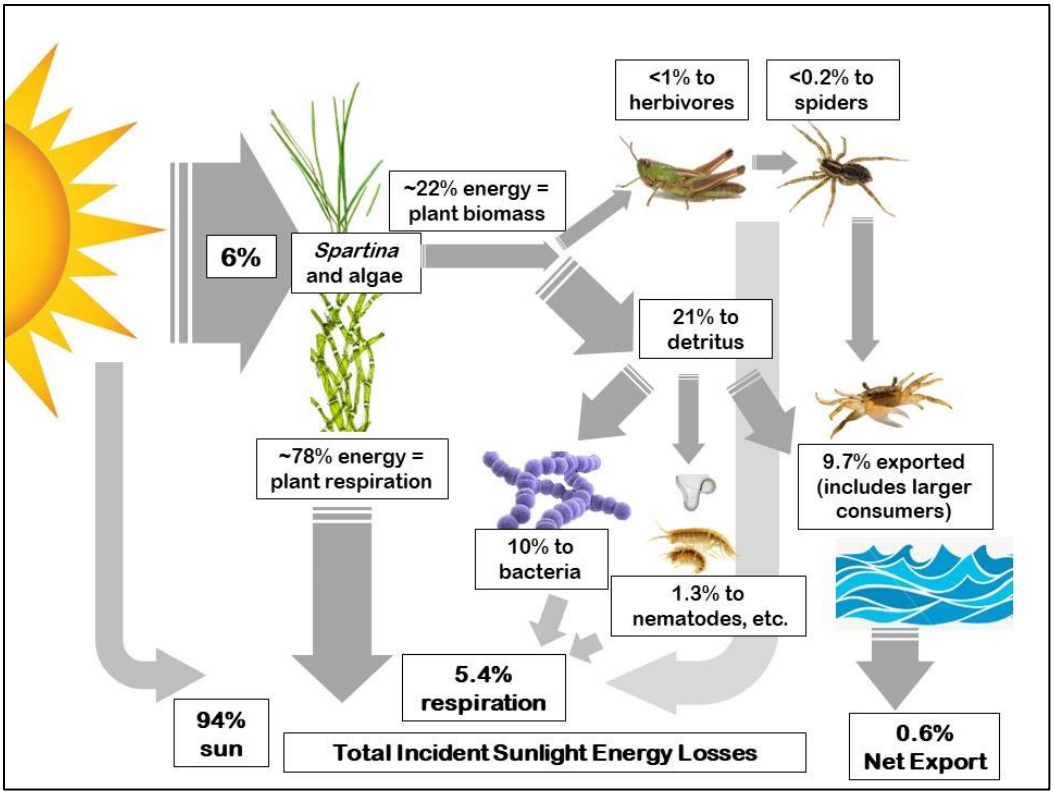

Figure 1.1. Energy-flow diagram in a Georgia, USA, salt marsh modified from Teal (1962) and Scott et al. (2014). Entering as light input, only 6% of this energy enters the primary production chain (as 93% is used in high primary production, i.e., photosynthesis). Of the *Spartina* production, almost 80% is lost as respiration, with only 22% making it to the consumers. Most of this 22% enters a detrital web, with less than 1% being directly consumed by herbivores. Of the 21% to detritus, almost 60% is respired by bacteria alone. Only 0.6% of the original light energy is exported from the salt marsh food chain to the coastal ocean.

Foraminifera are an abundant, therefore important, component of the salt-marsh meiofauna. They are unicellular, often testate protists found in all marine and most brackish coastal environments, with worldwide occurrences that date to the Cambrian (Buzas and Culver, 1991). This long geologic history, with high evolutionary rates, good preservation potential (agglutinated species), and ease of collection and storage makes foraminifera ideal environmental bioindicators (Barbieri et al., 2006). The importance of benthic salt marsh foraminifera for reconstructing coastal paleoenvironments and sea level (Scott et al., 2001, 2014) was first determined from high-resolution studies in

Chezzetcook Inlet, Nova Scotia (Scott and Medioli, 1980a, b). Their vertical distribution in a tidal marsh corresponds to elevation above sea level, allowing a paleo-sea level estimate with an accuracy of ± 5 cm (Scott and Medioli, 1980a). Most studies of foraminifera focus on their taxonomy, assemblages and distribution (Arnold, 1974; Gooday et al., 1992) and the validity of environmental interpretations based on relating generalized modern distributions to abiotic conditions remain unverified until the biological factors that influence foraminifera are understood, including their complex feeding habits (Myers, 1943; Arnold, 1974; Gooday et al., 1992; Goldstein, 1999; Mojtahid et al., 2011). Few studies have looked at meiofaunal and foraminiferal interactions (e.g., Dupuy et al., 2010) and, despite an "urgent need for future studies" on this theme (Cesbron et al., 2016), no major study has emerged since Chandler (1989). In that 1989 study, foraminifera, harpacticoid copepods, and nematodes were 95% of the meiofauna and consumed enough detritus and bacteria to void the sediment of nutrients, emphasizing their ecological importance (Chandler, 1989). This thesis addresses the important knowledge gap only ever examined by Chandler.

1.2 Study location and evolution of thesis

Two salt marsh systems in Nova Scotia, Canada (Figure 1.2) were selected for study. Chezzetcook Inlet was chosen on account of the long baseline of abiotic data collection and high-resolution records of foraminiferal assemblages and their Holocene history (Scott et al., 1980a). Chezzetcook is a mature (5000 years) salt marsh on the Atlantic Coast, and has a surface elevation of approximately 1 m ASL, and slow modern sedimentation rate. Here we define it as mesotidal, although it would be classified as low-

mesotidal following Hayes, 1975, 1979. My second system is the Windsor marsh, a young (<50 years), macrotidal salt marsh in the Minas Basin of the Bay of Fundy. This marsh exhibits high sedimentation rates due to creation of the Windsor Causeway in 1968-1970 (Van Proosdij et al. 2009). It has a surface elevation of 5 – 6 m ASL.

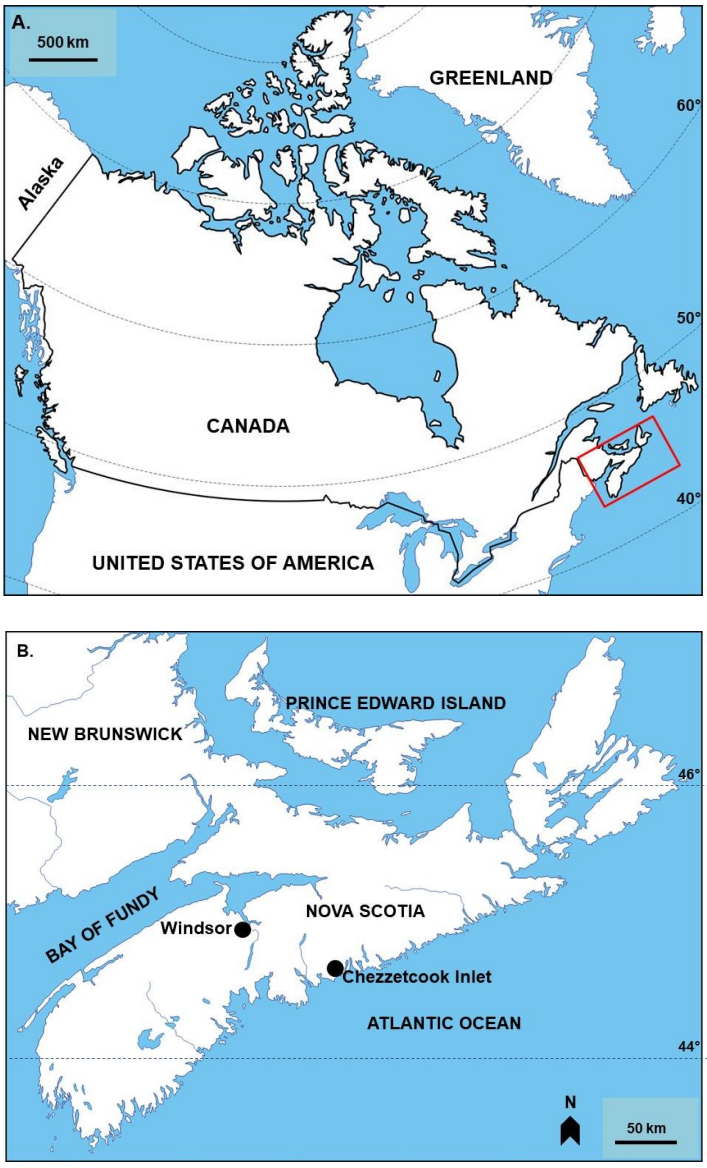

Figure 1.2. (A) Map of Canada, with (B) showing enlarged red box. Locations of Windsor and Chezzetcook Inlet marshes in Nova Scotia shown in (B).

The original intention was to examine benthic salt marsh foraminifera as living communities, in order to assist high-resolution sea-level studies and environmental monitoring. However, it became increasingly apparent that a much broader approach was needed to explore effectively the sediment ecological dynamics of foraminifera and biotic controls on their distribution and assemblages. In addition to foraminifera, the marsh "sediment" includes associated meiofauna and phytodetritus, which need to be included in any realistic analysis of habitat, connectivity and energy-flow. Remarkably, after decades of detailed studies of marsh plants, macrofauna, and standing stocks of foraminifera, the "sediment" is still considered a uniform depositional compartment by many researchers, although it is clear that vegetation distribution and height plays a large role in trapping of suspended sediment and the fauna it supports (Stumpf, 1983; Chen et al., 2016). In salt marsh sediments, the high abundance of foraminifera implies that they play a large and probably fundamental role in the conversion of phytodetrital energy for the salt marsh food web, but this idea has not been rigorously tested in a higher-latitude cool temperate marsh with harsh winter conditions, as most studies have occurred south of Nova Scotia (e.g., California, USA: Bradshaw, 1968, and Phleger, 1970; Florida, USA: Buzas, 1978, and Weinmann and Goldstein, 2016).

This thesis is divided into four independent but related topics concerning salt marsh ecology and foraminifera. These are: (1) the development and validation of a laboratory mesocosm salt marsh to examine seasonal-scale trends in community composition of foraminifera, replicating Chezzetcook Inlet assemblages and distributions; (2) development of structural binary food webs for Chezzetcook Inlet and Windsor Causeway salt marshes at different levels of taxonomic resolution and spatial

distinction; (3) validation of these food webs using $\delta^{13}C$ vs $\delta^{15}N$ stable isotope analysis; and (4) feeding and biomass analysis pertaining to living benthic agglutinated salt marsh foraminifera. Collectively, the four topics, which are outlined in more detail in the next section, provide the first comprehensive biological analysis of foraminifera and associated meiofauna in a cool temperate salt marsh in an attempt to better understand the "small food web". Determining the factors that control the dynamics of the often mentioned, but rarely studied, meiofaunal populations will increase our knowledge of their ecological niches and their roles in the temperate salt marsh food web, with application to current, future, and past environmental changes.

1.3 Chapter outlines and objectives

Chapters 2 through 5 are written as stand-alone papers, for submission to peer-reviewed journals. Because of this format, some aspects are repeated in each chapter.

1.3.1 Chapter 2: *Development of a salt marsh mesocosm to study spatio-temporal dynamics of benthic foraminifera*

Abiotic factors that govern the assemblages and distributions of key indicator salt marsh foraminifera are well-understood (Barbieri et al., 2006, Strachan et al., 2016). Chezzetcook Inlet provides decades of background research on assemblages linked to abiotic factors, but little is known about biotic controls on foraminiferal distribution. Cesbron et al. (2016) pointed out the urgent need to understand biotic controls on living foraminiferal populations, and Kemp et al. (2017) stressed that ecological insights into salt-marsh foraminifera are needed to improve the quality of foraminifera-based reconstructions of relative sea-level.

An important step to addressing knowledge gaps of biotic controls involves designing and validating a representative laboratory mesocosm. Chezzetcook Inlet is in a cool, temperate climate zone prone to prolonged winter freezing and ice conditions, which precludes regular year-round monitoring. Mesocosms assist in addressing complex problems beyond the scope of small-scale laboratory studies but too difficult for *in situ* field analysis (Pennington et al., 2004). I developed a mesocosm salt marsh in the Aquatron Facility at Dalhousie University to monitor foraminiferal assemblages and distributions with greater regularity and under more rigorous controls than field sampling allows.

The chapter addresses the knowledge gaps in three ways: (1) designing a fully-functioning salt marsh mesocosm for a cool-temperate ecosystem in a laboratory setting to allow year-round access for sampling of foraminifera and associated meiofauna; 2) rigorously testing if the laboratory mesocosm shows similar foraminiferal assemblage patterns to field samples; (3) assuming a successful outcome of the laboratory mesocosm experiment, using a mesocosm to monitor meiofaunal biotic effects (predation and competition) on foraminiferal assemblages.

Jen Frail-Gauthier is the primary author of the chapter. Other contributions are from David Scott for experimental design. Frail-Gauthier collected and analyzed all samples, carried out statistical analyses, and created all figures. Supervisory committee members provided manuscript advice and helped address key concerns and questions.

1.3.2 Chapter 3: *Taxonomic resolution and tidal gradients in food webs for two temperate salt marshes: how much detail is enough?*

Food-web analysis is a robust and informative way to address structural and functional differences in ecological communities. The analysis can determine how community structure changes along geographical and environmental gradients and in response to anthropogenic disturbance (e.g., Vinagre and Costa, 2014; Tao et al., 2015; Wood et al., 2015). Studies in salt marsh ecology commonly consider the ecosystem as a whole. They need also to examine separately the key tidal zones from mudflats to the high marsh, each of which has different primary producers and a gradation of marine to terrestrial consumers (Vinagre and Costa, 2014).

The chapter is the first attempt at creating salt marsh food webs that include the meiofaunal species which comprise a large part of the benthic sediment and process most of the basal marsh production (see Coull, 1973). Foraminifera exploit phytoplankton or detritus, whichever is in highest abundance (Lesen, 2005). They form a vital trophic link in marine communities and are known prey of fish, most meiofauna, and small macrofauna (Lipps, 1983; Culver and Lipps, 2003).

The chapter compares two different salt marshes in Nova Scotia (Windsor and Chezzetcook, Figure 1.2B) by using food webs to explore differences in ecological structure and function. We address (1) the amount of taxonomic detail needed to capture ecosystem structure, that is, how important taxonomic resolution of foraminifera and meiofauna is to the food web resolution; (2) the importance of spatial gradients for whole marshes and their separate tidal zones; and (3) differences in food webs for the young, macrotidal marsh at Windsor Causeway in the Bay of Fundy, and for the old, mesotidal

marsh at Chezzetcook Inlet on the Atlantic Coast. This is also, to our knowledge, the first high-resolution species list created for either of these two marsh systems, and one of the first to provide this level of detail anywhere, except for the detailed parasite web of Lafferty et al. (2006) in Carpinteria salt marsh, California. The modern food-webs can be compared to fossil records in well-preserved marsh sequences from Cretaceous through Tertiary time.

Jen Frail-Gauthier and Tamara Romanuk designed the study. Frail-Gauthier and undergraduate students did sample collections, and Frail-Gauthier verified species identifications. Frail-Gauthier created all binary food webs and analyzed them statistically. Frail-Gauthier wrote the manuscript, with reviews from supervisory committee members. Statistical advice for statistical software PRIMER was provided by Dr. Vladimir Kostylev from the Bedford Institute of Oceanography.

1.3.3 Chapter 4: *Use of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes within and between two temperate salt marshes in Atlantic Canada to examine patterns of food web structure and function*

Binary food webs include overall predator-prey dynamics but cannot quantify or capture this information in the sediment record. Here, we tackle this problem by examining stable isotopes (SI) for the three primary food sources (vascular plants, algae, sediment organic matter) and for small consumers (mostly foraminifera, meiofauna, and small invertebrates) of the two temperate salt marshes in Nova Scotia, analysing mudflat to high marsh zones. These SI analyses are a useful tool for investigating trophic interactions of animals and their food sources (Peterson and Fry, 1987; Post, 2002; Claudino et al., 2013), tracing carbon sources (Canuel et al., 1995; Chmura and Aharon,

1995; Connolly et al., 2005) and determining organic matter (OM) sources in heterotrophic organisms and sediments (Coffin and Cifuentes, 1999; Goñi and Thomas, 2000). Stable isotope data derived from fossil plant and animal material are used to infer paleoenvironments and to correlate geological records. They also can clarify the detritus-based food web structure set out in Chapter 3.

Stable isotope analysis addresses long-term feeding patterns and flow of organic matter through the food web. In contrast, feeding studies and gut content analyses give a snapshot of consumer feeding relationships, especially in systems dominated by omnivorous and detritivorous lower-level consumers (Schmid-Araya et al., 2016). The SI analysis contributes to an ongoing debate (Park et al., 2015) about the trophic role of basal sources and consumers and how their energy production moves to the larger fauna in the ecosystem. The high-resolution study in this chapter explores constraints on using SI data for paleoenvironmental interpretation in fossil records.

The main SI-related topics examined for the two salt marshes are (1) the patterns and magnitudes of variability in the C and N stable-isotopic composition of the plants, organic matter (OM) sources, and meiofaunal to small macrofaunal communities, collected from all habitat types, and (2) the relative importance of the "small food web" components across salt marshes with different tidal regimes and across tidal zones.

Jen Frail-Gauthier and Tamara Romanuk designed the study. Frail-Gauthier and BSc Honours student Emily Baker collected, analysed and identified all organisms and prepared samples for Stable Isotope Analysis. Frail-Gauthier and Baker analysed data and

Frail-Gauthier statistically and graphically separated the data. Frail-Gauthier wrote the text, with reviews from supervisory committee members.

1.3.4 Chapter 5: *Mesocosm and microcosm experiments on the feeding of temperate salt marsh foraminifera*

Foraminifera are important biostratigraphic tools and key proxies for interpreting the paleoecology of ancient seas and fluctuations in relative sea level (RSL). Many basic questions about feeding, growth and reproduction remain unresolved since the earlier work of Arnold (1974), particularly for agglutinated marsh species and other benthic foraminifera (Kitazato and Bernhard, 2014). Most studies examine environmental variables, which are considered to be the key controls on the distribution of foraminifera, but ecological variables may drive the species gradients, assemblages and distributions (Kemp et al., 2017). For example, the notoriously high patchiness of foraminifera (Lee, 1974) may be governed by food availability, feeding methods, competition with meiofauna, commonly-cited abiotic factors (salinity, elevation; see Chapter 2), or a combination of these. Previous conclusions on behavioural, feeding, and biotic interactions of "salt marsh benthic foraminifera" apply to a restricted part of the total assemblage (mostly calcareous mudflat species, e.g., *Ammonia*, Pascal et al., 2008). They fail to consider most of the agglutinated species that are widespread across the salt marsh, often in high abundances.

Chapter 5 considers three topics related to agglutinated salt marsh foraminiferal biology: (1) identifying inexpensive, low-maintenance, non-terminal methods for distinguishing living organisms in a mesocosm culture setting; (2) using Transmission Electron Microscopy (TEM) to investigate feeding modes in agglutinated foraminifera, to

elucidate and validate conclusions in Chapters 3 and 4; and (3) exploring feeding habits of salt marsh foraminifera and their overall importance, in terms of biomass and abundance in the salt marsh sediments. This set of observations will contribute to a fuller understanding of agglutinated and key calcareous salt marsh foraminiferal responses within their ecological niches, as well as their response to environmental changes affecting their food sources and elevational distribution. The results also address the contribution of meiofaunal biomass to carbon budgets and sediment energy fluxes.

This study was developed by Jen Frail-Gauthier, with initial guidance and advice from David Scott. Frail-Gauthier created culturing and feeding experiments and examined TEM images. Alastair Simpson supervised the TEM preparation. Frail-Gauthier analysed data and wrote the text. Peta Mudie provided light micrographs and interpretations of foraminifera form and feeding behaviour, and committee members provided valuable insights and comments to the structure of the chapter.

1.3.5 Chapter 6: *Conclusions* provides a synthesis of the findings of Chapters 2 – 5, addresses caveats of the studies and raises key points for future research.

1.4 Overview

A key objective of this thesis is to expand knowledge of trophic interactions that influence the spatial and temporal population dynamics of cool-temperate salt marsh foraminifera. Understanding these dynamics is a pre-requisite for future development after the pioneering Quaternary paleo-sea level studies (Scott et al., 2001 and references therein). I tackled these unknowns for modern environments using a variety of interdisciplinary methods which bring together geological and biological information that

is often disconnected in studies of salt marshes and foraminifera. Comprehensively, these chapters examine for the first time the biological dynamics of salt marsh foraminifera, and fill a major, long-term data gap in the field.

CHAPTER 2: DEVELOPMENT OF A SALT MARSH MESOCOSM TO STUDY SPATIO-TEMPORAL DYNAMICS OF BENTHIC FORAMINIFERA

2.0 Abstract:

Abiotic controls on salt marsh foraminifera assemblages are well-understood, especially for paleoenvironmental interpretations, but few studies have addressed the biology of foraminifera and associated meiofauna. To address this, we designed a laboratory saltmarsh mesocosm to allow frequent sampling of living salt marsh foraminifera, replicating high- and low-salinity marsh areas of Chezzetcook Inlet, eastern Canada, in a temperate region with three months of winter freezing. To make a rigorous assessment of how well the mesocosm replicated the natural salt marsh, the mesocosm foraminiferal assemblages and associated meiofauna (63–500 μm fraction) were compared statistically with field datasets collected in 1976 to 1978. Total (living + dead) foraminiferal assemblages from four tidal mesocosm zones show that the foraminiferal populations are more abundant than in comparable field sites, but species diversity is similar. Overall, few differences were noted between 1970s field data and the frequently sampled laboratory marsh samples over two years. Consistently higher mesocosm total abundances may reflect the absence of winter ice simulation. Other differences may be related to limited laboratory simulation of salinity fluctuations in the field where stream flow is variable and precipitation adds another variable. Within these environmental limitations, the mesocosm successfully replicated zonal distributions of foraminifera and relative abundances of dominant species, and the laboratory system provides a reliable platform for future experiments on faunal responses to specific changes, including temperature and nutrient enrichment.

2.1 Introduction

2.1.1 Salt marsh laboratory mesocosms

Tidal salt marshes have a global occurrence and have important environmental value. There is a focus on the tide-controlled zonation of dominant species that include grasses, invertebrates, and foraminifera (Scott et al., 2014). Salt marshes are studied for investigating changes in biodiversity (including invasive species), nutrient dynamics, carbon cycling, and potential for buffering shoreline erosion. Soft waterlogged mudflat substrates are only accessible at low tide, and boreal and Arctic marshes are remote and commonly frozen for several months a year, precluding regular and frequent sampling (Scott et al., 2014).

To compensate for these difficulties in accessibility, I designed and constructed a laboratory salt-marsh mesocosm to explore biological interactions and the role of physical parameters, with applications to salt-marsh restoration, climate change, and sea-level rise. Self-contained mesocosms can also be valuable for testing the impact of pollution without damaging the wetland ecosystem and adjacent ocean, such as the effect of herbicide on salt-marsh plants (Liu et al., 2005) and the effect of desalination effluent on seagrasses (Marín-Guirao et al., 2011). Mesocosms are experimental systems > 1 m^2 to ca. 5 m^2 in area, thus can contain multiple trophic levels of interacting organisms. They can maintain more ecological complexity than microcosms, and are less expensive and more time-effective than whole-ecosystem studies (Odum, 1984; Ahn and Mitsch, 2002). Scott et al. (2014) reviewed the use of experimental salt-marsh mesocosms for planning restoration, exploring storage of blue carbon (as defined in McCleod et al., 2011), and

filtering terrestrial runoff. For this chapter, the mesocosm focus is on salt marsh foraminifera, rather than environmental experimentation.

2.1.2. Salt marsh foraminifera

Foraminifera are testate protists found in all marine and brackish environments, with worldwide occurrences that date to the Cambrian (Buzas and Culver, 1991). Benthic salt marsh foraminifera are particularly useful for reconstructing coastal paleoenvironments and sea level (Scott et al., 2001, 2014).

Marsh foraminifera (both assemblages and indicator taxa) are used to reconstruct past sea level because their vertical distribution in a tidal marsh corresponds to elevation above sea level, giving a paleo-sea level estimate with an accuracy of ±5 cm (Scott and Medioli, 1980a). Moreover, most marsh foraminifera are arenaceous (agglutinated) and they preserve well in the lowered pH of marsh sediment. In ecological studies, living foraminifera provide a good "contemporary database" for assessing howforaminiferal assemblages represent past environments (Camacho et al., 2015). For example, they can be used as proxies for harbour pollution history (Dabbous and Scott, 2012) and for monitoring thermal or toxic effluent (Scott et al. 2001; McCann et al., 2017). Marsh foraminifera are abundant (thousands) in 10 ml sediment samples, yielding statistically significant populations (Phleger, 1960) and allowing compact storage of samples (Scott et al., 2001).

2.1.3. Objectives

Cesbron et al. (2016) pointed out the urgent need to understand biotic controls on living foraminiferal populations. The work undertaken for my thesis follows this directive in seeking to better understand the role of foraminifera in the food web (see Chapters 3 – 5)

and evaluate current, past (paleoenvironmental) and future changes (Papaspyrou et al., 2013).

This chapter addresses three main questions: (1) Can a fully-functioning salt marsh mesocosm for a temperate ecosystem be created in a laboratory setting to allow year-round access for sampling of foraminifera and associated meiofauna? 2) Does the mesocosm show similar foraminiferal assemblage patterns to field samples? (3) Can a mesocosm be used to monitor meiofaunal biotic effects (predation and competition) on foraminiferal assemblages?

In order to utilise a laboratory salt-marsh mesocosm, the system must be shown to replicate a natural salt marsh with a reasonable degree of confidence. To assess the degree of confidence, a rigorous statistical comparison was made between mesocosm data and data from two field transects at Chezzetcook Inlet. To answer questions 1 and 2, foraminiferal data for the mesocosm and field were compared by season and by elevation zone with respect to tidal inundation, based on the total abundance of all foraminifera and the relative abundance of key taxa. To answer question 3, the body of data was assessed qualitatively (see Chapter 5) to evaluate generic similarities and differences between the mesocosm and the natural marsh.

2.2. Study area and mesocosm

Chezzetcook Inlet is a tidal wetland located 45 km east of Halifax (44°42'N, 63°15'W) on the Atlantic shore of Nova Scotia, and is approximately 7 km long and 2 km wide. The area is inundated with diurnal mesotides (1.5–2 m) twice daily, filling and draining through a series of channels. Physical parameters were described in detail by Scott and Medioli (1980a, b) and Chague-Goff et al. (2001).

The inlet shows a characteristic vertical zonation of vegetation that is determined by the sediment height above mean sea level and the tidal range (Chapman, 1960; Scott et al., 2014). High, middle and low marsh zones are characterized by distinctive floras, dominated by *Spartina patens* in the high marsh zone and *Spartina alterniflora* in the low marsh zone. Sedimentation rates have been measured as 1.3 mm yr^{-1} in the middle marsh zone (Scott and Medioli, 1980a) and 2.8 mm yr^{-1} by Chmura and Hung (2004).

Chezzetcook Inlet has been a key study location for benthic salt marsh foraminifera since the late 1970s. However, the temperate marsh experiences winter freezing and snow cover, making it impractical to study foraminifera for up to three to four months per year. Previous studies (Scott and Medioli, 1980b, figs. 2–18) have data gaps of multiple months every year. Biological studies of the microfauna are also disrupted during these times as foraminifera are difficult to maintain in microcosms for long periods (personal observation). To fill these data gaps, a mesocosm was developed to simulate the Chezzetcook marsh. Preliminary trials using "fish tank experiments" with recirculating seawater were unsuccessful. In 2005, a larger mesocosm with a continuous flow of harbour seawater, as well as simulated tidal and light cycles to maintain a year-round marsh, was set up in the Aquatron Facility at Dalhousie University (https://www.dal.ca/dept/aquatron/about.html). To our knowledge, this is the first large-scale laboratory salt marsh designed to allow year-round culturing of foraminifera.

Validating a mesocosm is important for experimental work (Pennington et al., 2004). After establishing the feasibility of the system, a subsequent (2010) laboratory marsh was constructed for regular surface sampling from marsh zones and for fine-scale monitoring of foraminifera and associated meiofauna as addressed in Chapter 5. These

data are needed to investigate the faunal community, including taxa with functional groups and trophic positions similar to foraminifera. Details of this work are reported elsewhere (Frail-Gauthier and Mudie, 2014). Here we present the foraminiferal mesocosm results to assess the degree of success in replicating field conditions in a controlled setting.

2.3 Methods

2.3.1. Field sampling for mesocosm development

Marsh slabs (sizes listed in section 2.3.2) were taken in December, 2005 with a machete and shovel from two salinity regimes within Chezzetcook inlet (Fig. 2.1): inner marsh area with lower tidal water salinity (0 – 20 psu) towards the head of the inlet (Transect 1) and outer marsh area with higher salinity (20 – 30 psu) nearer the inlet entrance (Transect 2), in an area previously studied since the 1970's. Transects were chosen based on proximity to road and ease of marsh access. At each transect, four slabs of marsh were removed. The slabs represent high, middle and low marsh zones based on characteristic floral and tidal elevation studies of Scott and Medioli (1980 a, b).

High marsh is characterized by dominance of *Spartina patens*, middle marsh by mixed *Spartina patens* and *Spartina alterniflora*, and low marsh by the dominance of *S. alterniflora*. A mudflat slab was taken from the lowest parts of the transects to representthe unvegetated channel margin.

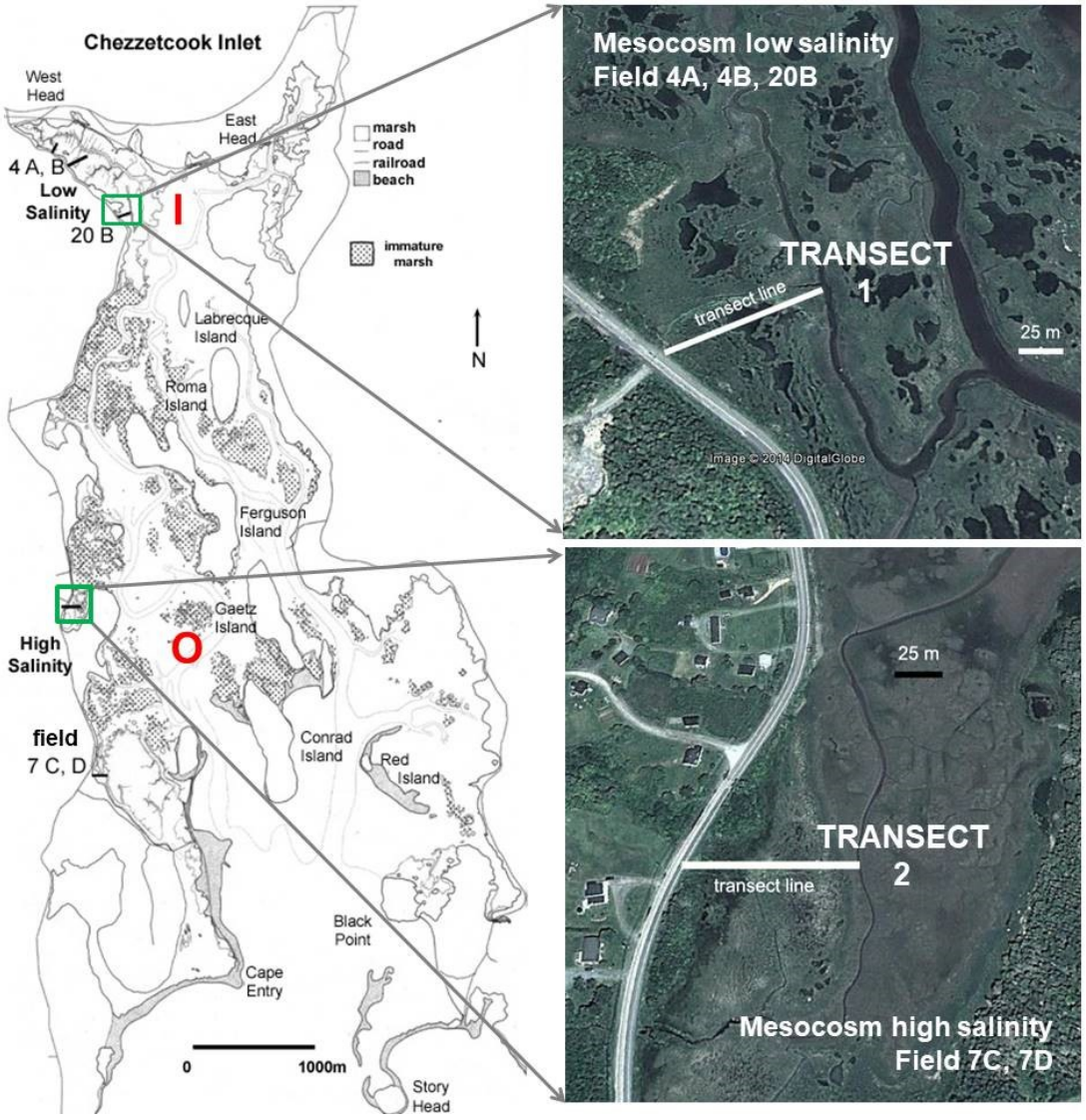

Figure 2.1. Map of Chezzetcook Inlet, showing the two transects used for this study (after Scott and Medioli, 1980b). Red "I" and "O" are the Inner and Outer inlet, respectively. Arrows link green squares of the transect areas to Landsat (Google Earth) images of the transects sampled for the laboratory mesocosm. Top: low-salinity transect (inner inlet), bottom: high-salinity transect (outer inlet). Numbered stations 4, 20 and 7 are reported in Scott and Medioli (1980b).

Marsh slabs were placed in prepared holding containers made at the Dalhousie University Aquatron Facility. For high, middle, low, and mudflat zones for each transect, a slab c. 0.5 m^2 (49 x 41.5 x 20 cm thick, but x 10 cm thick for the mudflat) was placed in

a plexiglass (acrylic thermoplastic) box and transported to the Aquatron for immediate setup.

2.3.2 Mesocosm Preparation

Laboratory Marsh Design:

A mesocosm was constructed (Figure 2.2) using two fiberglass tanks (208 cm long x 56 cm wide x 47 cm high) placed side by side in an Aquatron wet lab. The elevations were 40, 28, 18 and 5 cm high for the high, middle, and low marsh zones and the mudflat, respectively. These heights correspond to elevations above MSL to approximate the field tidal inundation conditions, where high marsh zones are barely covered by tidal water daily. A 12 cm space at the end of the tanks accommodated the main drain, with an emergency overflow drain and a screen to trap debris and prevent clogging of the drain, which would slow the lowering of tidal water. The mesocosms were examined at least weekly for possible equipment problems, with drains and pipes cleared of debris to maintain constant water flow.

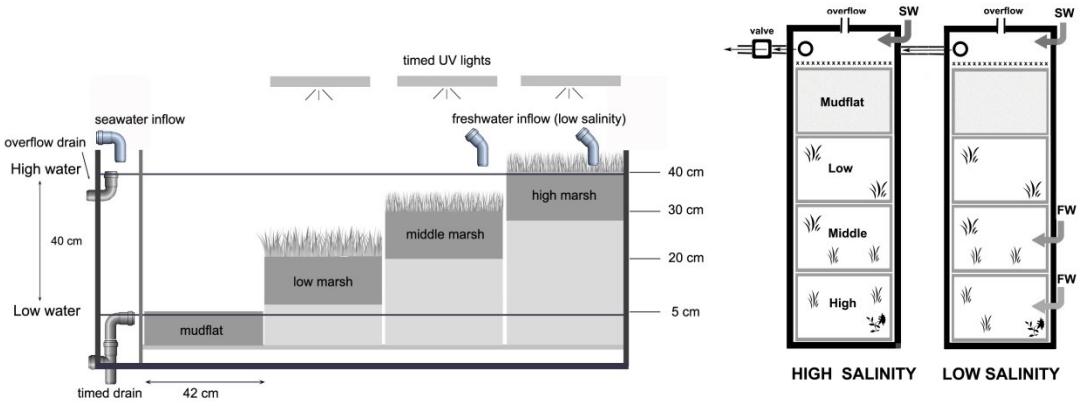

Figure 2.2. Diagrams of the mesocosm in the Aquatron at Dalhousie University. The side-view diagram is vertically exaggerated. Only the low salinity high and middle marsh zones receive freshwater input. Left: Side-view of one tank. Height measurements are approximate tidal levels; Right: Top-view of both tanks side-by-side. SW = salt water input; FW = fresh water input; ⋯ = screen.

Tidal Simulation and Fresh Water Input:

Ambient sea water from the Northwest Arm, Halifax, flowed in continuously at the lowermost (mudflat) end of each tank. The drain opening/closure valve regulated the rise and fall of artificial tides. The tanks were connected by side drains feeding to one main drain with a 230 PSI Ball valve (Chemline Plastics Ltd, PASR00). The valve opened and closed the drain based on programmable timers (Intermatic HB77R) set to 6-hour intervals. Filling to a high-water mark at 44.5 cm took five hours, and drainage also took five hours. Two high tides and two low tides were simulated at the same times each day; the timers were set at 7 a.m. and 7 p.m. to provide low tide in the middle of the day and facilitate sampling. The tidal cycles were the same for both transects, but Transect 1 samples received direct continuous fresh, non-chlorinated water over the high and middle marsh zones, which indirectly flowed onto the lower marsh zones to simulate freshwater runoff at the inlet head. Inputs of sea- and freshwater were adjusted to maintain appropriate water levels through the tidal cycle, but no provision could be made to replicate precipitation, which amounts to 1358 mm yr^{-1} at Halifax and is distributed year-round.

Ultraviolet Light:

Ultraviolet light bulbs (1500 W Metal Halide (MH) bulbs) 63 cm above the high-water mark were set on timers to simulate daylight cycles. To control environmental parameters as closely as possible, light was kept at a constant cycle. Three UV lights covered the high, middle and low marsh zones of each tank, which received eight, seven, and six hours of direct light, respectively. Times were based on D. Scott's evaluation (pers. comm.) of light intensity received at mudflat elevations, with the high marsh

exposed for more of the tidal cycle. In total, the mesocosm received 12 hours of UV light per day. The mudflat received the peripheral light from the low marsh. The differences in duration and intensity of light were designed to replicate the relative amounts of direct sunlight a natural marsh experiences when immersed in turbid tidal water (the mesocosm did not experience these suspended sediments). The mudflats receive the fewest hours of unfiltered direct sunlight in contrast to the high marsh that is covered by a thin layer of water on average every 3 – 4 tidal cycles.

Temperature and Salinity:

Water temperature was based on the input of ambient sea water (continuously recorded by the Aquatron Facility), and air temperature was laboratory room temperature which fluctuated around 20°C. Salinity was maintained through the ambient sea water, except in the low salinity marsh, and salinity of water near each slab was recorded in parts per thousand (ppt) at the time of sampling using a Goldberg refractometer calibrated to seawater salinity. Results report the salinity as practical salinity units (psu) which are essentially identical in the observed salinity range of parts per thousand (ppt).

2.3.3. Sediment sampling

Surface sediment samples were taken at irregular but frequent intervals (weekly, biweekly, or monthly) from December 2005 to November 2007 in all eight marsh segments to examine foraminiferal assemblages over time. A 10 cm^3 volume gives enough foraminifera (>300 individuals) to provide a statistically significant representation of the given marsh zone (Phleger, 1960). We used pseudoreplication by taking six random ~2 cm^3 samples, combining them, then removing a total sample size of

10 cm^3, in order to smooth out minor spatial variation in foraminifera (Debenay and Guillou, 2002; Duchemin et al., 2005; Morvan et al., 2006). The top centimeter of sediment was sampled and considered as representative of the living foraminifera, although some taxa burrow deeper (Scott et al., 2001; Tobin et al., 2005). Samples were taken at low tide to prevent loss of sediment in the water column on removal.

Samples were washed with tap water through 500, 63 and 45 μm sieves, retaining the sediment on the two lower sieves. The coarsest mesh removed large pieces of debris, roots and grasses; the 63 μm sieve traps material of intermediate size and captures most foraminifera, also preventing clogging and overflow of sediment on the 45 μm sieve; and fine silt and clay passes through the 45 μm sieve that also captures smaller foraminifera. The >45–<500 μm sediment fractions were immediately fixed with formalin and stained with 2 ml Rose Bengal solution (2.5 ml powdered Rose Bengal in 250 ml distilled water), using minimum amounts of water to reduce use of fixative and stain while maintaining a 10% minimum fixative solution. At least 1 ml of borax buffer was added to prevent dissolution of calcium carbonate tests (Murray, 2006). Samples were kept in stain and fixative for at least 24 hours, and then washed over a 45 μm sieve to remove excess stain and formalin solution. Samples were stored with minimal water to which 70% ethanol solution and 1 ml borax powder was added. The samples were sealed in plastic 150 ml hospital-grade vials to prevent evaporation of the ethanol, bacterial growth, and aggregation of detrital organic matter (Scott et al., 2001).

2.3.4 Sample examination

The high number of foraminifera per sample (some exceeding 8000 per 10 cm^3) required use of a settling column wet-splitter to divide samples into manageable fractions of 1/6, 1/9, 1/18 or 1/36 (Scott and Hermelin, 1993). At least 300 individuals were needed per sample split to represent the entire sample population statistically, although counts of 100 ensure a 99% probability of recording the main species (those >5%; Fatela and Taborda, 2002). Samples were examined wet under a binocular dissecting microscope. Living (bright pink Rose Bengal in multiple chambers) and dead (not stained or weakly stained; see Bernhard, 2000) foraminifera were counted and each species was recorded as living or dead. In this study, totals of living plus dead are used in all calculations. This provides information on environmental features at the time of sampling and also incorporates the death assemblage that is used in paleontological analyses (Morvan et al., 2006; Strachan et al., 2015). Foraminifera were identified to genus or species level using the taxonomy of Scott and Medioli (1980a), corrected by more recent studies (e.g., Müller-Navarra et al., 2016; Lei et al., 2017) that combine *Trochammina macrescens* f. *macrescens* and *T. macrescens* f. *polystoma* into *Jadammina macrescens*.

2.3.5 Field to mesocosm comparison

In order to assess the success of the mesocosm in replicating field conditions, spatial and temporal foraminiferal assemblage data were compared with 1976-1978 data from Chezzetcook Inlet (Scott and Medioli, 1980 a,b). In the 1980 study, the authors made repeated seasonal counts for five transects over three years, and the transects closest to the mesocosm sample sites were used for comparison with the mesocosm data (Table

2.1). We used elevation above mean sea level (ASL) and marsh vegetation to make appropriate comparisons of field and mesocosm samples. Although Field Station 20B is physically located on mesocosm Transect 1 (inner estuary low salinity), it matches the elevation and flora of our Transect 2 high salinity middle marsh zone and was therefore used for field-mesocosm comparisons of the Transect 2 samples.

Table 2.1. Sample locations and parameters used for comparison of field (*Scott and Medioli, 1980b) and corresponding laboratory mesocosm section. ASL – above (mean) sea level. Pat = *Spartina patens;* alt = *Spartina alterniflora;* Cyp = *Cyperaceae* (sedges)*;* Jun = *Juncus* (*gerardii* and *balticus*)*;* Pot = *Potentilla anserina;* Sol = *Solidago sempervirens;* Sal = *Salicornia* sp./*Sarcocornia* cf. *perennis.*

Chezzetcook Inlet Field (F) (1976 – 1978*)					**Mesocosm (M) 2005 – 2007**		
Field Sites Inner Inlet (I) Outer Inlet (O)	**Notation in text and figures**	**Field Elevation ASL (m) in a ~1.2 m tidal range**	**Notable plants**		**Inner Inlet (I) samples= Transect T1 ; Outer Inlet samples= Transect T2**	**Notation in text and figures**	**Mesocosm Elevation (m) in a 40 cm tidal range**
F-I, High Marsh Zone (Site 4A)	4A	0.8–0.9	Cyp, Pot, Sol, Jun, pat	→	**M-T1, High (H) Marsh Zone (Low Salinity)**	T1-H	0.38
F-I, Middle Marsh Zone (Site 4B)	4B	0.75–0.8	Cyp, Pot, Sol, Jun, pat	→	**M-T1, Middle (M) Marsh Zone (Low Salinity)**	T1-M	0.28
F-I, Middle Marsh Zone (Site 20B)	20B	0.7	Sal, pat	→	**M-T2, Middle (M) Marsh Zone (High Salinity)**	T2-M	0.28
F-O, Low Marsh Zone (Site 7C)	7C	0.3–0.5	alt	→	**M-T2, Low (L) Marsh Zone (High Salinity)**	T2-L	0.18
F-O, Mudflat Zone (Site 7D)	7D	-0.1–0	alt (if any)	→	**M-T2, Mudflat (MF) Zone (High Salinity)**	T2-MF	0.05

2.3.6. Data analysis

Data are presented as total (living + dead) foraminiferal counts, and as relative abundances of the most common taxa. Data are mean values per season (fall+winter, spring, and summer periods), pooled over the three sampling years in the field and two years in the mesocosm, and mean values per tidal zone (Table 2.1). Fall+winter is the interval from end-September to end March; spring is from early April to mid-June; and summer is from mid-June to end-September. Fall and winter samples were combined due to the low number of field samples during these seasons every year. Statistical differences between and among locations, zones, and seasons were determined using XLSTAT in Excel for non-parametric tests (Kruskal-Wallis for *k* samples, Mann-Whitney for 2 samples, significance value of $p < 0.05$) as the data did not follow a normal distribution, even when transformed in a variety of ways. Cluster analysis and non-metric multidimensional scaling of Euclidean distances on square-root transformed relative abundances of foraminifera were performed using PRIMER v.6.0. They were used to examine foraminiferal communities against selected environmental parameters: location (field or mesocosm), marsh zone (linked to elevation), and season (fall+winter; spring; and summer). ANOSIM of Euclidean distances of square-root transformed relative abundances of common foraminifera was also used in PRIMER to examine differences in the three parameters.

2.4 Results

The mesocosm prospered for two years, which was the duration of the experiment, showing good promise for a laboratory system. Although all environmental parameters

were controlled except for ambient water temperature that followed fluctuation in Northwest Arm of Halifax Harbour (Figure 2.3) and there was no winter ice or change in daylight hours and intensity, the vegetation followed a seasonal cycle of growth and death (Figure 2.4). Freshwater temperatures were above 2.5°C in winter months (lowest at end-February to early March) and below 22°C in summer months, peaking in early August (Figure 2.3). Seawater temperature had more variability on short-term scales (days) and between the two years. Overall, the lowest temperatures were in February-March (2.7°C in 2006, ~1°C in 2007) and the highest temperatures were in early September (~19°C in 2006, 14°C in 2007).

The mesocosm floral zones replicated the field floras. High marsh contained *Spartina patens*, Cyperaceae (sedges; *Carex* sp.), *Potentilla anserina, Limonium carolinianum*; mid-marsh contained *S. patens*, *Juncus* spp., and *Salicornia* sp./*Sarcocornia* cf. *perennis*; and the low marsh contained *Spartina alterniflora*. Macrobiofilms (thick green and blue-green algal mats) were common on both the low marsh and mudflats of both mesocosm tanks.

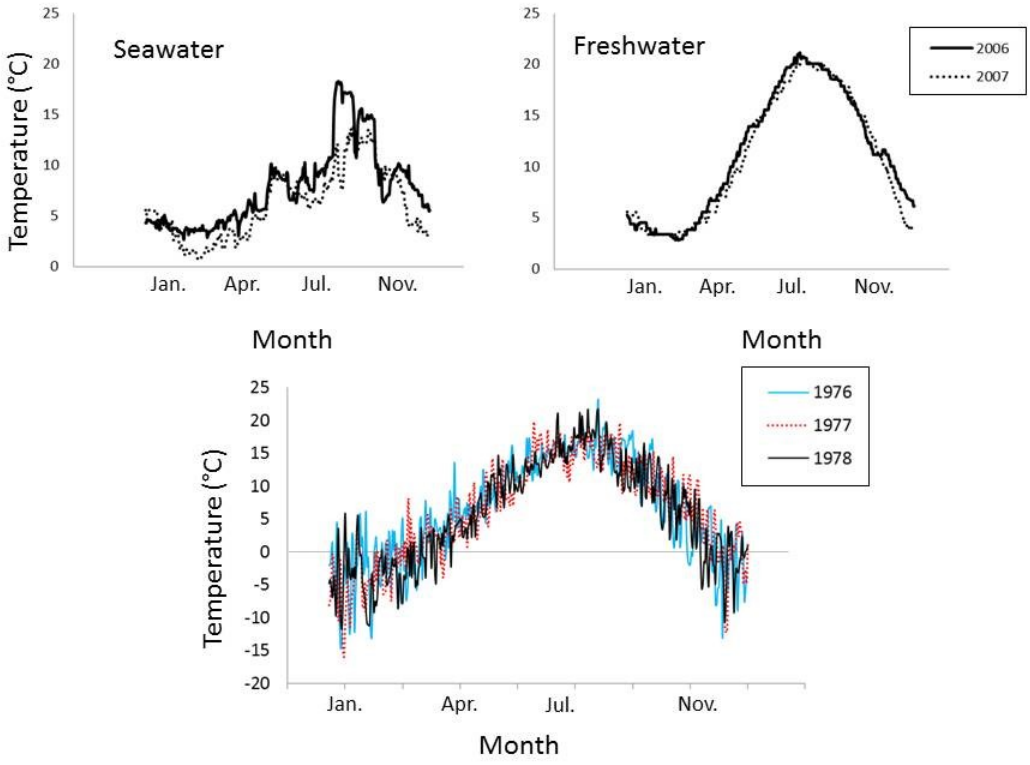

Figure 2.3: TOP: Water temperature profiles of incoming seawater and freshwater in the Aquatron Facility for 2006 and 2007. BOTTOM: Temperature profiles for mean daily air temperatures from nearby (<30 km away) Sandy Cove (Halifax), N.S., 1976-1978.

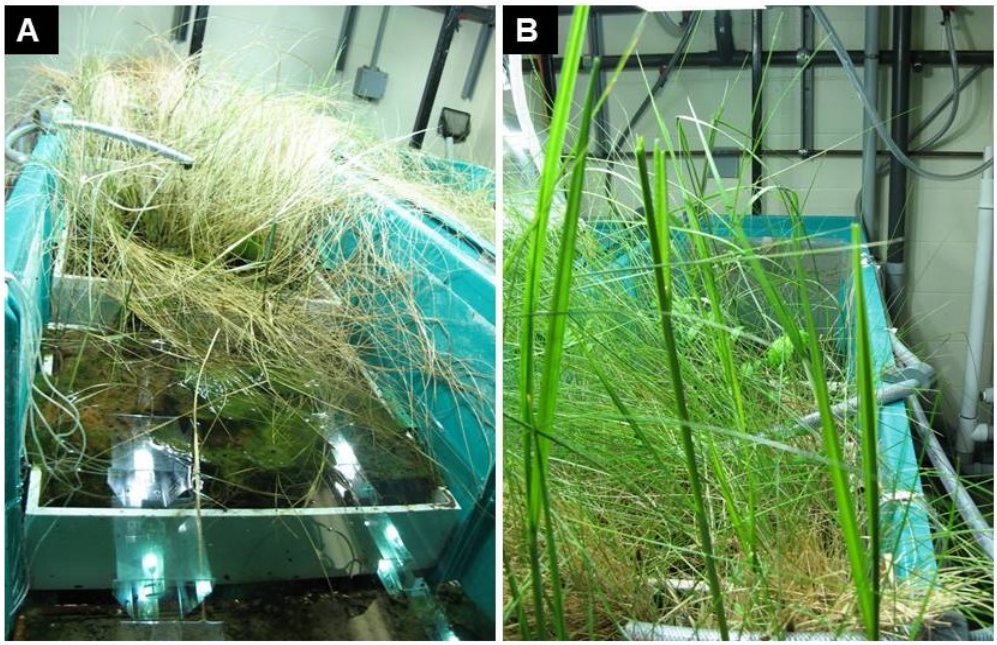

Figure 2.4: Low salinity transect (A) in winter (February), and (B) in spring (May). A is oriented to show the mudflat with algal mats in the foreground; B shows the high marsh in the foreground (with notable sedges, *Spartina patens,* and others (e.g. *Potentilla anserina*).

2.4.1 Salinity comparisons

Overall, average salinities are similar for the field and mesocosm in any given season (Figure 2.5). Inner Inlet high and middle marsh zones 4A, 4B, and Mesocosm Transect 1 have lower salinities (generally ~ 5 psu, except for the summer field samples at ~ 15 psu). Outer Inlet marsh areas (7C and 7D) and Transect 2 have higher salinities of ~ 25 psu, with the mudflat having salinities closer to 30 psu (Figure 2.5). The one exception is field site 20B, which groups variably with the low salinity marsh area in winter, and the high salinity area in summer, with an intermediate spring position matching that of the summer Inner Inlet sample value of c. 15.

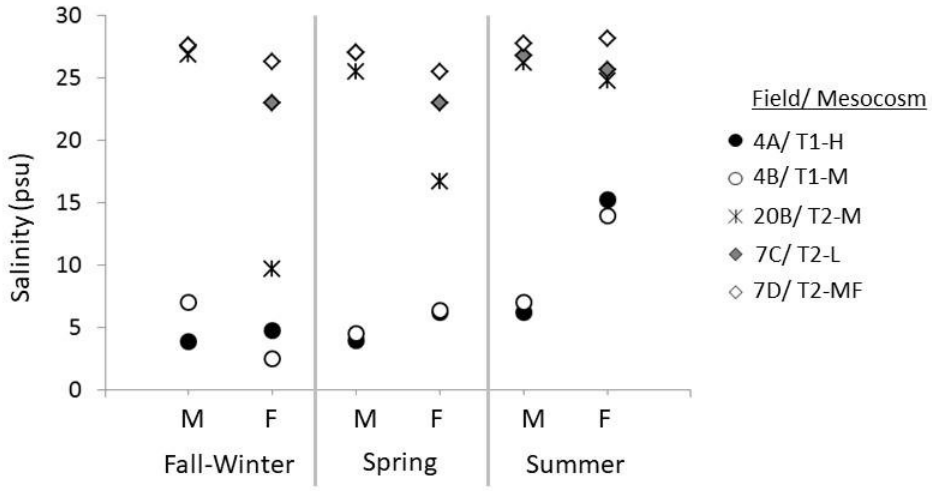

Figure 2.5: Average salinities (psu) for each marsh elevation for each season for the laboratory mesocosm (M) and field (F) samples. Average salinities (psu) for each marsh zone (H, M, L, MF) for each season for the mesocosm (M = T1 and T2 samples) and field (F, sites 4A, 4B, 20B, 7C and 7D) samples. See Table 2.1 for notations.

To examine average seasonal salinities with tidal elevation, the data were separated by marsh zone (Figure 2.6). Across seasons in any given zone, salinities fluctuated less for the mesocosm than for the field. Between the field and the mesocosm, station 20B appears to have the largest discrepancies, although station 7C low marsh also has large differences between the mesocosm and field (25 to 30 psu for mesocosm, 20 to 25 for field; Figure 2.6). Additionally, stations 4A and 4B have higher salinities in the summer in comparison to the mesocosm (Figure 2.6).

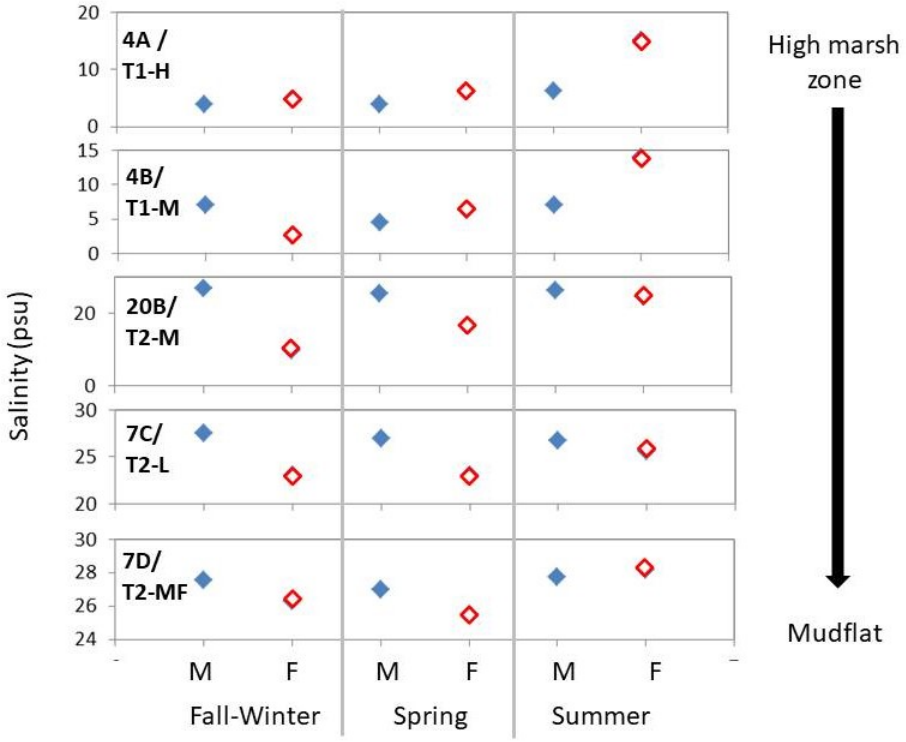

Figure 2.6: Average salinities (psu) for each marsh zone in each season measured during 2005-07 in Mesocosm (M; T1 and T2) samples and 1976-78 Field (F; 4A through 7D) samples. See Table 2.1 for additional notations.

Water salinities for the field samples (1976-1978) show significant differences across seasons for the Inner Inlet high-middle marsh zone sites (4A, 4B) and middle marsh site (20B). All have significantly higher salinity ($p=0.003$ or 0.004) in summer than in fall+winter and spring (Table 2.2). The low marsh field samples (7C and 7D) do not have significantly different salinities across seasons ($p =0.351$ and 0.166). For all seasons, there are significant differences ($p<0.001$) across marsh zones: (4A=9.8, 4B=8.9, 20B=17.5, 7C=23.9, 7D=26.7), with salinity increasing towards lower elevations (low marsh and mudflat) (Table 2.2).

In the mesocosm, seasonal differences of salinity are not significant for each zone ($p>0.05$). However, there are differences across the four marsh zones when seasons are

combined, with higher marsh areas having significantly lower salinity than the lower marsh areas ($p<0.0001$; Table 2.2).

Comparison of mesocosm and field salinities of each zone, regardless of season, shows some significant differences (Table 2.2). Low salinity inner high marsh zones (4A and T1-H) values are significantly lower in mesocosm than field ($p=0.017$), but the low salinity middle marsh zones (4B and T1-M) are not different ($p=0.383$). Both middle marsh zones (20B and T2-M) and the outer low marsh zones (7C and T2-L) are significantly higher between mesocosm and field. The mudflat (7D and T2-MF) salinities are not significantly different between the mesocosm and field ($p=0.544$).

Table 2.2. Salinity comparisons across seasons (top panel), zones (bottom panel), and between the field (4A – 7D) and mesocosm (T1 and T2; zones defined in Table 2.1) (bottom right). Statistically different differences ($p<0.05$ for Kruskal-Wallis or Mann-Whitney non-parametric tests) are bolded. FW = Fall+winter; Sp = Spring; Su = Summer. More statistical details can be found in Appendix A Table A-1.

FIELD mean salinity values (psu)				**Kruskal-Wallis significance**	**MESOCOSM mean salinity values (psu)**				**Kruskal-Wallis significance**
	F-W	**Sp**	**Su**			**F-W**	**Sp**	**Su**	
4A	4.75	6.25	15.22	**p = 0.003**	**T1-H**	3.85	4.0	6.25	p=0.544
4B	2.5	6.38	14.0	**p = 0.004**	**T1-M**	7	4.5	7	p=0.60
20B	9.67	16.72	24.75	**p = 0.021**	**T2-M**	26.85	25.5	26.25	p=0.715
7C	23.0	23.0	25.7	p = 0.351	**T2-L**	27.57	27	26.75	p=0.878
7D	26.3	25.5	28.2	p = 0.166	**T2-MF**	27.5	27	27.75	p=0.795

FIELD zonal salinity mean values (psu)	**Kruskal-Wallis significance**	**MESOCOSM zonal salinity mean values (psu)**	**Kruskal-Wallis significance**	**Mann-Whitney significance of FIELD vs MESOCOSM for each zone**
4A: 9.8		T1-H : 4.6		**p=0.017**
4B: 8.9		T1-M : 6.6		p=0.383
20B: 17.5	**p<0.0001**	T2-M : 26.5	**p<0.001**	**p=0.000**
7C: 23.9		T2-L : 27.2		**p=0.01**
7D: 26.7		T2-MF : 27.5		p=0.544

2.4.2 Seasonality in foraminifera

The total abundance of foraminifera and the relative abundance of the dominant taxa have varying significance levels when considered by season. For all samples, there are no significant seasonal patterns on square-root transformed data using either cluster analysis or multidimensional scaling (MDS) methods (Figure 2.7), and ANOSIM results show no differences across *all seasons* ($R=0.016$, $p=0.075$). However, when looking at the pairwise comparisons of *individual seasons*, the fall+winter versus spring samples shows significant differences in seasonal foraminiferal abundance and composition ($R=0.043$, $p=0.03$). Although the data did not follow a normal distribution, MANOVA (multivariate analysis of variance) results show that seasonal variability explains little of the variability in the data ($p=0.127$ for seasons compared to $p<0.001$ for inlet locations (I vs. O) and tidal zones (H, M, L, and MF).

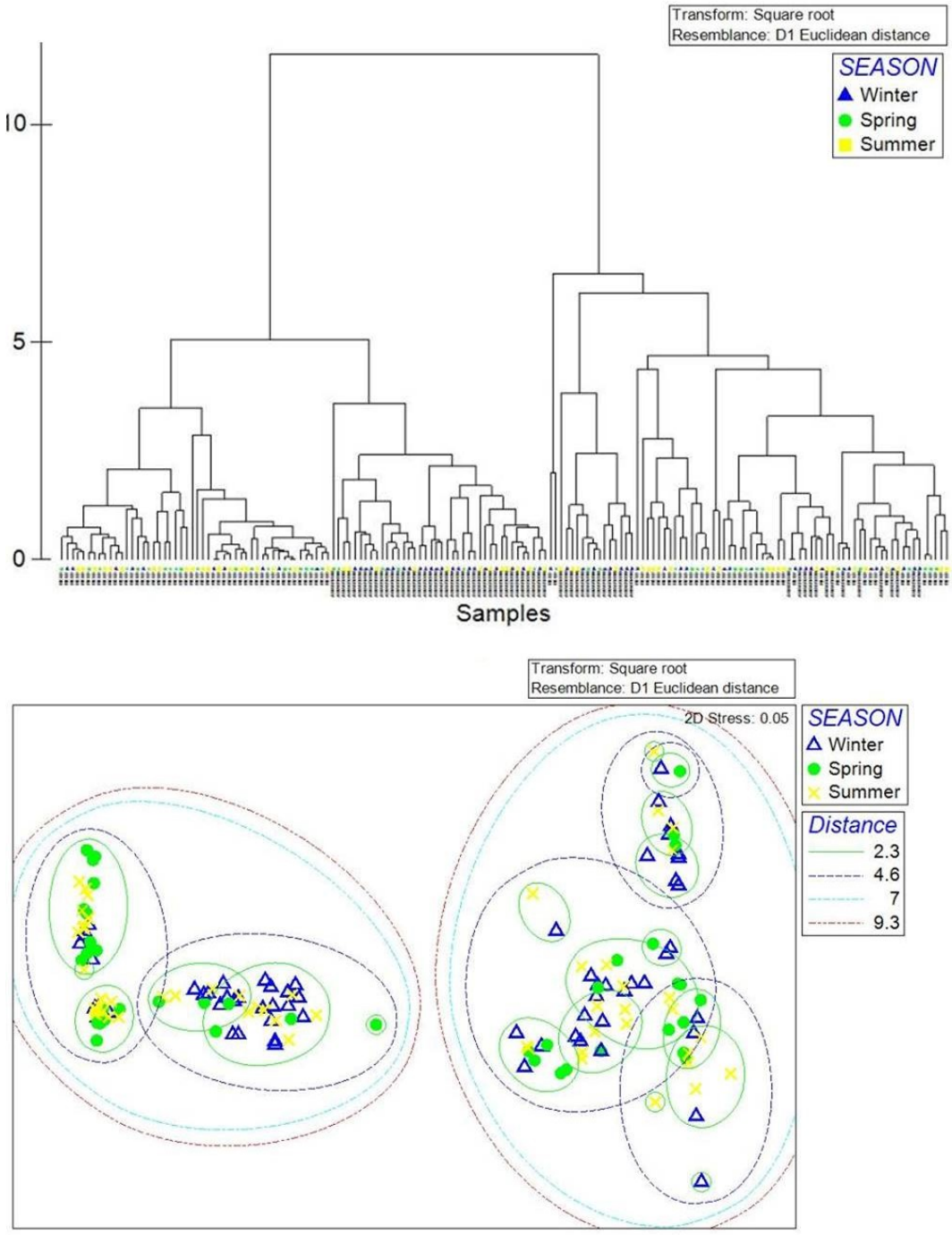

Figure 2.7: Seasonal (fall+winter, spring, summer) distributions determined by Cluster diagram (top) and non-metric MDS plot (bottom) of the Euclidean distances of square-root transformed relative abundances of foraminifera for all samples (field and mesocosm).

Field sample data show that total foraminiferal abundances are significantly different across seasons (Figure 2.9; Table 2.3). For field 4A (I, high marsh), foraminifera

are significantly more abundant in summer than in fall+winter and spring. For field 4B (Inner Inlet middle marsh zone), summer abundance is also significantly higher. Middle, low marsh and mudflat zones (20B, 7C, and 7D) show no significant difference in abundance across seasons. In contrast, the mesocosm seasonal data show no significant differences in abundance for each marsh zone across seasons (Table 2.3).

Relative abundances of taxa in field and microcosm have varying significance across seasons (Table 2.3). For the field, relative abundances of *Trochammina inflata* + *Jadammina macrescens*, *Tiphotrocha comprimata*, and *Haplophragmoides manilianensis* show no seasonal difference in the Inner Inlet high marsh zone (4A; Fig 2.13), but *T. comprimata* is slightly higher in the spring at the middle marsh zone (4B) (Fig. 2.13). For taxa in the Outer Inlet middle marsh (20B), low marsh (7C) and mudflat (7D) zones, relative abundances also show no significant seasonal change. However, the three calcareous taxa *Helenina anderseni*, *Haynesina orbiculare*, and *Elphidium* spp. Have higher spring values for the mudflat zone although the values are not significant due to high standard deviations (Fig. 2.13, Table 2.3).

Similarly, relative abundances of mesocosm taxa show few significant differences by season (Table 2.3). *Tiphotrocha comprimata*, *Trochammina inflata* + *J. macrescens*, and *Miliammina fusca* show no significant seasonal change in the Inner Inlet high marsh zone T1-H (p-values > 0.4; Figure 2.13). In the middle marsh zone (T1-M), *T. comprimata* is significantly less abundant in fall+winter ($p = 0.03$). Outer Inlet middle marsh (T2-M), low marsh (T2-L) and mudflat (T2-MF) zones show no significant seasonal differences (Figure 2.13).

Table 2.3. Seasonal comparisons of the average total abundances (top), and average relative abundances of main species of foraminifera (bottom) in field (4A through 7D) and mesocosm (T1 and T2; zones defined in Table 2.1). Statistically different results ($p<0.05$ for Kruskal-Wallis or Mann-Whitney non-parametric tests) are bolded. FW = Fall-winter; Sp = Spring; Su = Summer. *high standard deviation around mean. Additional statistical detail (e.g. standard deviations) given in Appendix A, Table A-1.

FIELD Average total foraminiferal counts across seasons				**Kruskal-Wallis significance**	**MESOCOSM Average total foraminiferal counts across seasons**				**Kruskal-Wallis significance**
	F-W	**Sp**	**Su**			**F-W**	**Sp**	**Su**	
4A	1660	1319	2735	**p=0.027**	T1-H	6392	6705	4425*	p=0.173
4B	1128	832	2135	**p=0.015**	T1-M	3618	3615	3228*	p=1.0
20B	1065	1780	1612	p=0.277	T2-M	8075*	6516*	5911	p=0.295
7C	2257	2260	2533	p=0.956	T2-L	4535*	4275	4266	p=0.810

FIELD Average relative abundances (%) of main foraminifera across seasons					**MESOCOSM Average relative abundances (%) of main foraminifera across seasons**				
Trochammina inflata + *Jadammina macrescens*									
	F-W	**Sp**	**Su**	Significance		**F-W**	**Sp**	**Su**	Significance
4A	75.8	68	74.9	p=0.365	T1-H	63.3	63.1	60.5	p=0.461
4B	77	72	77	p=0.153	T1-M	67.3	57.7*	66.8	p=0.9
20B	7	4.8	4.6	p=0.503	T2-M	52.1	53.5	46.8*	p=0.509
7C	3.1	0.8	4.2	p=0.342	T2-L	4.0	2.9	2.9	p=0.216
Tiphotrocha comprimata									
	F-W	**Sp**	**Su**	Significance		**F-W**	**Sp**	**Su**	Significance
4A	16.7	17.2	13.9	p=0.463	T1-H	14.5	18.0	15.8*	p=0.434
4B	17.6	21.4	16.2	**p=0.048**	T1-M	7.6	12.6	11.8	**p=0.033**
20B	3.5	5.3	3.5	p=0.328	T2-M	22.1	23.6	18.8	p=0.539
Miliammina fusca									
	F-W	**Sp**	**Su**	Significance		**F-W**	**Sp**	**Su**	Significance
20B	87	87.8	88	p=0.926	T1-H	13.3	10.5	13.5*	p=0.447
7C	77.9	87	79.8	p=0.46	T1-M	20.4	26.4*	16.9	p=0.95
7D	69.3	79	74.5	p=0.499	T2-M	22.9	27.5*	24.7	p=0.928
					T2-L	86.4	88.0	93.7	p=0.056
					T2-MF	60.2	56.9	49.4	p=0.313
Calcareous species (*Elphidium* spp. + *Helenina anderseni* + *Haynesina orbiculare*)									
	F-W	**Sp**	**Su**	Significance		**F-W**	**Sp**	**Su**	Significance
7C	16.5	8.7	9.5	p=0.744	T2-L	5.9	6.7*	1.7	p=0.721
7D	12.6	15.4*	7.2	p=0.64	T2-MF	8.9*	19.3	22.7*	p=0.117

2.4.3. Zonal differences for foraminifera: Mesocosm vs. Field

Combining the data for all seasons, there are significant differences in abundance of foraminifera across tidal zones in both the field and mesocosm data (Figure 2.8). For the field, Outer Inlet low marsh zone site 7C has significantly higher total abundances than the other Field zones (2461/10 ml; $p=0.016$). In the mesocosm samples, the Transect 2 middle marsh (T2-M) has significantly higher (7234/10 ml) and the mudflat (T2-MF) has significantly lower (862/10 ml) foraminiferal abundances than the other zones ($p<0.0001$), in contrast to the field abundance distributions.

Overall, the mesocosm has higher abundances of foraminifera (Figure 2.8) than the field in all zones except the mudflat, and in all seasons ($p<0.0001$). Most mesocosm samples have over twice the field abundances, on average. However, the field mudflat (7D) has almost double the average abundance of foraminifera than the mesocosm mudflat (T2-MF Mesocosm = 862/ 10 ml, Field: 1520/ 10 ml, $p=0.07$).

Marsh zonation (elevation) appears to exert the most important control on relative abundances of foraminifera in both mesocosm and field. Euclidean distances (Figure 2.10) show clear zonal clusters, with the Inner Inlet low salinity sites (4A/T1-H, 4B/T1-M) separated from the Outer Inlet high salinity sites (7C/T2-L, 7D/T2-MF). This distinction reflects foraminiferal species distribution (Figs. 2.12, 2.13), with *T. inflata* + *J. macrescens* and *T. comprimata* dominating the inner area, and *M. fusca* and calcareous species dominating the outer area. For the middle marsh zone 20B, field samples cluster with the low marsh zone and mudflat, whereas comparable mesocosm samples (T2-M) cluster with the high and middle marsh zones (Figure 2.11).

ANOSIM results show that differences in foraminiferal relative abundances are due to both growth location (field vs. mesocosm; $R=0.821$, $p=0.001$) and elevation (marsh zone; $R=0.888$, $p<0.001$). In contrast to differences in total abundances, and seasonality across tidal elevation, relative abundances of foraminifera show more significant zonal differences (Figure 2.12; Table 2.4). Three exceptions with no significant difference are *T. comprimata* in the low salinity high marsh zone (4A), *M. fusca* in the high salinity low marsh zone (7C) and calcareous species in the mudflat zone (7D) (Table 2.4). Only calcareous species and *M. fusca* in the field samples show no significant zonal differences. *T. inflata* + *J. macrescens* and *T. comprimata* are significantly more abundant in high marsh zones (4A, 4B) than middle and low marsh zones (20B, 7C) in the field, but are much higher in the mesocosm middle marsh zone (T2-M) in comparison to field samples or other mesocosm zones. *M. fusca* is found in all mesocosm zones but has significantly higher relative abundance in lower (T2-L and T2-MF) than higher (T1-H, T1-M, T2-M) zones (Table 2.4 and Figure 2.12).

Table 2.4. Comparison of the average relative abundances (%) of dominant foraminifera from the zones (elevation; 4A high marsh through 7D mudflat) and location (field or mesocosm). *Calcareous species include *Elphidium* spp., *Helenina anderseni*, and *Haynesina orbiculare.* Statistically significant differences ($p<0.05$) are shown in bold. More statistical data in Appendix A Table A-3.

Species	Field	Elevation comparison	Mesocosm	Elevation comparison	Field – Mesocosm comparison
Trochammina inflata + *Jadammina macrescens*	4A: 72.3 4B: 75.1 20B: 5.4 7C: 2.8	**p<0.0001**	4A : 62.4 4B : 65.4 20B : 50.8 7C : 3.4	**p<0.0001**	4A: **p=0.007** 4B: **p=0.016** 20B: **p<0.0001** 7C: **p=0.041**
Tiphotrocha comprimata	4A: 15.8 4B: 18.6 20B: 4.19	**p<0.0001**	4A :15.5 4B : 9.7 20B : 21.3	**p<0.0001**	4A: p=0.926 4B: **p<0.0001** 20B: **p<0.0001**
Miliammina fusca	20B: 87.6 7C: 81.1 7D: 74.6	p=0.069	4A: 12.9 4B: 20.2 20B: 22.2 7C: 88.7 7D: 56.7	**p<0.0001**	20B: **p<0.0001** 7C: p=0.171 7D: **p=0.002**
Calcareous species*	7C: 12.0 7D: 11.1	p=0.828	7C: 4.8 7D: 14.3	**p=0.007**	7C: **p=0.021** 7D: p=0.198

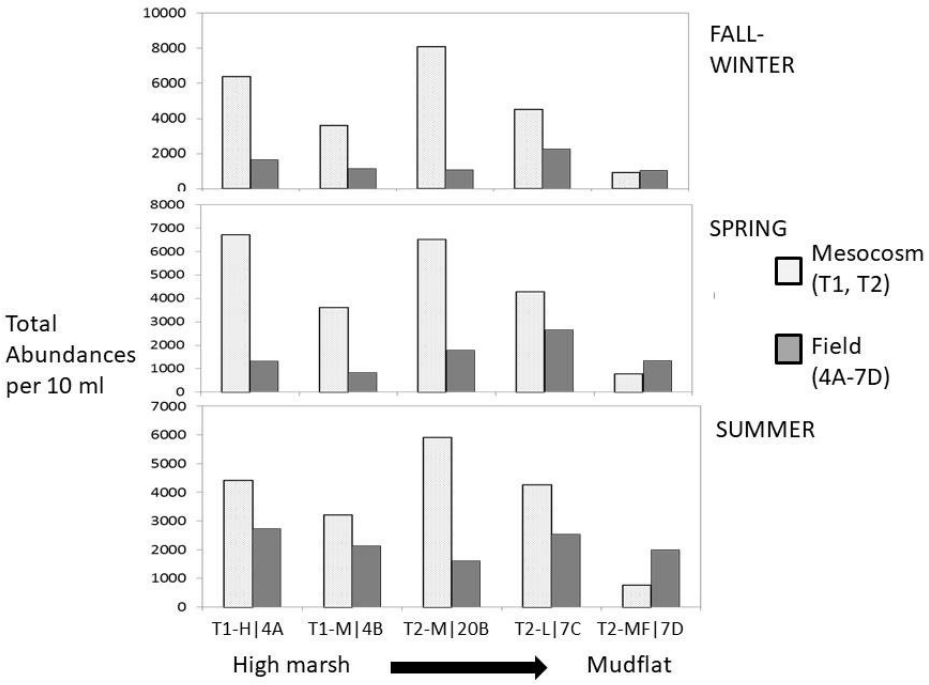

Figure 2.8: Average total abundances of all foraminifera across each zone, for each season of the mesocosm (T1 and T2; see Table 2.1 for notations) and field (4A through 7D) samples. H – High marsh, M = Middle marsh, L= low marsh, MF = mudflat.

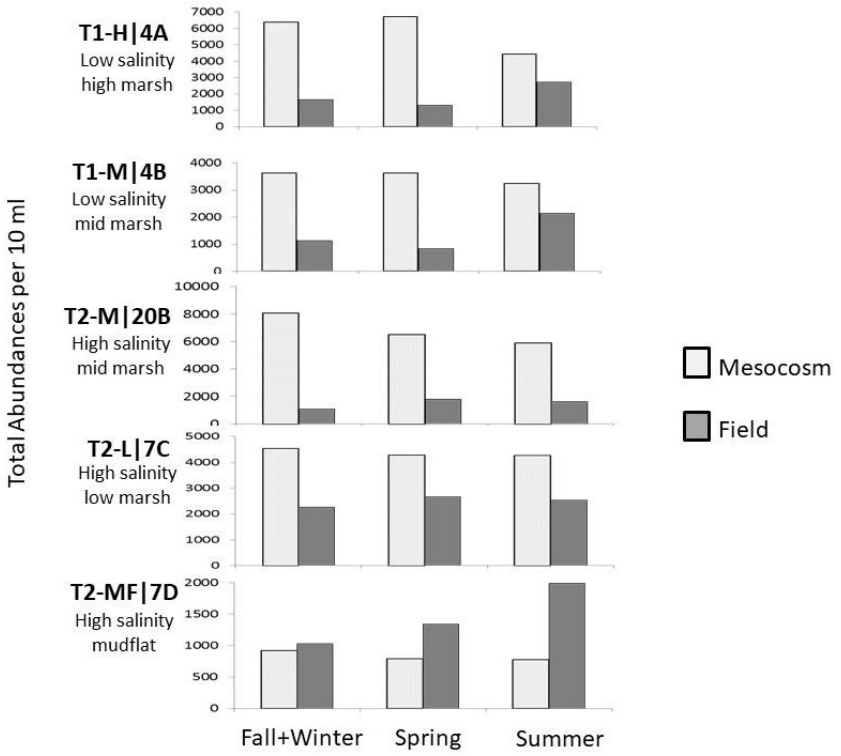

Figure 2.9: Average total abundances (per 10 ml) of all foraminifera in mesocosm (T1, T2) and field (4A – 7D) for seasons across each elevation. H = high; M = middle; L = low; MF = mudflat zones.

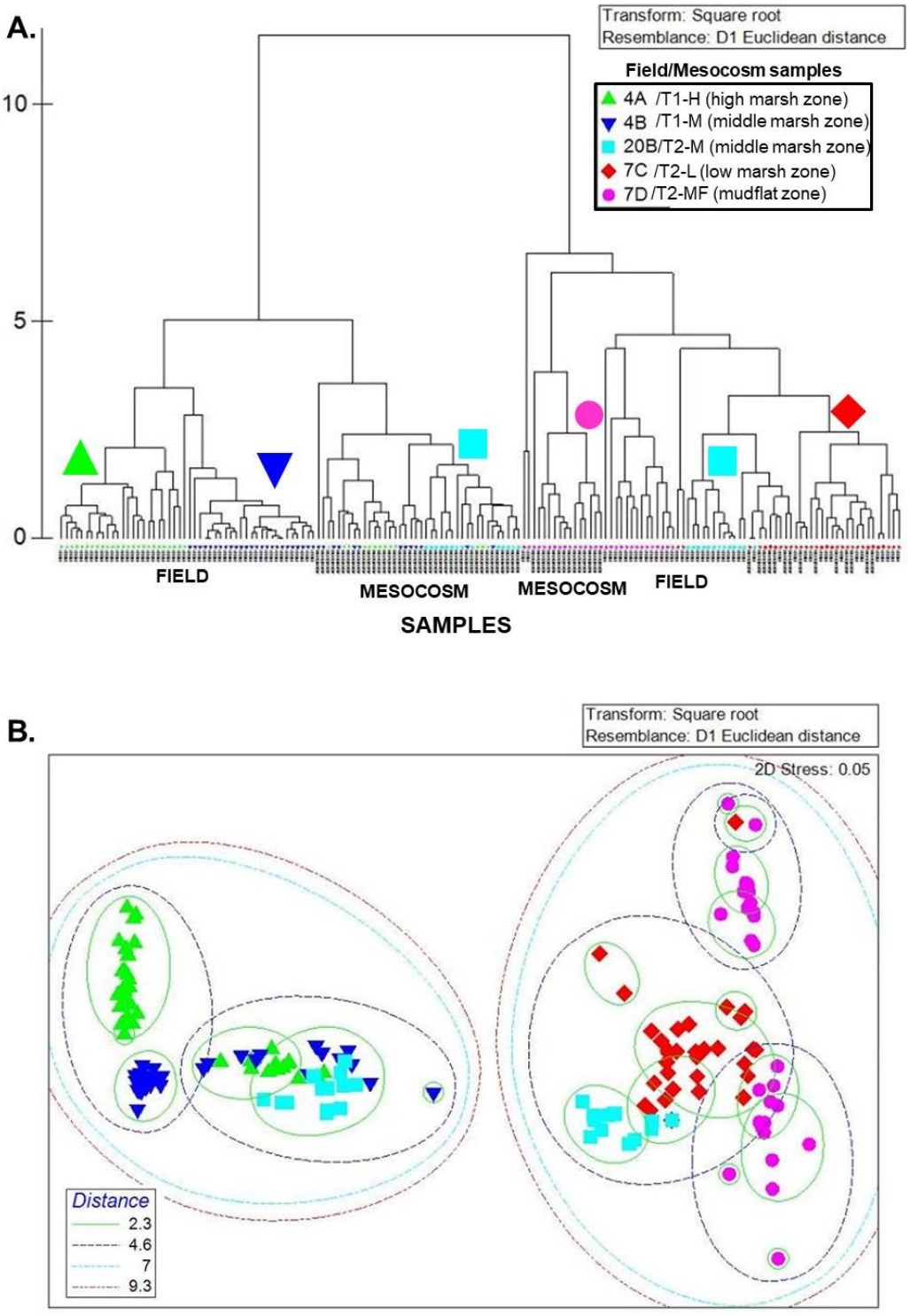

Figure 2.10: Cluster diagram (A) and non-metric MDS plot (B) of Euclidean distances of square-root transformed relative abundances of foraminifera in all samples (field and mesocosm). H = high; M = middle; L = low; MF = mudflat zones.

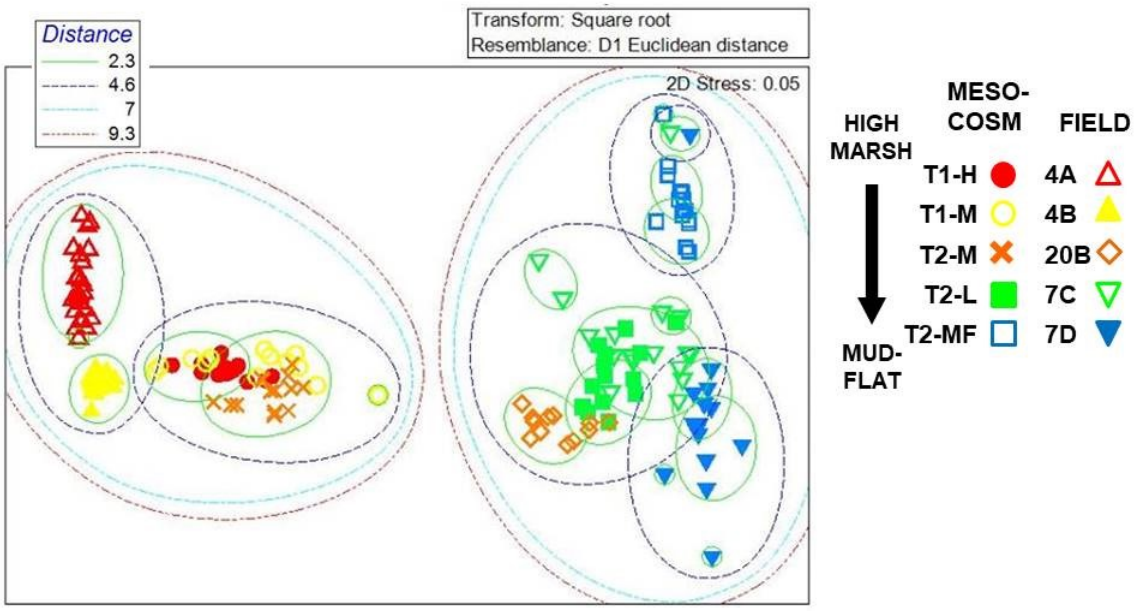

Figure 2.11: Non-metric MDS plot (B) of Euclidean distances of square-root transformed relative abundances of foraminifera separated for the lab and field, across elevation zones (4A-7D). H = high; M = middle; L = low; MF = mudflat zones.

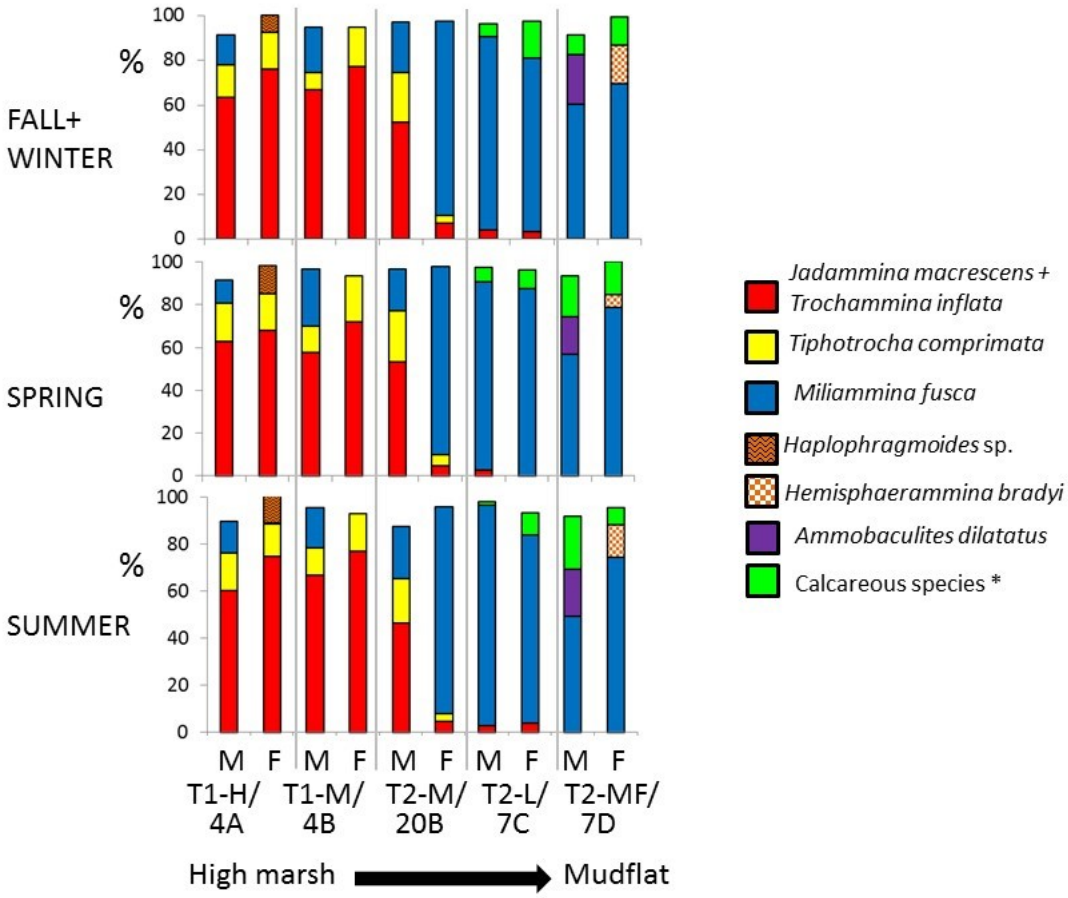

Figure 2.12: Average relative abundances (%) of dominant foraminifera (>5% of total) in mesocosm (M: T1, T2, H (high), M (middle), L (low) and MF (mudflat) zones) and field (F; 4A – 7D) samples for each season across each zone. *Calcareous species: total of relative abundances of *Helenina anderseni*, *Haynesina orbiculare*, and *Elphidium* spp.

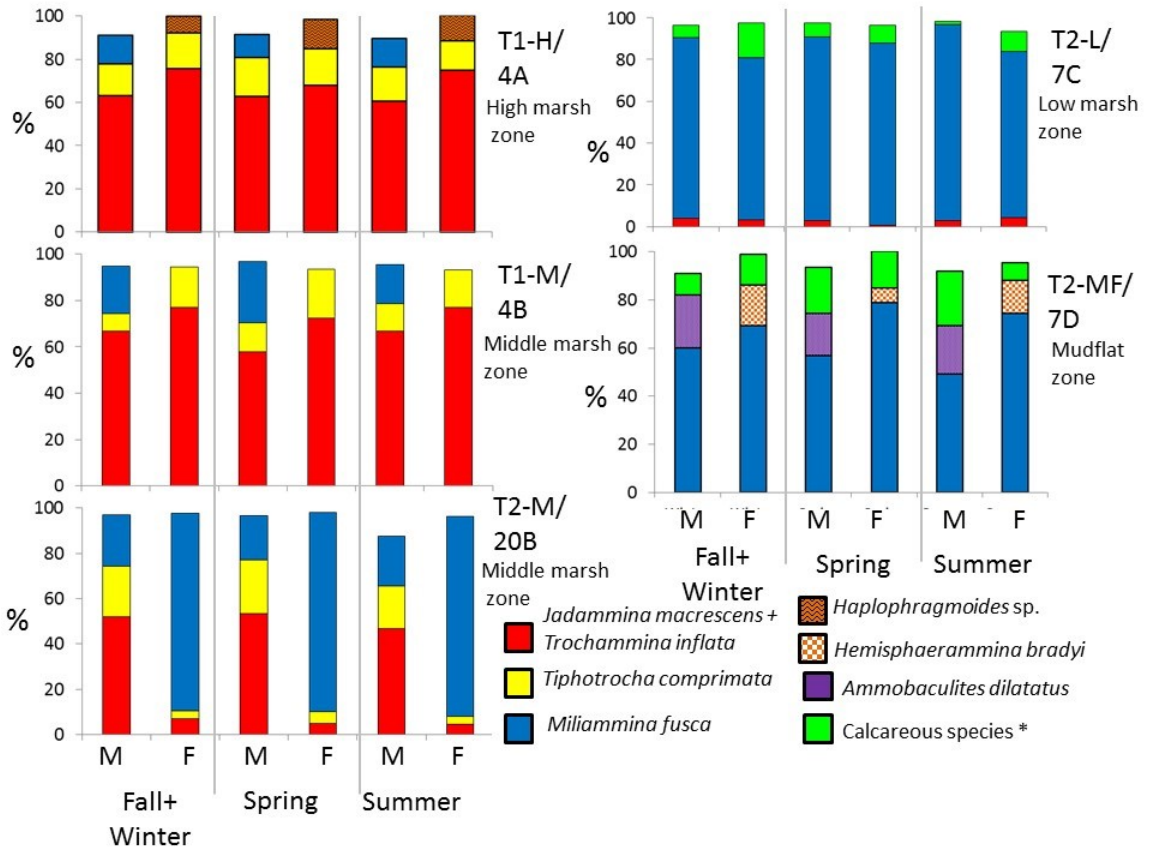

Figure 2.13: Average relative abundances (%) of dominant foraminifera (>5% of total) in mesocosm (M) and field (F) foraminifera for each zone (M: T1, T2, H (high), M (middle), L (low) and MF (mudflat) zones; F: 4A through 7D) over each season. Calcareous species same as figure 2.12.

2.4.4 Key results

1) Established with field slabs from a natural marsh, the laboratory mesocosm remained viable (live vascular plants in correct elevational zones, abundance of live foraminifera and meiofauna) over the full two-year period of investigation. Although some laboratory environmental parameters were invariable, mesocosm vegetation followed a strong seasonal cycle and continued to flourish (Fig. 2.4). The systematic foraminiferal results showed that distinctive assemblages were maintained in marsh zones defined by tidal inundation.

2) Salinity values were broadly concordant between mesocosm and field sites. In both field and mesocosm, average salinity was lower in the high and middle marsh zones than in the lower zones and mudflats (Figs. 2.5-2.6). However, seasonal changes in salinity were significant in the field (except in the lower zones of the outer inlet (7C and 7D), which had > 20 psu in all seasons: Table 2.2). There were no significant seasonal differences in the mesocosm.

3) Comparing elevation zones, salinity and foraminiferal results show a generally good match between comparable mesocosm and field zones. The mesocosm high salinity middle marsh zone (T2-M) and field site 20B showed the least good fit, with considerable differences in salinity and foraminifera (total abundances, relative abundances).

4) Comparing seasonal results, foraminiferal total and relative abundances showed few clear seasonal distinctions, either for zones or for combined mesocosm and field samples (Fig. 2.7; Table 2.3). Mesocosm foraminifera total abundances also show no significant difference across seasons for each zone (Fig. 2.9).

5) Combining data from all seasons, there are significant differences in foraminifera across elevational zones, as well as some differences between results for field zones and comparable mesocosm zones (Table 2.4, Figs. 2.10-2.13). Total abundances of

foraminifera in mesocosm samples are significantly higher than those in field samples, except for greater abundance in field mudflat samples.

6) Despite some differences, elevational zones emerge as the most important control on foraminiferal distributions and assemblages for both field and mesocosm (Figs. 2.10-2.11). The high and middle marsh zones cluster separately from the low marsh and mudflat zones. An exception is 20B/T2-M where 20B clusters with low marsh and mudflat zones whereas T2-M clusters with high and middle marsh zones.

2.5 Discussion

2.5.1. Comparison to other salt marsh mesocosms

This work examines foraminiferal spatial and temporal foraminiferal assemblages in a laboratory setting. Overall, the analysis of salinity and foraminiferal patterns confirms the similarity between the mesocosm and the natural salt marsh at Chezzetcook Inlet. For example, despite the indoor laboratory location and uniformity of air temperature and light regimes in the mesocosm, the temperate salt marsh plants replicated seasonal cycles of vegetation over two years. Although not subject to freezing temperatures, the plants died off during the fall-winter months (October to March) and regenerated as shoot and leaf growth during the spring and summer, indicating a different endogenous response from the solar or lunar rhythms reported for marsh nekton (Rountree and Able, 2007). Mesocosm foraminiferal changes do not show statistically significant differences across seasons, although there are some differences. For example, there are more calcareous species in the spring and summer in comparison to the fall-winter in the mesocosm

mudflat. A change in relative abundances of calcareous species over different seasons also was found at Chezzetcook (Scott and Medioli, 1980b) and in other temperate salt marshes, such as Cowpen Marsh, UK (Horton and Edwards, 2003), and North Norfolk, England (Saad and Wade, 2017). Averaging the data over two years, seasonal foraminiferal assemblages in the mesocosm show less seasonal variation than the field samples. The vegetation in the mesocosm did exhibit marked seasonality, however (Fig. 2.4). This may reflect the marked seasonal temperature changes of incoming ocean water available in the Aquatron. If so, these findings suggest that, other than natural cycles, average water temperature is a more important driver of seasonal change in a cool-temperate marsh than air temperature and light, which were held at summer values in the mesocosm. The lack of significant changes in mesocosm foraminifera across season may also be driven by the constant amount of incoming light, which replicates neither seasonal sunlight cycles nor short-term changes due to storms or winter ice cover.

There have been few other comparable marsh mesocosm studies over the last 30 years. They range from simple to complex, located in the field, greenhouses, or laboratories. Mesocosms are not expected to be exact replicas of the natural system, but are representative enough to answer questions too complex for small microcosm or culture analyses, and impossible to define in field studies (Pennington et al., 2004). Padgett and Brown (1999) used a similar engineering design to the present mesocosm, including continuous seawater inflow and a timed drain, to simulate tidal cycles for an outdoor mesocosm in the warm climate of North Carolina. Their study examined the effect of soil drainage and organic content on the growth of cordgrass *Spartina alterniflora*, using different proportions of clean sand and peat moss to manipulate

substrates for seedling rhizome growth. Growth was successful and monitored over a year. Other similar designs to the present mesocosm involve a modular system with a high, middle, low marsh and/or mudflats, though they use recycled seawater in reservoir tanks to create diurnal tides (see Pennington et al., 2004; Cleveland et al., 2012). A simpler approach (Sharpe and Baldwin, 2012) used a greenhouse mesocosm with small, shallow pans and artificial seawater, in warm temperate Chesapeake Bay. Marsh soil containing wild seeds was injected onto the pans and studied to determine the effects of salinity and inundation on salt marsh plant growth; the impact on biodiversity, freshwater and oligohaline communities were also studied. Marsh plant growth was successful over a year, and inundation frequency did not significantly influence species richness or biomass. The results were considered useful for forecasting saltmarsh plant community response to sea-level rise, but the long-term effects of artificial seawater were not evaluated.

Salt marsh mesocosms are also important for use in pollution studies where toxins can be tested without damage to the natural environment and the impacts of invasive species can be studied without harming the native marsh. Some mesocosms are used as a baseline for responses of the system to a contaminant or chemical, such as the use of vegetable oil biodiesels to clean oil spills on different sediment types (Pereira and Mudge, 2004). Though conclusions could not be made, these studies showed that field work with oil spills and trial remediation techniques is often not practical. In coastal wetlands, secondary impacts of attempts to clean up the oil spills can be more damaging than just letting the environment recover without intervention. Although it takes longer

for the wetlands to recover naturally, this approach may be preferable to using physically or chemically-invasive clean up methods (Dowty et al., 2001).

Other mesocosms use field transplants to monitor the growth of salt marsh plants or mangroves under quasi-controlled abiotic conditions in the field where plots are subject to nutrient enrichment that simulates eutrophication of coastal waters (Feller, 1995). Cleveland et al. (2012) examined the effects of silver nanoparticles on phytoplankton, *Spartina alterniflora*, and a variety of small invertebrates, following the design of Pennington et al. (2004) who studied the impacts of an agricultural insecticide on a salt marsh ecosystem. This modular estuarine mesocosm design was also used to examine how antifouling chemicals that kill photosynthetic organisms impact primary consumers (DeLorenzo et al., 2009). Though these mesocosm studies answer questions about cause-and-effect in salt marsh ecosystems, none have directly compared the results to archival field data, and we are not aware of other mesocosm studies that focus on foraminifera.

Although a mesocosm has many advantages, it is a challenge to create and manipulate salt marshes in a small setting because natural low-energy tidal environments experience strong fluctuations in physical parameters. No published study over the last 20 years has demonstrated that a mesocosm can fully replicate the field. For logistical reasons and simplicity, Pennington et al. (2004) and DeLorenzo et al. (2009) did not modify the tidal inundation levels over the course of their experiments and they did not attempt to completely replicate short- and long-term weather variability. They also kept air temperature at ambient conditions, and salinity constant at 20 psu.

The shortcomings of mesocosms, however, may be outweighed by the advantage of frequent sampling under standard conditions, allowing rigorous experiments on mitigation of human impacts such as pollution and biological invasions. This knowledge is currently needed in a time of intense coastal development and wetland loss (Scott et al., 2014). Nova Scotia has already lost over 65% of all salt marshes (Bowron et al., 2009), and there is an urgent need to understand, conserve, and hopefully re-establish these important ecosystems. The present mesocosm shows that temperate-region salt marsh plants and foraminifera continue to grow well for at least two years in laboratory conditions, providing opportunity for experiments under conditions that cannot be regulated in a natural marsh (e.g., storm occurrences, invasions, anthropogenic pollutants). In a controlled environment, key parameters can be manipulated and specific causes and effects can be monitored. Future work could regulate physical parameters, such as daylight, salinity, and tidal height, to investigate the importance of specific parameters (abiotic or biotic). Although the laboratory mesocosm does not precisely replicate field conditions, the results show that it provides a reasonable representation of a temperate salt marsh system that has been extensively studied *in situ*.

2.5.2. Field versus mesocosm foraminiferal comparisons and implications.

A primary purpose of the mesocosm study was to investigate the spatio-temporal dynamics of temperate saltmarsh benthic foraminifera from the Chezzetcook type locality under year-round controlled conditions. The mesocosm allowed the first year-round sampling of foraminiferal assemblages over a two-year period that included fall and winter, in comparison with 1976–1978 field sampling (Scott and Medioli, 1980a,b) that

contained 3-month winter gaps. Total foraminiferal assemblages from four mesocosm zones show a similar diversity to the field sites, with a similar zonal distribution for four agglutinated and three calcareous taxa (Figs. 2.12 and 2.13). These zonal patterns are crucial for determining high-resolution sea-level change in fossil records (e.g., Scott and Medioli, 1980a) and are discussed further below.

Important biological limitations of the mesocosm include the absence of most insects and other macrofauna (e.g., crabs, fishes), the use of seawater filtered to remove larger planktonic diatoms, and the absence of potential nutrient inputs from windblown dust and pollen (Frail-Gauthier and Mudie, 2014). Gnats and midges were common in the mesocosm, both as larvae and adults, and gastropods were numerous, but bivalves, fish and birds were missing. Nevertheless, there are relatively few differences in foraminiferal results between the 1970s field data and mesocosm data obtained over two years. A probable explanation is that marsh foraminifera are generalistic detrital, bacterial and phytoplankton feeders (Chandler, 1989; Lesen, 2005) and found ample plant detritus and microbiota in the mesocosm (see Chapter 5 on results of feeding experiments).

The largest difference in foraminiferal patterns was the higher mesocosm total abundance for all zones and seasons, except for the mudflat (Figure 2.8). Although marsh temperatures were not measured in the field, there was most probably equilibrium between air temperature and surface water temperature for the well-mixed, shallow marsh and mudflat (Fig. 2.3). Assuming that marsh foraminifera are not light-sensitive as they do not depend on photosynthetic symbionts as a sole food source, temperature showed the largest differences between field and mesocosm. Hence, periods of freezing likely slowed Chezzetcook foraminiferal population growth from November through March,

when temperatures dropped below freezing of seawater at -2^{o}C. Additionally, temperate marshes have reproductive blooms throughout the year (most often in the spring and early fall). These population blooms cause large changes in total and relative abundances, with the magnitude depending on which species have reproduced. However, paralic foraminifera do not have consistent life cycles, leading to a seasonal variability that is not necessarily replicated interannually at the same location (Morvan et al., 2006). In the winter, post-mortem transport and storms in paralic settings may decrease the total abundances for the following year. In the present laboratory mesocosm, the lack of tidal flushing, freezing and storm replication apparently kept numbers consistently much higher than the field, potentially reaching the carrying capacity of the population (described in Murray, 2003) in each salt marsh zone. In the mesocosm, temperatures may have been consistently high enough to allow the foraminifera to steadily thrive, as temperature is known to be a key factor in inducing foraminiferal reproduction (Bradshaw, 1968). Additionally, warmer soil conditions in the mesocosm allow for continual soil decomposition by bacteria, providing a consistent food supply for foraminifera.

The minimal abundance differences in the mesocosm mudflat samples, however, are difficult to explain. Environmental stresses, particularly large salinity fluctuations, increase as elevation ASL increases, leading to a lower diversity of species but much higher abundances of a few well-adapted key indicator species (Horton and Murray, 2007; Martins et al., 2014; Strachan et al., 2017). In the mudflat, biological interactions (competition, predation) may play a bigger role in controlling foraminiferal assemblages than in the middle and high marshes, as biotic factors may exert a more direct control on

foraminifera than abiotic factors in this environment (Hohenegger et al., 1989). However, Alve (1999) found that biotic control was a primary factor regulating marsh interactions whereas physical factors were more important in the mudflat ecosystem.

With increasing species diversity, there can be an increase in foraminifera interspecific competition (Matera and Lee, 1972; Martins et al., 2014) and differential rates of feeding on microalgae may cause large fluctuations in calcareous species such as *Ammonia* and *Haynesina* (Wukovits et al., 2017). On the mesocosm mudflat surface, there is also a higher diversity of potential foraminiferal predators, especially non-selective deposit-feeding polychaetes and grazing snails such as *Ecrobia truncata* and small *Littorina littorea* that were seen non-selectively consuming foraminifera (personal observations, Buzas, 1978). Species such as *Elphidium* spp. can be dense, and are epiphytic on soft, easily flushed sediments such as fecal pellets (Linke and Lutze, 1993); in the mesocosm, they formed dense colonies on filamentous algal mats (from examining samples of algae under the stereomicroscope). The highly unstable calcareous mudflat populations show high post-mortem dissolution because of low environmental pH, and are easily removed from the mudflat surface by storms. These factors could explain their larger seasonal changes in the field than in the mesocosm. The summer increase in calcareous numbers is pronounced in the field due to the higher salinity and pH (Scott and Medioli, 1980b; Horton and Edwards, 2003; Camacho et al., 2015).

Salinity also fluctuated less in the mesocosm than in the field. The combined effect of no freezing and more uniform salinity may result in a less-stressful physical environment favouring higher reproductive rates (Weinmann and Goldstein, 2016). *Trochammina inflata* shows a positive correlation with salinity in Nova Scotia (Table

2.4), but a negative correlation with salinity in other areas (Horton and Murray, 2007), which demonstrates the within-species variability across different localities. In general, agglutinated taxa predominate in lower salinity water (0 to 30 psu) and calcareous species in higher salinity water (Horton and Murray, 2007). When comparing different marshes with similar elevational zones, salinity appears to be the biggest cause for variability of foraminiferal assemblages, as in Connecticut, USA (Edwards et al., 2004) and Caminha, northwest Portugal (Fatela et al., 2009). The importance of salinity as a distributional control of foraminifera is also confirmed by the review of Debenay and Guillou (2002).

2.5.3. Foraminiferal zonation

Overall, elevation above sea level is the most important parameter affecting foraminiferal zonation in both the field at Chezzetcook Inlet and the mesocosm (Figures 2.10 – 2.11), rather than temporal changes. The same dominance of spatial rather than temporal effects is found in the Yellow Sea, China (Lei et al., 2017), Norfolk, England (Saad and Wade, 2017) and in the well-studied Cowpen Marsh, UK (Horton and Edwards, 2003). For ecosystems, elevation is not an exact environmental parameter itself, as it is related to salinity, inundation, sediment type and particle size, and pH (Edwards et al., 2004; Fatela et al., 2009; Camacho et al., 2015; Strachan et al., 2016; Saad and Wade, 2017). Foraminiferal assemblages in salt marshes are specific to sites, regions, and localities, making global comparisons challenging. The distribution of modern assemblages needs to be defined for a specific marsh before attempting to interpret paleoenvironmental conditions for that marsh (Edwards et al., 2004). The Chezzetcook work of Gehrels et al.

(2005) shows that tide gauge data were much more variable than estimates of sea-level interpretations based on high-marsh foraminiferal zonations.

In general, specific zonal trends are seen in salt marshes around the world, although salinities and elevations vary. Because some species are dependent on multiple factors, key assemblages need to be used rather than individual taxa (Edwards et al., 2004). At Chezzetcook Inlet, high and middle marshes are dominated by calcareous *Jadammina macrescens* (= *Entzia macrescens* Brady, 1870) and *Trochammina inflata* (4A/T1-H, 4B/T1-M; Figures 2.12 – 2.13), and low marsh and mudflats are dominated by arenaceous *Miliammina fusca* and diverse calcareous species. Also the arenaceous agglutinated *Ammobaculites* is common in the mesocosm mudflat (T2-MF); this taxon is a common tidal flat species in other salt marshes around the world (Strachan et al., 2017).

In cool-temperate marshes of Nova Scotia, high and middle marsh fauna *J. macrescens* and *T. inflata* are distributed most strongly in accord with elevation, rather than salinity or other environmental factors (as in accordance with results from Horton and Murray, 2007), making this assemblage the best for determining paleo-sealevel rise. This relationship to elevation has been extensively validated around the world: for Chezzetcook Inlet (Scott and Medioli, 1980a), Galpins salt marsh, Natal South Africa (Strachan et al., 2015, 2016, 2017), Guadiana Estuary, southeastern Portugal (Camacho et al., 2015), Cowpen Marsh, UK (Horton and Edwards, 2003), Connecticut, USA (Edwards et al., 2004), and the Bay of Tumlau, German North Sea (Müller-Navarra et al., 2016). Though the same general low marsh and mudflat assemblages are also common throughout these salt marshes, they are more susceptible to variability within and between sites and are not as useful for paleoenvironmental reconstructions. Rather than

elevation, these assemblages tend to follow other environmental variables, such as a higher salinity, higher pH, a sandier substrate, and more biological interactions (Saad and Wade, 2017 and references therein).

Common middle – low marsh faunas (*Tiphotrocha comprimata*, *M. fusca*) are more variable in their distributions between the field and mesocosm (Figures 2.12 – 2.13). This may explain the disparity seen between T2-M and field site 20B. Though these two sites were considered comparable due to similar elevations and visible *Spartina* grass cover (mostly *patens* with mixed *alterniflora*), they are differentiated based on their foraminiferal assemblages (Figures 2.11 – 2.13). The field site has an assemblage with strong low-marsh affinities and the mesocosm equivalent has a middle-marsh assemblage. The zonal distribution of *T. comprimata* varies between sites (within and between marshes) and it is often found in low – high marsh transition zones in areas of higher salinity (Edwards et al., 2004). *Miliammina fusca* is known to outcompete other species (Scott and Medioli, 1980b) and can be found throughout the marsh, under a range of various environmental conditions (Murray and Alve, 1999).

2.5.4. Value of laboratory salt marsh mesocosms, limitations, and future work.

Overall, the present mesocosm provides a robust artificial marsh with similar foraminiferal assemblage patterns across elevational gradients that are found in the field (Chezzetcook) and in other marshes around the world. This was an exploratory test to validate its resemblance to field assemblages and distributions, which needs to be established before future experimental work (Pennington et al., 2004). Detailed mesocosm experiments for paleontological interpretations might investigate preservation

potential, dissolution / diagenesis related to pH and water composition, and paleoclimatic inferences for preserved foraminifera in cores as a result of controlling for climate-related factors.

Limitations to replicating a temperate salt marsh are common drawbacks seen in other mesocosms (section 2.5.1). Excluding winter ice devalues key seasonality trends (though seasonality is not the major determinant of salt marsh foraminifera zonation, as previously discussed). Future studies replicating freezing conditions could provide more details about biological limits and seasonal cycles of foraminifera, or could manipulate temperatures for examining climate change. Other issues with the present mesocosm are related to salinity. Future experiments could involve changes in tidal inundation and variable freshwater input to better replicate natural conditions.

Another key factor that could account for the foraminiferal differences between the mesocosm and field is the constant high amount of UV light in the mesocosm. Although salt marsh foraminifera are known to be heterotrophs, some species may harbour diatom photosymbionts (e.g., calcareous *Haynesina germanica*, Jauffrais et al., 2017). The high amount of light in the mesocosm, which does not change seasonally or replicate storms or cloudy days, may cause increased algal production and promote foraminiferal abundance, especially for the calcareous forms associated with algae in the mudflat. Future experiments could investigate this issue.

2.5.5. Biological and ecological analysis of mesocosm foraminifera

Related to question 3, the initial mesocosm setup was not designed to explore the biotic relationships of foraminifera and associated meiofauna (published in Frail-Gauthier and

Mudie, 2014). The mesocosm data are also potentially important in providing controlled calibration of marsh foraminifera and meiofaunal remains recovered in palynological residues from the same samples (Frail-Gauthier and Mudie, 2014). The organic, chitinous faunal remains (microforaminiferal linings, nematodes, crustacean eggs, mandibles of ostracodes and larval insects) are part of a rapidly growing field of palynological study of NPP (non-pollen palynomorphs; Mudie et al., 2011). The organic-walled zooplankton remains in palynological samples are a crucial component of sequence-stratigraphic analysis used in petroleum exploration where preservation of microfossils is variable, and for verification of marine vs. freshwater designations in ancient seas, e.g., the Paratethys (Orszag-Sperber, 2006) and in periodically isolated marine basins like the Black Sea (Londeix et al., 2009).

Future studies considering the modern distributions of salt marsh foraminifera need to incorporate their associated benthic community (meiofauna) to see if competition and predation play a role (Papaspyrou et al., 2013). In Arachon Bay in southwest France, foraminifera account for 7% of oxygen uptake in mudflat sediments, emphasizing their noteable metabolic role (Cesbron et al., 2016). They are more ecologically and biologically important than previously assumed, and contribute to the salt marsh ecosystem through herbivory, dissolved organic matter (DOM) uptake, bacteriovory, and deposit feeding, and Cesbron et al. (2016, p. 33) consider that it is "…urgent to study these topics in more detail". These biological interactions may help to explain the small-scale spatial heterogeneity common in salt marsh foraminiferal analyses and to examine the variability seen in low-marsh and mudflat assemblages. Biotic effects are considered

in Chapters 3 – 5. Unpublished foraminifera and meiofauna counts from the mesocosm are archived for use in future publications.

2.6. Conclusions

A salt marsh mesocosm using samples from the well-studied Chezzetcook Inlet, Nova Scotia, provides a quantifiable test of how well natural foraminiferal assemblages and distributions were replicated in a controlled laboratory setting. Mesocosm results matched relative abundance trends of foraminifera at equivalent field sites to a significant degree. High and middle marsh zones yielded the most comparable results.

Mesocosms are a potentially important experimental tool for examining specific ecological and environmental questions in detail, and the first step is to show that they are valid representatives of the natural environment. Over two years, the temperate climate laboratory mesocosm maintained high abundances of key representative zonal taxa (*Jadammina macrescens*, *Trochammina inflata*, *Miliammina fusca*). These high total abundances may reflect the fairly constant environmental parameters that favor foraminiferal reproduction in the mesocosm, and also the lack of storms and strong tidal flushing. The duration of tidal inundation may be a more important physical determinant than salinity and water temperature, and it appears that light is not a limiting factor for key marsh foraminifera that are omnivorous or primarily detrital feeders. Though foraminiferal species distributions throughout the marsh zones follow a strong physical gradient, small-scale spatial and temporal heterogeneity is common in foraminiferal assemblages.

Although the mesocosm was not designed to explore biotic factors, foraminiferal assemblages are highly constrained by biological factors (food, competition, predation, reproduction). This is especially true for zones with high variability within and between marshes throughout the world (i.e., low marsh and mudflat assemblages). These interactions need to be accurately defined in order to fully understand salt marsh foraminiferal distribution patterns, and are explored in later chapters in this thesis.

CHAPTER 3: TAXONOMIC RESOLUTION AND TIDAL GRADIENTS IN FOOD WEBS FOR TWO TEMPERATE SALT MARSHES: HOW MUCH DETAIL IS ENOUGH?

3.0 Abstract:

Sufficient taxonomic detail is crucial, but rarely examined, for correct interpretation of the structure, function and dynamics of ecosystems. Salt marshes are extremely productive, highly heterogeneous coastal ecosystems, with large spatial gradients controlled by tides. The cool, temperate region of Nova Scotia, Canada, has macrotidal marshes in the Bay of Fundy and mesotidal marshes on the Atlantic coast. Here we compiled high-, medium- and low-resolution metafood webs for a young macrotidal Fundy marsh at Windsor, and a mature mesotidal Atlantic marsh at Chezzetcook Inlet, and high-resolution webs made for tidal zones in each marsh. The species list for these two marshes includes 281 taxa and almost 6000 feeding links. The high-resolution webs contain nodes down to the highest taxonomic detail possible; medium-resolution webs exclude foraminifera, and low-resolution webs amalgamate basal and invertebrate species into 50% fewer nodes. To compare our salt marsh food webs, we use the niche mode which predicts food web properties by assigning species to a feeding hierarchy. The species-rich (S>100) high-resolution marsh webs have significantly higher *% Herbivores* than predicted by the niche model; however, the low-resolution webs are a better fit for the niche model, indicating that current food-web predictor models do no fully capture ecosystem dynamics in species-rich webs with a high number of links. The low-resolution webs over emphasize higher trophic-level groups and increase the web

connectance by taxonomic aggregation, leading to interpretations with reduced validity of the marsh ecosystem structure and function. Food webs for each tidal zone in the two marshes show that low marsh and mudflat are more similar to each other than to the more terrestrially-influenced middle and high marshes. Although there are no significant differences between the marsh metawebs, the food-web structure of the young Windsor marsh, with extensive low marsh, favours restoration within a short period. This study emphasizes the need for using high-resolution food webs for detrital-based bottom-up salt marsh systems and the need to examine spatially heterogeneous tidal-marsh food webs in smaller increments (tidal zones) along the elevational and salinity gradients.

3.1. Introduction

Food webs are complex networks of feeding interactions that occur between and among species coexisting within an ecosystem (Dunne, 2009; Baskerville et al., 2011). They are a model of the underlying architecture of energy flow through an ecosystem. By assembling and analyzing food webs, researchers study a network that involves interactions between consumers and between consumers and producers, across spatial and temporal scales (Baskerville et al*.,* 2011). The world's most spatially diverse ecosystems are estuaries (Vinagre et al., 2017), including salt marshes (Scott et al., 2014). Because of the tidal range and terrestrial influence, salt marshes are extremely heterogeneous in terms of salinity, temperature, substrate, and other factors, which in turn generate a heterogeneous distribution of plants and animals and complex food-web interactions. As food webs are a network, species or another taxonomic entity (e.g., genus/family) are represented as nodes. Feeding interactions are links between nodes.

Thus, an ecosystem can be emperically modeled in its entirety (Dunne, 2009) and its component habitats compared (Vinagre and Costa, 2014). Additionally, community organization can demonstrate the resilience of the ecosystem towards extinction, changes in population dynamics, and disturbance (Baskerville et al., 2011; Coll et al., 2011; Schmidt et al., 2011). Food-web analysis is a robust and informative way to compare structural and functional differences in ecological communities. It can demonstrate how community structure changes along geographical and environmental gradients and in response to anthropogenic disturbance (e.g., Vinagre and Costa, 2014; Tao et al., 2015; Wood et al., 2015).

Many food-web parameters are sensitive to the level of taxonomic detail, and food webs may undersample the natural system or overwhelm the analysis by including every possible feeding link (Layer et al., 2010). A low-resolution web uses groups of taxa that represent functional groups, size classes, or similar aggregates. Many food web studies focus on the pelagic zone (e.g., fishes) and examine the whole ecosystem with fine-tuned vertebrate taxa and often only the larger invertebrates (e.g., crabs), but the inclusion of benthic biota and invertebrates is key to proper interpretation of ecosystem functioning (Sanchez-Hernandez et al., 2015). Smaller salt-marsh fauna and lower trophic groups are often combined as "detritus" or "small invertebrates" despite disparity of ecological function. I am the first to include, in a salt-marsh food web, the meiofaunal species (usually less than 1.0 or 0.5 mm but greater than 0.063 mm), which comprise a large part of the benthic sediment (see Coull, 1973).

Foraminifera, harpacticoid copepods, and nematodes can make up 95% of the meiofauna and can consume enough detritus and bacteria to void the sediment of

nutrients, emphasizing their ecological importance (Chandler, 1989). In San Francisco Bay, foraminifera are quick to exploit either phytoplankton or detritus, whichever is in highest abundance (Lesen, 2005). In general, these foraminifera form a vital trophic link in marine communities and are known prey items of fish, most taxonomic groups of invertebrate meiofauna, and small macrofauna (Lipps, 1983; Culver and Lipps, 2003). Although these meiofauna represent only 10% of the biomass of macrofauna in mudflats, they have over 1.5 times the throughput and two times the secondary energy production (Leguerrier et al., 2003). There are many studies on foraminiferal (and meiofaunal) distributions but few on their specific ecological roles (Lesen, 2005). Meiofauna and small macrofauna are the major food source of the larger macrofauna (fish and birds) that use salt marshes as feeding and nursery grounds. Although small-scale food sources are a crucial component of ecosystem dynamics, their inclusion in food webs has yet to be assessed.

Previous studies of spatial gradients and scales in food webs have covered latitudinal changes between warm temperate and tropical regions (e.g., Marczak et al., 2011, for salt marshes), physical parameters (e.g., pH, Layer et al., 2010), anthropogenic disturbance (e.g., seagrass beds, Coll et al., 2011), and estuarine salinity (Vinagre et al., 2017). For salt-marsh food-web ecology, spatial gradients related to the tidal regime must be included because the seaward gradient of salinity and other physical and chemical factors correspond to changes in the biological communities (Bergamino and Richoux, 2015). For example, the dependence of consumers on salt-marsh grasses, algae or seagrasses will change across zones (Olsen et al., 2011). Food web studies normally do not focus on the small-scale biology, and interpretations of the entire ecosystem are based

on properties heavily biased to large scales and thus lack details about small-scale variability and site-specific differences (Vinagre et al., 2017). Thus, food webs need to be examined not only for an entire salt marsh but also for component zones from mudflats to the high marsh (Vinagre and Costa, 2014).

3.1.1. Objectives

In order to address the aforementioned concerns, we compare cool temperate marshes at Windsor and Chezzetcook in Nova Scotia, which have strongly contrasted age, tidal and ice regimes on the macrotidal Bay of Fundy and the mesotidal Atlantic coast, respectively (Fig. 3.1). We use food webs to explore salt-marsh ecological structure and function in terms of three key questions. Firstly, how much taxonomic detail is needed to capture ecosystem dynamics? Specifically, how important are the foraminifera, meiofauna, and small macrofauna to the food web? Low-, medium-, and high-resolution food webs are compared to investigate these questions. Secondly, how important are spatial gradients when comparing the food webs of entire marshes (termed here metawebs) with component tidal zones from the mudflat to the high marsh? Thirdly, how do high-resolution food webs differ for a newly-formed marsh in a macrotidal setting (Windsor) and an old, stable mesotidal marsh (Chezzetcook)? We also provide the first highly-resolved taxonomic species list (excluding endoparasites and rare transients such as humans and their pets) for each marsh, constituting a baseline for future monitoring.

3.2 Study areas: Windsor and Chezzetcook marshes

The Windsor marsh (Figure 3.1) is a young salt marsh developed after the construction of a tidal barrier. Windsor Causeway is a rock structure built in 1970 across the Avon River estuary at Windsor (45°00'N, 64°08'W). The estuary is in the Minas Basin in the upper reaches of the Bay of Fundy (Fig. 3.1), a large macrotidal system with estuaries and bays where semidiurnal tidal height exceeds 15 m (Table 3.1). Sediment load (>150 mg L^{-1}; Daborn et al., 2003) is high in the basin due to strong currents and winter ice action that erodes tills and cliffs (Amos and Long, 1980). A sedimentation rate of 15 cm mos^{-1} in front of the causeway (BoFEP, 2008; Bowron et al., 2009) slowed to 0.5 cm mos^{-1} in the early 2000s (van Proosdij, 2005). The mudflat grew rapidly, reaching an average elevation above sea level of 4.70 m (Townsend and van Proosdij, 2002) and an area of over 1 km^2. Ten years after causeway completion, *Spartina alterniflora* appeared in an isolated patch, and by 1992, over 30 patches existed. Between 1995 and 2001, *Spartina* covered from 41,000 m^2 to over 390,000 m^2 of the mudflat. Based on satellite estimates using polygons in Google Earth®, visible *Spartina* cover in 2015 was over 1 km^2 (1,000,000 m^2), not including cover along the outer banks (see Figure 3.1).

Low marsh predominates at Windsor (Tables 3.1 and 3.2). A measured transect from the rock levee to the main tidal channel is approximately 90 m long, with a barren mudflat 20 m, low marsh 60 m, and narrow high marsh <10 m long. The mid marsh usually found in mature marshes is an abrupt, barely distinguishable transition from low to high marsh. The extensive low marsh at Windsor probably reflects the high tidal elevation, the young age (mature Fundy marshes have less low marsh [Byers and Chmura, 2007]) and a high sedimentation rate that allows mudflat colonisation by the

rapidly-spreading halophytic grass *Spartina alterniflora*. Newly restored marshes in the Bay of Fundy also exhibit large monospecific zones of *S. alterniflora,* with minimal floral diversity in the upper marsh (Smith et al., 1980; Bowron et al., 2009).

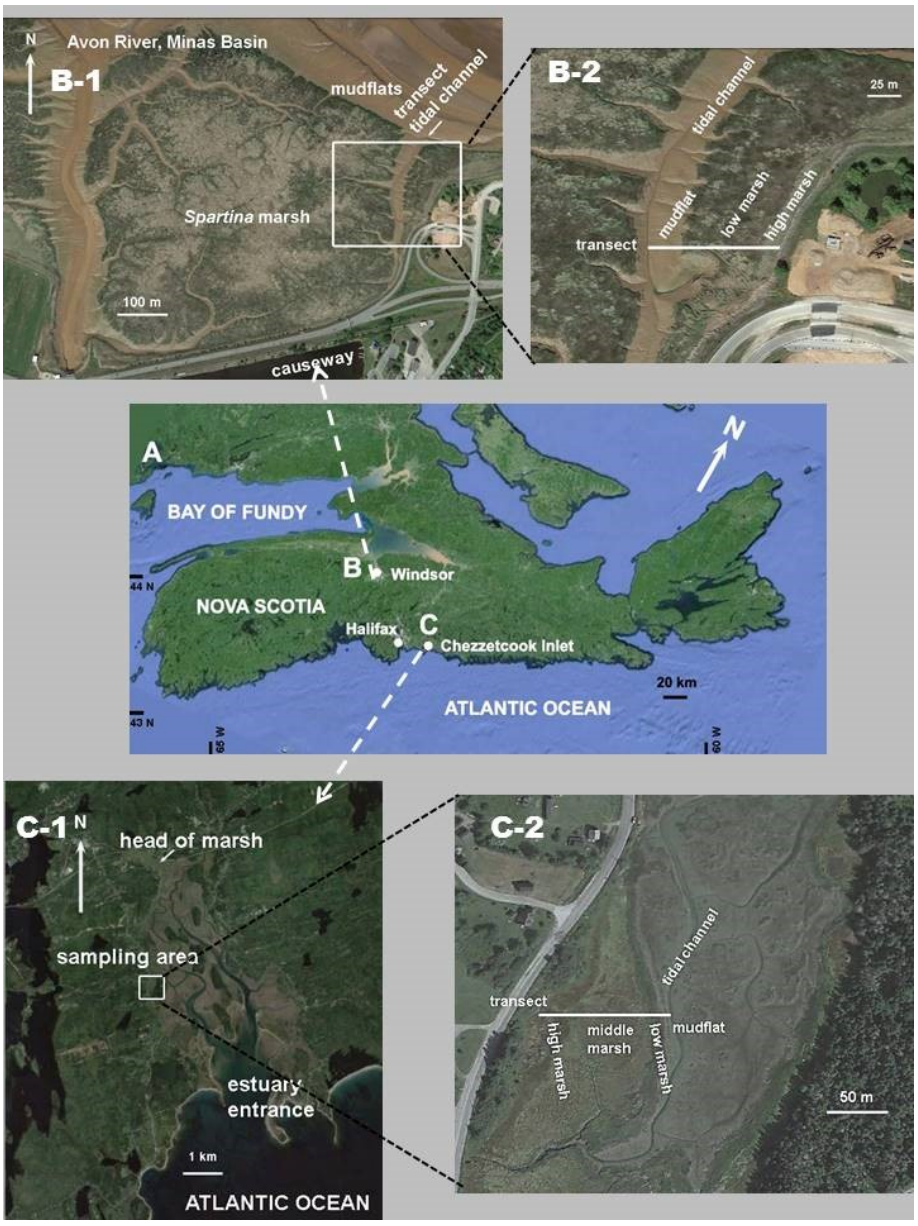

Figure 3.1. (A) Map of Nova Scotia showing locations of Windsor Causeway and Chezzetcook Inlet marshes. (B) Windsor Causeway marsh in the Minas Basin, Bay of Fundy, north of the constructed causeway. (C) Chezzetcook Inlet on the Eastern Shore of Nova Scotia, Atlantic Ocean. White squares are locations of sampling transects of B and C, which are enlarged in B-2 and C-2, respectively. Images from Google Earth (DigitalGlobe).

Table 3.1: Parameters for Chezzetcook (Atlantic Ocean) and Windsor (Bay of Fundy) salt marshes in Nova Scotia, Canada. MSL = Mean Sea Level. Windsor data from Daborn et al. (2003) and Chezzetcook data from Scott and Medioli (1980a).

Property	**Chezzetcook**	**Windsor**
Latitude	44˚44'23 N	44°59'75 N
Area	~14 km^2	~1 km^2
Transect zone widths*	Mudflat: 5 m Low marsh: 2 m Middle marsh: 50 m High marsh: 20 m	Mudflat: 20 m Low marsh: 60 m High marsh: 9 m
Age	~4000+ years	~40 years
Sea surface temperature	Monthly average 0.5 –15.6 ˚C Annual average 7 ˚C	Monthly average 0.6 –17 ˚C Annual average 8 ˚C
Salinity[+] (psu)	10 – 33	15 – 27
Organic Matter (%)[†] in mudflat	>15%	<10%
Water nutrients*	Nitrate – 0.6 mg L^{-1} Phosphate – 2.0 mg L^{-1}	Nitrate – 2.9 mg L^{-1} Phosphate – 20.0 mg L^{-1}
Tidal range	1.5 – 2 m	15 m
Mean elevation	<2 m above MSL (shallow slope to main channel)	4.7 m above MSL (steep slope from *Spartina* low marsh to main channel)
Winter ice	Thin (<20cm) depending on snow amounts, flat over marsh surface	Thick (locally up to 4 m) with large ice and mud boulders

[+] Tidal water salinity where possible; if no water over area sampled, depressions were made and filled with water to sample, therefore salinity also reflects porewater.
[†]Organic matter % is from loss on ignition by Daborn et al. (2003) and Scott and Medioli (1980a).
*From measurements taken in July 2016, analyzed in the Aquatron Facility.

Table 3.2. Descriptions of the vertical salt marsh zones from sampling transects of Chezzetcook Inlet and Windsor Causeway, Nova Scotia, Canada.

Zone	Chezzetcook Inlet Transect	Windsor Causeway Transect
Mudflat	Mesotidal; silty mud with 15% organic matter; anoxic below few mm depth. Long flood duration; flanks main tidal channels. Rare *Spartina alterniflora.* Green algal mats common. Surface sediment feeders (shore flies, mudsnails), burrowers (clams and worms) common. At flood tide fish occur throughout; many birds feed on epifauna and infauna at low tide.	Macrotidal; clayey silt mud with <10% organic matter (Partridge, 2001; Daborn *et al.* 2003). Rare green algal mats; sediment oxidised >20 cm. Wide, deep tidal channels are a vector for fish. At low tide, many migratory birds feed on meiofauna and smaller macrofauna (*Corophium* amphipods and *Hediste* polychaetes).
Low Marsh	Smallest section of marsh; floral cover exclusively *S. alterniflora* which tolerates periodic sediment anoxia (Bertness, 1991). Green algae and cyanobacterial films in bare areas. Periwinkles, crustaceans and worms common. Fish shelter and feed here (DFO, 2012).	Mudflat abruptly transitions to tall monospecific *S. alterniflora* (>1m; Daborn et al., 2003). Upper areas with green algal mats and shallow (<5cm) anoxic subsurface sediment. Most mudflat fauna also occur here. Insects and spiders locally abundant at low tide. Juvenile migratory fish here at high tide.
Middle Marsh	Largest section, with visible transition from *S. alterniflora* to *S. patens* which dominates the mid-marsh. *Salicornia*/*Sarcocornia, Distichlis* and rushes (*Juncus*) present. Insects, spiders, amphipods and pulmonate coffee bean snails dominant invertebrates. Meiofauna and foraminiferans less diverse, but more abundant, than in low marsh	Not represented at Windsor
High Marsh	Weeks without tidal submersion. Root peat. Floral diversity is high; rushes (*Juncus*) displace *S. patens* at the highest elevations; reeds and sedges abundant. Meiofaunal and foraminiferal abundances low. Spiders and insects diverse.	Infrequent submersion. Smallest marsh zone; dominated by *S. patens*. Insects, spiders and amphipods are common invertebrates. Annual glasswort (*Salicornia maritima*) occurs throughout open pan (barren) areas.

The Chezzetcook marsh is in Chezzetcook Inlet (44.70°N, 63.25°W) on the storm-exposed Atlantic Coast (Fig. 3.1) and formed as a drowned drumlin field following

the ice-sheet retreat of the last glaciation (Scott 1977). The uppermost part of the salt marsh is over 4000 years old, and the outer marsh accretes seaward as sedimentation exceeds erosion (Orford et al., 1991). The inlet is 7 km long and 2 km wide, with ca. 14 km^2 of mudflats and salt marshes (Table 3.1). The measured transect from the terrestrial zone to the middle of the mudflat tidal channel is approximately 80 m long, with the barren mudflat 5 m, low marsh 2 m, an extensive middle marsh 50 m, and high marsh 20 m long (Table 3.1). The area is inundated twice daily by low-mesotides (mostly < 2 m) with water of normal marine salinity (30 – 35 psu) distributed through a channel network (Fig. 3.1C). Terrestrial transitional (storm tide zone), high and middle marsh zones are extensive. *Spartina patens* (salt marsh hay) and *Juncus gerardii* (black rush) dominate the middle and high marsh flora, with *Solidago sempervirens* (seaside goldenrod) and many Cyperaceae (sedges, e.g. *Carex palaeceae*). *Spartina alterniflora* exists in the lowest zones, often in narrow bands (less than 5 m) adjoining tidal channels. Glasswort (annual *Salicornia* spp.) is scattered through the low and middle marsh areas, especially covering bare areas produced by sea ice or windrows of seaweed wrack.

The two salt marshes contrast in other ways (Table 3.1). Both have a similar cool temperate climate, but the Windsor marsh has an average annual water temperature about 1 ^{o}C warmer (8 ^{o}C). The entire grass surface of the Windsor marsh is completely removed by ice each winter (see photographs in van Proosdij, 2005), and the seasonal *Spartina* growth (> 1 m height, and biomass; Daborn et al., 2003) greatly exceeds that of Chezzetcook (ca. 50 cm). Windsor marsh has higher water column nutrient levels (Daborn et al., 2003 and Table 3.1), better drainage (no pannes or ponds of standing water), and a deeper anoxic layer (> 10 cm below surface compared to < 1 cm at

Chezzetcook, personal observation based on dark colour change and hydrogen sulfide smell). These variables are preseumed to play an important role in the high *Spartina* growth at Windsor (Daborn et al., 2003). Additionally, these differences allow a robust test of food-web characteristics in marshes from different settings within the same cool-temperate climate regime.

Almost 65% of Nova Scotia marsh area has been destroyed since European settlement. In the Bay of Fundy, 80% has been destroyed since the early 1600s when Acadian agricultural diking began, and less than 15% of original salt marsh area remains within the Minas Basin study area (Gordon, 1989). However, the high marsh elevation, high tidal range, and rapid sedimentation rate (average of 1.3 cm yr^{-1}) give Bay of Fundy marshes resilience to disturbance and promise for low-maintenance restoration (Byers and Chmura, 2007). The Windsor Causeway marsh is one of the most productive in Atlantic Canada (Daborn et al., 2003), and was selected for food-web analysis of a newly-formed salt marsh with a high sedimentation rate (6 cm yr^{-1} or more). In contrast, the Chezzetcook marsh is a low-lying, mature mesotidal marsh representing 200 to thousands of years of sedimentation and plant growth (Chague-Goff et al., 2001). Sedimentation rates are relatively slow, ca. 5 mm yr^{-1}, about 1–2 mm yr^{-1} higher than the rate of sea-level rise (c. 3 – 4 mm yr^{-1}). The marsh has experienced only minor human encroachment since European settlement began c. 1600 AD and is a good reference site for a temperate, relatively undisturbed climax marsh (Chague-Goff et al., 2001). Creating highly-resolved food webs for these two contrasting marshes in cool-temperate areas, approaching the northern range of *Spartina* grasses, broadens the applicability of these food web models and the understanding of these ecosystems.

3.3 Methods

3.3.1 Sample collection and examination

A total of at least 250 samples were collected from the two salt marshes at low tide at monthly or twice-monthly intervals throughout spring, summer and fall seasons for six years from 2011 through 2016. During sample collection, shallow infaunal samples (<5 cm sediment depth) were collected along a vertical transect line 90 m long, divided into vertical zones by vegetation cover and floral composition (Tables 3.1 and 3.2), from the tidal channel to the terrestrial transition. Two 500 ml and two 50 ml sediment samples were taken per zone from random, haphazardly picked locations to account for small-scale spatial heterogeneity as was verified throughout the literature, most recently with Vinagre et al. (2017). During the 1 – 2 hour collection times, highly mobile macrofauna such as insects, arachnids, amphipods and gastropods were collected on site using a net, covered container, or by hand, and unidentified macrofauna were preserved in 75% ethanol or by freezing.

In the lab, the sediment fauna was separated by size using 250, 63, and 45 μm sieves. Small samples (10 ml) were washed gently through stacked sieves using filtered sea water from the Aquatron facility at Dalhousie University. Washed samples were viewed under a Zeiss dissecting microscope (10 – 40x) to identify the taxa. Organisms were identified to the lowest taxonomic level possible using guides and resources available (e.g., Gosner, 1978; Scott and Medioli, 1980a; Sept, 2008). Macrofauna (insects, fish, birds and mammals) that could not be brought back to the laboratory or were not seen at the time of collection were added to the species list based on published local information (e.g., Bromley and Bleakney, 1984; Hatcher and Patriquin, 1981), and

lists provided by A. Hebda, Nova Scotia Museum of Natural History. Species lists compiled by collection on one day in each of five consecutive summers (2012 – 2016) by undergraduate students in a Coastal Ecology field course at Dalhousie University were also added to the taxa, after identifications were confirmed and/or corrected by the lead author.

3.3.2 Food-web construction

Feeding links for all taxa were determined from published literature, online resources (Encyclopedia Online (eol.org), World Register of Marine Species (WoRMS; marinespecies.org), FishBase (fishbase.ca), the Cornell lab of Ornithology (allaboutbirds.org), and personal observations of feeding behavior in the field and in the laboratory (as done in other food-web studies, e.g., van der Zee et al., 2016). Predator-prey lists were made for 281 taxa (Appendix B-1 and Supplement B-1) and used to generate a binary matrix that quantifies predator-prey interactions (Supplement B-2). According to Wood et al. (2015), feeding links determined for one zone of the marsh are applicable where taxa occur together in another marsh zone.

Overall, 16 food webs were constructed: (1) high-, medium- and low-resolution meta food webs combining data from Chezzetcook and Windsor (hereafter called NS webs), (2) separate high-, medium, and low-resolution meta food webs for each marsh, and (3) high-resolution food webs for four zones at Chezzetcook and three zones at Windsor (Figures 3.4 and 3.5). The metaweb combines feeding relationships that are integrated over large spatial scales (the entire salt marsh, or, both marshes combined) to include all energetic links among taxa that co-occur in at least part of the landscape for the 6-year time interval. We used FoodWeb3D to generate and analyze the food webs,

written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab (www.foodwebs.org, Yoon et al., 2004).

Low-resolution food webs combined the species into groups based on overall taxonomic similarities. These groups were given new ID numbers to distinguish them from taxa in the high- and medium- resolution food webs. For example, all 21 polychaete taxa were grouped into a "polychaete" trophic category (see Appendix B-2 for combinations), and 12 amphipod taxa, 11 copepod taxa, and 4 nematode taxa were similarly grouped. This approach replicates many salt-marsh ecological studies in which groups of smaller, taxonomically unrelated animals are based on size (e.g., "sediment meiofauna" or "zooplankton"). Endoparasites (such as trematodes in gastropods) were not included in the present study. Humans and domestic animals (cats, dogs) were excluded because they do not necessarily reflect natural feeding interactions within the system (as was also done by Vinagre and Costa, 2014), although sporadic fishing, clamworm collecting, and clam digging occur at both marshes. We omitted rare transient species such as some birds that appear in small numbers once a year or less.

Because the role of foraminifera in the salt-marsh food web is a key focus of the present study, medium-resolution metawebs for Nova Scotia, Chezzetcook and Windsor were generated that excluded only the foraminifera. This step involved removing 13 taxa of mostly basal feeders (detritus, plankton, algae and bacteria: Lipps, 1983), although some species of foraminifera can be predatory on meiofauna (Dupuy et al., 2010).

High-resolution webs included all organisms down to the highest taxonomic level possible at a microscopic level (genus or species). This approach reduces over-representation of secondary consumers or predators, such as fishes, birds and mammals

(see Appendix B-1). Trophic compartments were resolved to the highest taxonomic level to which feeding links could be reliably established, based on literature and database searches or *in situ* and laboratory observations. Overall, we used 281 nodes for Nova Scotia salt marshes. In the Chezzetcook metaweb, 224 nodes (91.4%) were resolved to genus/species-level, and 21 nodes not resolved to this level include invertebrates (n=14) and sources (n=7), the latter comprising organisms that do not have prey items (plants, algae, microalgae, bacteria, detritus, and carrion). In the Windsor metaweb, 174 nodes (91.1%) were resolved to genus/species-level, and 17 nodes not resolved to this level include invertebrates (n=10) and basal sources (n=7).

3.3.3 Food-web properties

Seventeen properties were used to describe food-web structure, using FoodWeb3D (Table 3.3; Williams and Martinez, 2000; Romanuk et al., 2006). The number of nodes in each web was converted into 'trophic species', a common method used to reduce bias from uneven taxa resolution by grouping taxa with the same predators and prey into one "trophic species" (Williams and Martinez, 2000). In particular, three food-web properties (Table 3.3) were used to compare the eleven high-, medium-, and low-resolution food webs of Windsor and Chezzetcook marshes: number of trophic species (*S*); mean links per species (*L/S*); and connectance € (which is the proportion of realized to possible links per species; $C=L/S^2$).

Six node properties describe the percentages of feeding types in a food web: *Top*, *Inter* (=*Intermediate*), *Can* (=*Cannibal*), *Omn* (= *Omnivore;* i.e., taxa with food chains of different length from non-basal to basal species), *Herb* (=*Herbivore or Detritivore*), and *Bas* (=*Basal*). Trophic level properties in this study are the maximum and mean trophic

level (*TLMax* and *TLMean*), which both use short-weighted trophic position (*SW-TP*). The property *SW-TP* is the average of 'prey-averaged trophic position' (*PA-TP*) and the shortest trophic position. The averaged trophic position *PA-TP* gives a value of 1 + the mean trophic position of all the taxon's trophic resources. The shortest trophic position *SW-TP* gives a value of 1+ the shortest chain length from the consumer taxon to a basal taxon (Williams and Martinez, 2004). *SW-TP* can underestimate the actual trophic level, but it is considered the best fit for estimating flow-based webs (Williams and Martinez, 2004). Another measure of trophic properties is mean trophic similarity (*MeanSim*), which is the mean Jaccardian similarity calculated as the number of consumers and resources shared in common, divided by the pair's total number of consumers and resources (Williams and Martinez, 2000).

The standard deviation of mean generality (*GenSD*) defines the number of prey items for a species, and vulnerability (*VulSD*) defines the number of predators for a species. These two measures quantify the variability of species' normalized predator and prey counts (Schoener, 1989). Diet discontinuity (*DietDis*) is the number of triplets of species with an "irreducible gap", i.e., a gap in a consumer's diet that cannot be made contiguous because of the constraints imposed by other consumers' diets, divided by the number of possible triplets. Diet discontinuity is a measure of intervality which indicates the degree to which the species and their diets can be represented along a single dimension (Cattin et al., 2004; Stouffer et al., 2006). If the food web departs from this intervality, then the mechanisms behind the structure of the food webs are more complex than modelled, as the feeding modes span several dimensions. We also report the clustering coefficient (*CC*) which is one measure of 'small-world' network structure

(Watts and Strogatz, 1998; Dunne et al., 2002a; Camacho et al., 2002; Montoya and Sole, 2002; Williams et al., 2002). The clustering coefficient indicates where nodes are more likely to be clustered together than they would be in a random graph, with small path length between nodes.

Table 3.3. Description of food web properties of Network 3D (after Dunne, 2006).

Food web property		**Description**
Trophic Species	*S*	Number of species in the food web after being converted into a trophic web
Links/Species	*L/S*	Number of predator and/or prey links per species
Connectance	*C*	Proportion of actual trophic links to all possible links (L/S^2)
Link standard deviation	*LinkSD*	Standard deviation of links per species (L/S)
Clustering coefficient	*CC*	Probability that two taxa linked to the same taxa are also linked to each other
Percentage of top predators	*%Top*	Taxa with prey and no predators
Percentage of intermediate taxa	*%Inter*	Taxa with both predators and prey
Percentage of omnivores	*%Omn*	Taxa that prey on primary producers (basal taxa) and other consumers
Percentage of basal taxa	*%Bas*	Taxa with predators and no prey
Percentage of cannibals	*%Can*	Taxa that prey on their own species
Percentage of herbivores/detritivores	*%Herb*	Taxa that prey on basal taxa
Maximum trophic level	*TLMax*	Maximum trophic level in the food web using short-weighted algorithm (*SW-TP*)
Mean trophic level	*TLMean*	Average trophic level for *SW-TP*
Trophic similarity	*MeanSim*	Mean of total number of consumers and resources shared in common divided by the pair's total number of consumers and resources (Jaccardian similarity)
Diet Discontinuity	*DietDis*	Number of triplets of species with an "irreducible gap" (measure of intervality)
Generality standard deviation	*GenSD*	Number of prey of a taxa standardized by L/S
Vulnerability standard deviation	*VulSD*	Number of predators of a taxa standardized by L/S

3.3.4 Statistical analysis

For the 17 food web properties, comparisons were made for: (1) low-, medium- and high-resolution metawebs for both marshes combined (NS metaweb); (2) Chezzetcook versus Windsor marshes (metawebs); (3) high-resolution webs between marshes (3a) and within each marsh (3b). Values generated from FoodWeb3D were used for statistical analysis (Supplements B-3, B-4).

Direct comparison of web 3D properties is difficult because statistical significance cannot be determined (Dunne et al., 2004). To compare these properties across resolutions, marshes and tidal zones, we used the coefficient of variation (CV =standard deviation of the differences between the properties, divided by the mean of the property, multiplied by 100) (Vinagre et al., 2017). A CV greater than 10% indicates a significant difference in the food-web properties that are most affected by the comparison (Vinagre et al., 2017). As CV values for each web did not follow a normal distribution, we used Mann-Whitney nonparametric tests to evaluate the differences in CV across resolutions and zones (Supplement B-4). With PRIMER v. 6, we used non-metric multidimensional scaling (nMDS) and cluster analysis overlaid with normalized Euclidean distances of the food web properties to visually examine food-web differences between salt marsh zones and resolutions. We also used nMDS graphs to compare our food webs with previously published food webs, using eight common food-web properties (Table 3.4).

In addition to examining whole-web properties, we also examined statistical differences between and among salt marshes and resolutions, using the trophic level and connectivity values for each of the species nodes for each web. As these samples did not

follow a normal distribution, we used Kruskal-Wallis non-parametric sample comparisons (when examining differences of more than 2 samples), and Mann-Whitney non-parametric tests to examine differences between 2 samples. For both tests, we used significance values of $p<0.05$ (Appendix B-3). The program XLSTAT for Microsoft Excel was used to compute the tests.

Finally, we used the niche model (Williams and Martinez, 2000) to predict food web properties using only input parameters of *S* (trophic species number) and *C* (connectance) from the constructed food webs. In the niche model, species are sorted along a single niche axis (representing the feeding hierarchy) where the diet of a consumer lies in a defined section of the axis. For each web, Monte Carlo simulations were used (1000 generations of the niche model) to calculate the mean and standard deviation of the measured food web properties. If the normalized error (model error/ model SD) between the niche and empirical models is between -1 and 1 of the model standard deviation, the niche model is considered a good fit to the actual empirical web (Vinagre and Costa, 2014).

3.4 Results

3.4.1 High-, medium- and low-resolution food webs

We compiled 281 nodes (taxa or species) for the Nova Scotia (NS) metaweb, with 5995 feeding links (244 nodes and 4673 links for Chezzetcook; 191 nodes and 3778 links for Windsor). For all webs, the conversion of the number of species to trophic species was less than 10% of taxa. In terms of taxonomic diversity, invertebrates dominate the NS metaweb, with 58% of the species richness (Figure 3.2). There are slightly more fishes

and birds at Windsor, and four times the number of vascular plant species at Chezzetcook. The numbers of fishes, birds and mammals are the same for different taxonomic resolutions, but the number of invertebrate taxa decreases by over half between the high- and low-resolution webs (Figure 3.2).

Table 3.4. Food web topology for the three metawebs (Nova Scotia, Windsor, Chezzetcook) at three taxonomic resolutions. CV = coefficient of variation

Location:	**Nova Scotia (Windsor + Chezzetcook)**				**Windsor**				**Chezzetcook**			
Resolution:	High	Medium	Low	CV	High	Medium	Low	CV	High	Medium	Low	CV
Species Richness	281	268	123		191	183	100		244	231	105	
TS	271	256	123	*31*	182	173	98	*25*	232	217	105	*31*
L/S	20.68	20.55	15.05	*14*	18.61	18.27	12.61	*17*	18.35	18.22	14.28	*11*
C	0.08	0.08	0.12	*20*	0.10	0.11	0.13	*11*	0.08	0.08	0.14	*28*
LinkSD	0.59	0.57	0.50	*7*	0.50	0.48	0.50	*2*	0.62	0.60	0.46	*13*
CC	0.16	0.17	0.20	*10*	0.17	0.17	0.19	*5*	0.17	0.17	0.21	*10*
%Top	0.37	0.39	0	*71*	0.55	0.58	1.02	*30*	0.43	0.46	0	*71*
%Inter	86.0	84.77	91.06	*3*	90.11	89.02	88.78	*1*	83.62	82.49	90.48	*4*
%Omn	58.3	59.38	76.42	*13*	66.45	67.63	77.55	*7*	54.74	55.30	72.38	*13*
%Basal	13.65	14.45	8.94	*20*	9.34	10.40	10.20	*5*	15.95	17.05	9.52	*23*
%Can	17.71	18.75	24.39	*14*	19.23	20.23	23.47	*9*	17.68	18.90	26.67	*19*
%Herb	29.89	29.69	14.63	*29*	25.82	26.59	12.24	*31*	31.47	31.34	18.10	*23*
TL Max	4.22	4.20	4.05	*2*	3.95	3.92	4.06	*2*	4.20	4.19	4.02	*2*
TL Mean	2.39	2.39	2.78	*7*	2.57	2.53	2.85	*5*	2.32	2.32	2.77	*9*
MeanSim	0.08	0.08	0.11	*16*	0.10	0.10	0.12	*104*	0.09	0.09	0.12	*14*
DietDis	0.13	0.14	0.38	*53*	0.15	0.15	0.38	*48*	0.12	0.13	0.29	*43*
GenSD	1.15	1.14	0.78	*17*	0.98	0.97	0.70	*15*	1.21	1.20	0.82	*17*
VulSD	0.72	0.71	0.85	*8*	0.74	0.75	0.90	*9*	0.62	0.65	0.72	*6*

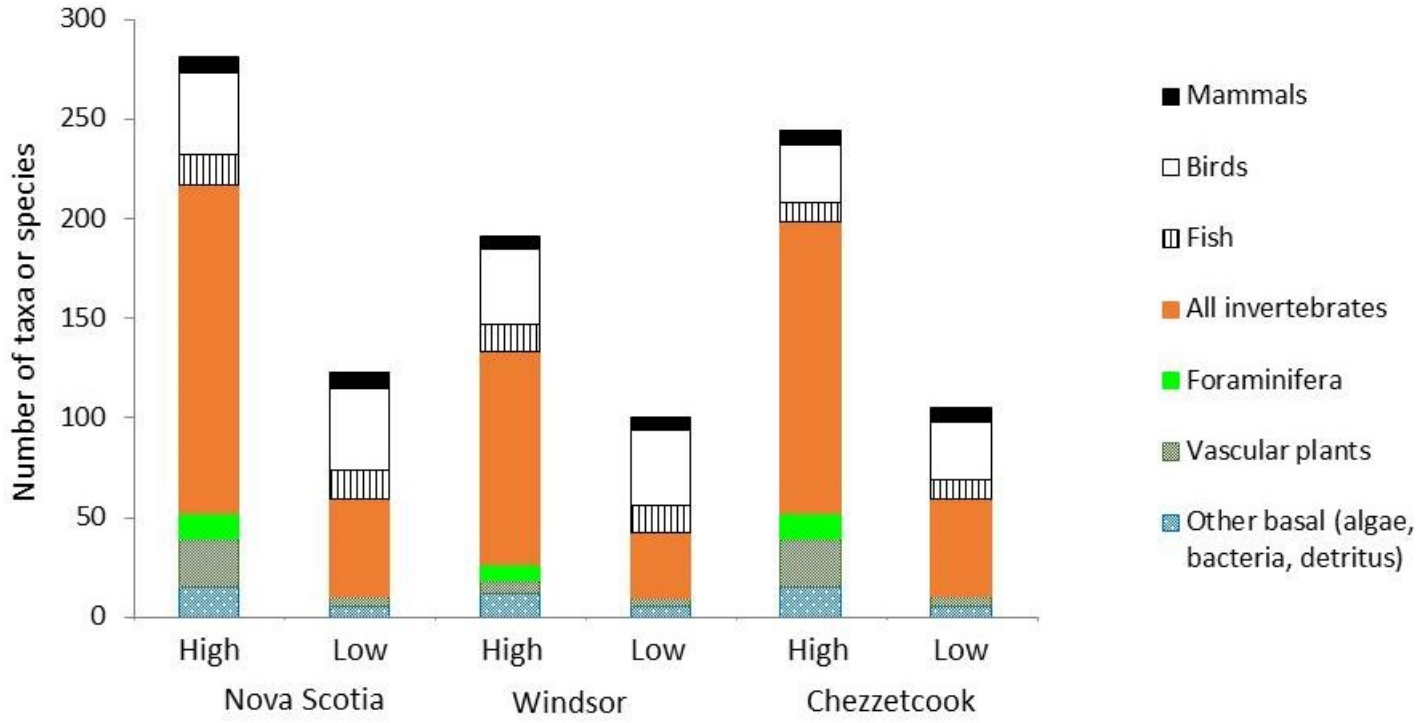

Figure 3.2. Numbers of taxa comprising the major taxonomic groupings in two salt marshes combined (Nova Scotia), and at the Windsor and Chezzetcook marshes across high and low resolutions (medium resolution not shown because it is identical to high resolution, minus the foraminifera, shown in green).

For food web structural properties, the larger number of nodes and links in the combined NS high-resolution web increases the link density (*L/S*) from approximately 18 in individual marshes to more than 20 links per species (Table 3.4). All other 16 property values (Table 3.4) for the NS web were intermediate between those of the Windsor and Chezzetcook marshes. Omnivory always exceeds 50% of the trophic groups, and the percentage of top predators (*%Top*) is below 1% except for Winsor mudflat. Trophically intermediate taxa (those with predators as well as prey) dominate the system (Table 3.4, *Inter*.), with approximately 85 to 90% of taxa. The most connected taxa in the NS metaweb is the mummichog bottom-feeding fish *Fundulus heteroclitus*, with a connectivity of 3.5 (the only node with a connectivity >3; Supplement B-3). Other highly connected taxa are dipteran flies (including chironomid midges and mosquitoes) with connectivity >2, and small crustaceans such as amphipods with connectivity >1.5. The high values reflect the intermediate and omnivorous feeding behaviour of these taxa, which dominate the functional groups. The most connected basal nodes are marine detritus (1.9) and phytoplankton (1.7), here comprising diatoms. Overall, 168 taxa had a connectivity less than 1, 89 taxa between 1 and 2, and 23 taxa between 2 and 3. Mean trophic level for the high-resolution web was 2.39. The only top predator (*%Top*) in the NS marshes metawebs is, surprisingly, one species of cnidarian because ectoparasites (e.g., biting flies and mites) feed on the mammals and large birds, and because the eggs, larvae or juveniles of predatory fish, birds and mammals are prey to various animals. The *MeanSim* of 0.08 indicates that, on average, the taxa do not have common predators or prey (0 = no common predators or prey; 1 = shared predators and prey).

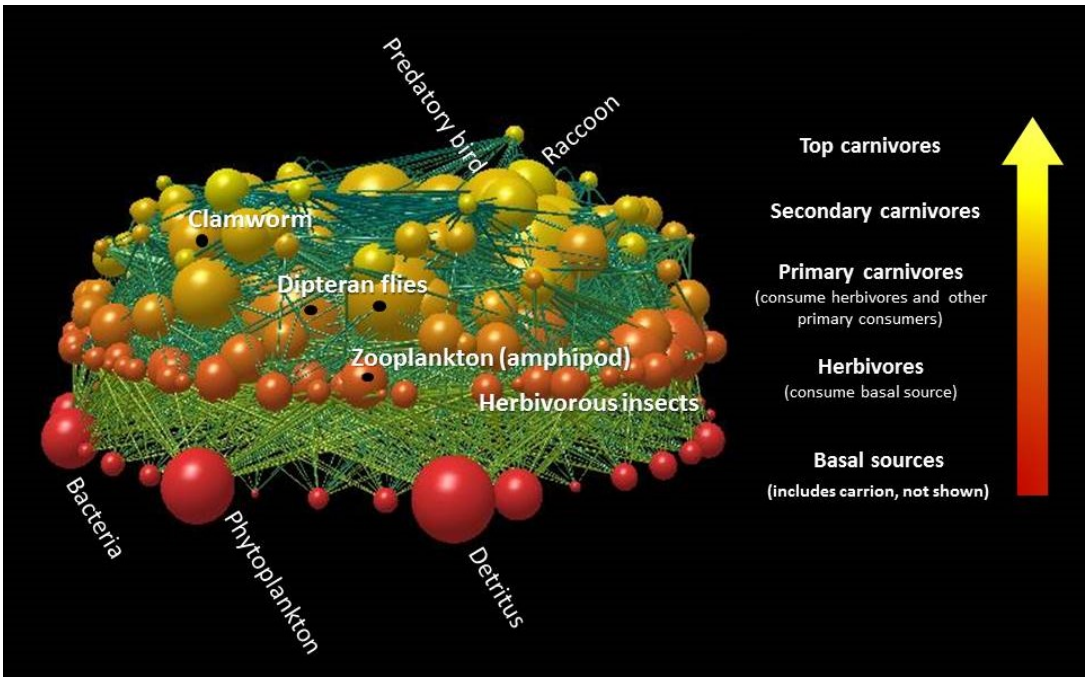

Figure 3.3: High-resolution Nova Scotia meta food web. Size of coloured nodes is indicative of connectivity. Lines connecting nodes are feeding links between nodes. Colour of nodes indicates trophic level, as shown by the arrow. Examples of highly connected and/or common trophic taxa are labelled beside their nodes, with black dots specifying nodes the labels may overlap.

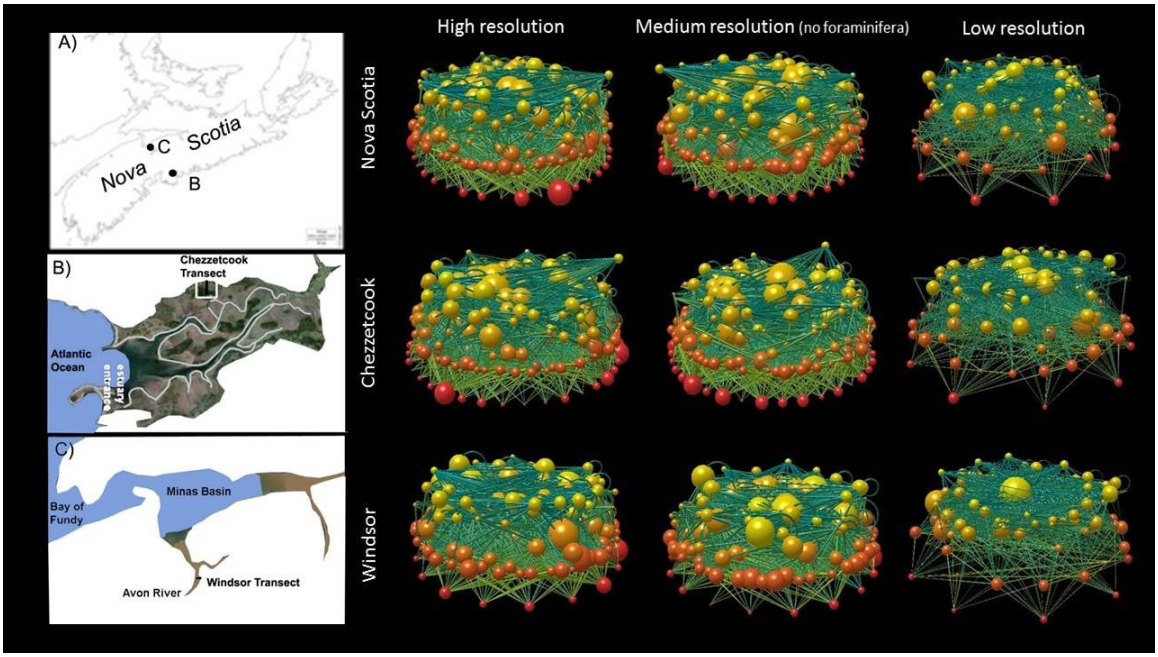

Figure 3.4: Food webs for Nova Scotia (A), Chezzetcook (B) and Windsor (C) marshes and varying levels of taxonomic resolution. Node size indicates connectivity; trophic levels are the same as in Figure 3.3.

Structural network properties changed little in the NS medium-resolution web without foraminifera, which are herbivorous and omnivorous (intermediate) taxa. The percentages of trophic groups changed by 1% or less (Table 3.4). The percentage of cannibalism increased slightly by 1.04 %, and intermediate species decreased by more than 1%. Visually, high- and medium-resolution food webs are similar (Fig 3.4).

More differences emerge in food web properties of the low-resolution NS web. The number of nodes decreased from 271 to 123 (5994 to 1851 feeding links), and no taxa had identical predators and prey. Links per species decreased to 15.05, and connectance increased slightly, to over 12% (Table 3.4). The percentage of top consumers only increased slightly, but all other functional groups changed by larger amounts (e.g., omnivores, intermediate and cannibal taxa all increased by more than 6%, whereas basal and herbivorous taxa decreased by more than 5%). The mean trophic level increased slightly from 2.39 to 2.78. Connectance was less than 1 for 76 taxa and between 1 and 2 for 42 taxa. The most connected taxon was the amalgamated "mosquitoes" (biting Diptera) group (3.26), followed by three other taxa of flies/midges with a connectance of between 2 and 3 (Supplement B-3).

Statistically for the NS metawebs, there are no significant differences across taxonomic resolutions for vertebrate and invertebrate trophic levels ($p = 0.39$, $p = 0.134$, respectively; Appendix B-3), but the invertebrate taxa show significantly higher connectance in the low-resolution NS web (high = 0.979, medium = 0.950, low = 1.158, $p = 0.026$). Vertebrate taxa have a significantly lower connectance in the low-resolution NS web, in comparison to medium and high resolutions (high = 1.386, medium = 1.375, low = 0.918, $p < 0.001$). Basal resources do not have significant differences in

connectivity across resolutions (high = 0.624, medium =0.596, low = 0.748, p = 0.063). For all resolutions, the differences between invertebrate and vertebrate taxa are significant for connectivity and trophic levels, with vertebrates always having a significantly higher trophic level than invertebrates ($p<0.001$ for all three resolutions). In terms of connectivity, vertebrates have a significantly higher connectance than invertebrates for high and medium resolutions ($p<0.001$) but a significantly lower connectance in the low-resolution NS metaweb ($p=0.031$; Appendix B-3).

In terms of the metawebs for Chezzetcook and Windsor separately, overall, patterns of change across resolutions are similar to those for the NS metaweb (Figure 3.4, Table 3.4). A notable difference is in the percentage of top consumers, which increased to more than 1% in the low-resolution Windsor web, the highest value across all resolutions and metawebs. The low-resolution basal taxa percentage increased by less than 1% from high resolution at Windsor, but decreased by 5% at Chezzetcook.

Regardless of resolution, Chezzetcook and Windsor show similar values of connectance but Chezzetcook has a slightly wider range across resolutions (8–14% versus 10–13% in Windsor). In terms of resolution, 11 of 17 properties for the NS web have a CV higher than 10% compared to 8 of 17 for Windsor, and 12 of 17 for Chezzetcook. Species richness, links per species and connectance all have large differences across resolutions. Overall, trophic level is significantly higher for the low-resolution Chezzetcook web in comparison to the medium- and high-resolution webs. Vertebrates have a significantly higher trophic level in low-resolution webs than they do in medium- and high-resolution webs(high = 3.067, medium = 3.037, low = 3.282, p = 0.006; Appendix B-3), whereas invertebrate trophic level differences are not significant

($p = 0.08$). The taxa with the highest connectance values for high- and medium-resolution webs are mummichog (fish), spotted sandpiper (bird), shrew (mammal), followed by biting flies. In the low-resolution web, biting flies have the highest connectance values, followed by shrews and raccoons (Appendix B-3).

The Windsor webs show significant differences across resolutions for vertebrate trophic levels, with a lower trophic level in low-resolution webs. As with Chezzetcook, vertebrates have significantly higher trophic levels in the low-resolution web than in the high- or medium-resolution webs (High = 3.216, Medium = 3.104, Low = 3.269, $p = 0.024$; Appendix B-3), and invertebrates do not have significant differences in trophic level across resolutions ($p = 0.328$). In all Windsor resolutions, invertebrates have a significantly lower trophic level than the vertebrate taxa ($p<0.001$). As with Chezzetcook nodes, invertebrates and vertebrates also have significantly different connectance in the Windsor resolutions, with invertebrates higher than vertebrates in the low-resolution web (1.259 vs 0.908, $p = 0.003$) and significantly lower than vertebrates in medium- and high-resolution webs ($p = 0.004$ and $p = 0.011$, respectively; Appendix B-3). The taxa with the highest connectance values for high- and medium- resolution webs are mummichog followed by biting flies, shrimp and spotted sandpiper. In the low-resolution web, biting flies have the highest connectance values followed by raccoons and amphipods.

Multidimensional scaling (Fig 3.5) shows high clustering of each marsh with high- and medium-resolutions. Overall, medium- and high-resolution webs are more similar than any are to the low-resolution webs.

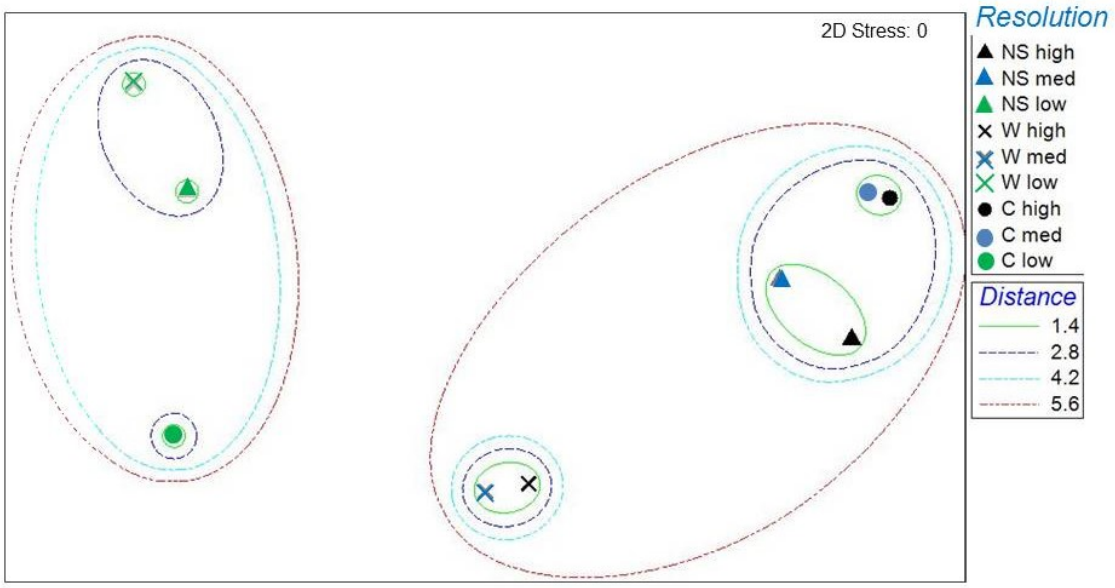

Figure 3.5. Non-metric multidimensional scaling analysis overlaid with normalized Euclidean distances from cluster analysis of food web properties of the three marshes and three resolutions. NS = combined Nova Scotian study sites; W = Windsor; C = Chezzetcook. Black = high resolution; green = low resolution; blue = medium resolution.

3.4.2 Comparison of high-resolution food webs between salt marshes and zones

Visual food webs show no major differences between and among the zones of Chezzetcook and Windsor (Fig. 3.6). Chezzetcook has more vascular plants and therefore more basal taxa than Windsor metawebs. In both Windsor and Chezzetcook, fish increase in taxonomic abundance in the low marsh and mudflat. Windsor has 10% more Top taxa whereas the other zones have ~1 *%Top*. Chezzetcook also has more Top taxa in the mudflat than in the upper zones of the marsh (Table 3.5). The coefficient of variation (CV, Table 3.5) shows that six of 17 food web properties are affected by spatial gradients (tidal zones) at Chezzetcook and seven at Windsor. In both saltmarshes, the *%Top* taxa have the biggest differences across spatial gradient, with more top predators in lower elevations. The percentage of basal taxa is also strongly affected by spatial gradient.

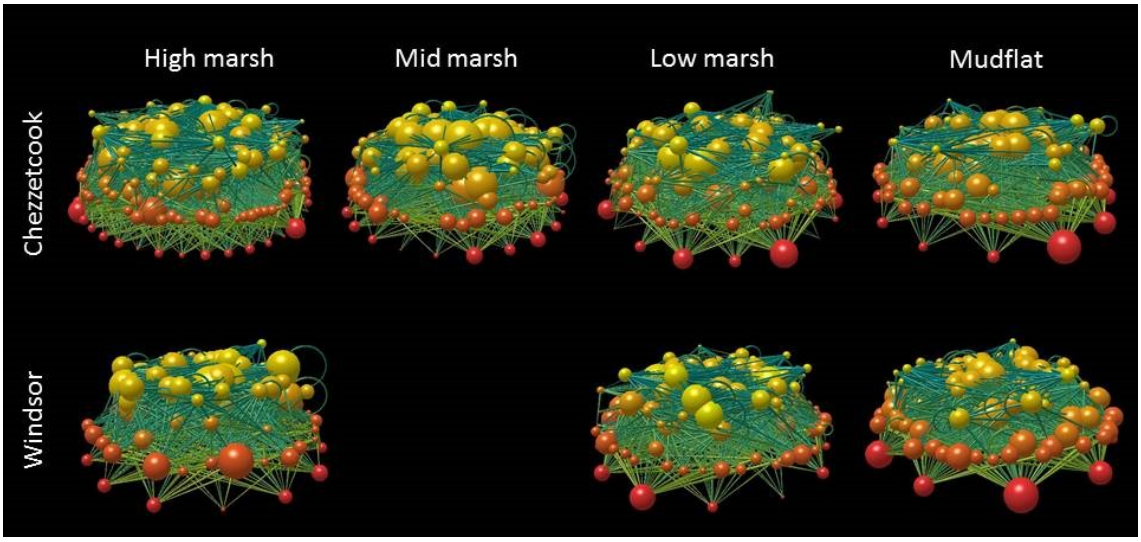

Figure 3.6. High-resolution food webs for Chezzetcook and Windsor marsh zones. Node size indicates connectivity; trophic levels are the same as in Figure 3.3.

Table 3.5. Zone-specific high-resolution food web topologies for Chezzetcook and Windsor salt marshes. Richness = species richness; CV = coefficient of variation.

Location:	**Chezzetcook**					**Windsor**			
Zone:	High Marsh	Middle Marsh	Low Marsh	Mudflat	CV	High Marsh	Low Marsh	Mudflat	CV
Richness	132	143	140	109		98	128	127	
TS	119	132	134	104	*10*	96	119	117	*9*
L/S	14.74	14.96	13.54	14.45	*4*	12.34	13.48	17.17	*14*
C	0.12	0.11	0.10	0.14	*13*	0.13	0.11	0.15	*13*
LinkSD	0.61	0.62	0.55	0.48	*10*	0.54	0.50	0.43	*9*
CC	0.20	0.20	0.16	0.16	*11*	0.19	0.16	0.17	*7*
%Top	0	0	0.75	4.81	*144*	1.04	0.84	10.26	*109*
%Inter	79.83	83.33	86.57	83.64	*3*	84.38	89.08	82.05	*3*
%Omn	55.46	55.30	54.48	61.54	*5*	60.42	63.87	69.23	*6*
%Basal	20.17	16.67	12.69	11.54	*22*	14.58	10.08	7.69	*26*
%Can	18.49	17.42	18.66	19.23	*4*	13.54	21.01	20.51	*19*
%Herb	28.57	28.79	32.09	30.77	*5*	26.04	28.57	24.79	*6*
TL Max	4.31	4.25	4.18	3.72	*6*	4.09	3.87	3.79	*3*
TL Mean	2.33	2.42	2.42	2.37	*2*	2.59	2.54	2.55	*1*
MeanSim	0.13	0.11	0.10	0.14	*13*	0.12	0.11	0.15	*13*
DietDis	0.11	0.13	0.14	0.16	*13*	0.13	0.13	0.19	*19*
GenSD	1.16	1.15	1.06	1.00	*6*	0.92	0.92	0.90	*1*
VulSD	0.65	0.69	0.66	0.66	*2*	0.77	0.77	0.78	*1*

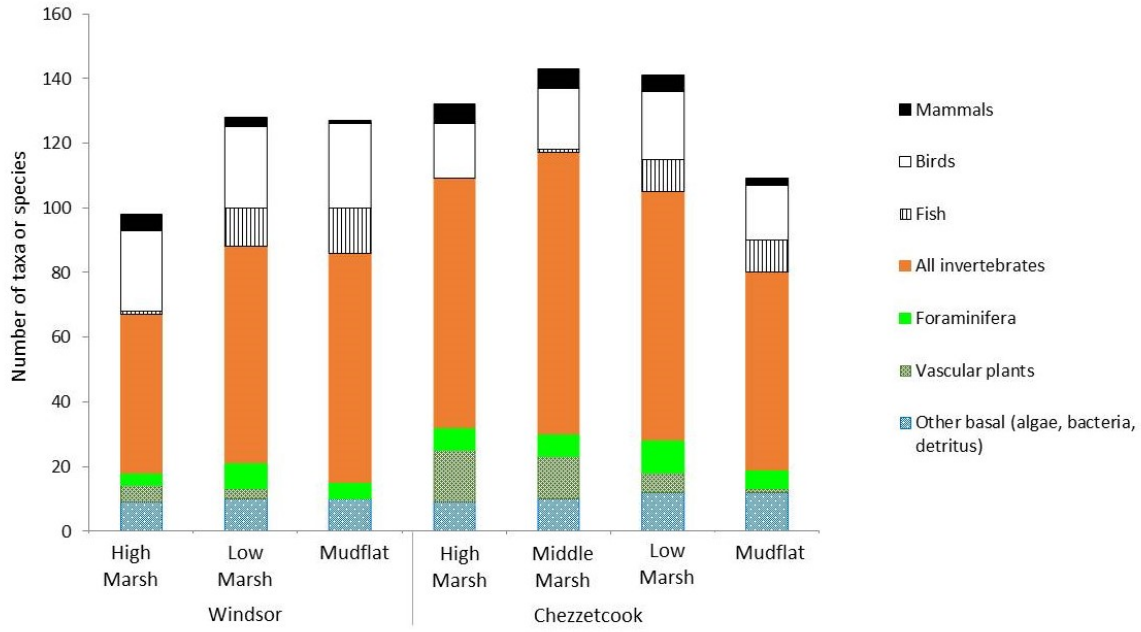

Figure 3.7. Zone-specific high-resolution taxonomic group distribution for Windsor and Chezzetcook.

The trophic level of vertebrate taxa is significantly higher at Windsor than at Chezzetcook (Windsor = 3.216, Chezzetcook = 3.067, p = 0.038; Appendix B-3), although the invertebrate taxa show no significant difference (Windsor = 2.514, Chezzetcook = 2.478, p = 0.514). Comparison of the same major taxonomic groupings by zone (Fig. 3.7) also shows no significant differences in trophic level between the two marshes for each group (e.g., fishes: Windsor = 3.042, Chezzetcook = 3.015, p=0.193). Connectivity of nodes, however, shows significant difference between Windsor and Chezzetcook. For example, insects and spiders, and birds each have higher connectance at Chezzetcook than Windsor (p = 0.031 and 0.036, respectively), whereas crustaceans and annelids each have higher connectance at Windsor than Chezzetcook (p = 0.025 and 0.001, respectively; Appendix B-3).

For Windsor, connectance of mammals, birds, fish and basal resources do not show significant differences across zones but crustaceans have significantly lower connectance values in the high marsh than in the mudflat and low marsh (HM = 0.427, LM = 1.114, MF = 1.092, $p = 0.008$). Foraminifera connectance values signficantly increase from high marsh to the mudflat (HM = 0.330, LM = 0.525, MF = 0.709, $p = 0.02$). In all zones, invertebrates have a significantly lower trophic level than vertebrates ($p<0.002$; Appendix B-3). The taxa with the highest connectance values change through the zones, with biting flies having highest connectance in the high marsh, and amphipods, shrimp, and polychaetes having the highest connectance in the mudflat.

For Chezzetcook, a few taxa show significant differences in connectance between zones. Insects and spiders show connectance decreases from high marsh (1.247) to mudflat (0.776; $p = 0.032$), and crustaceans and foraminifera show connectance decreases from high marsh to mudflat ($p < 0.001$ for both). Overall, as at Windsor, there is no significant difference in trophic levels across zones for vertebrate taxa ($p=0.499$), but invertebrate taxa show significantly lower trophic level from high marsh to mudflat ($p=0.044$). The taxa with the highest connectance values changes through the zones, with four species of birds having the highest connectance in the high marsh and mummichogs having the highest connectance in the mudflat and low marsh. In all zones, biting flies are within the top 10 most connected taxa (Supplement B-3).

Multidimensional scaling of food-web properties of the similarities of Chezzetcook and Windsor marshes and zones (Fig.3.8) shows that Windsor mudflat is most dissimilar, followed by Windsor high marsh and Chezzetcook mudflat. Chezzetcook

and Windsor low marsh zones are clustered together, followed by Chezzetcook high and mid marshes.

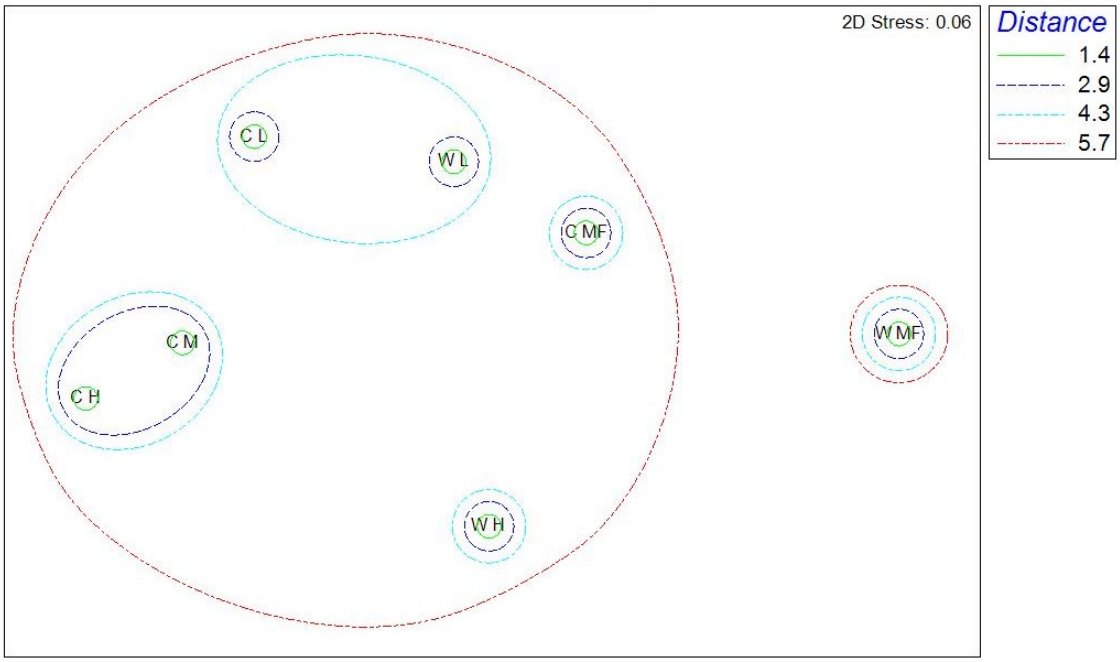

Figure 3.8: Multidimensional scaling analysis overlaid with normalized Euclidean distances from cluster analysis of food web properties of Chezzetcook and Windsor marshes and zones (C = Chezzetcook, W= Windsor; H= high marsh, M = mid marsh, L = low marsh, MF = mudflat).

The coefficient of variation is the spread of variability, and it is used to evaluate which parameters are responsible for the largest differences in foodweb properties across resolutions and tidal zones. Overall, when comparing the differences in resolution and zone properties for both marshes, the resolution variability was larger than zonal variability (Chezzetcook resolution CV = 19.8, zone CV = 16.06 p = 0.02; Windsor resolution CV = 19.18, zone CV = 15.24, p = 0.534; Appendix B-3). Although not significant for both marshes, the zonal variability at Chezzetcook was higher than zone variability at Windsor.

3.4.3 Niche model

Overall, the niche model of Williams and Martinez (2000) fits well to structural properties of trophic interactions (*L/S* and *C*) in the Nova Scotia marshes, but not to all types of species properties. For example, the niche model underestimates the percentage of basal groups and herbivores and overestimates the percentage of omnivores. The niche model fits the empirical webs better when zones are computed separately and show matches for 9–11 out of 14 properties (Table 3.6). Values for different resolutions show some differences in fit to the niche model (Table 3.7). The niche model appears to fit more closely for the low-resolution webs, with the highest number of food-web properties within niche model error, although the Nova Scotia webs contain more taxa than many other highly resolved webs (e.g., Dunne et al., 2004). To examine niche model fit with fewer taxa, we also ran the niche model against earlier, preliminary even lower-resolution webs for Chezzetcook and Windsor (data not shown in this paper). The niche model fits less well with those preliminary data than with the current low-resolution webs (only 6 and 7 of 14 properties, respectively, were within model error; Table 3.7). An overall summary of results is listed in Table 3.8.

Table 3.6. Niche model comparisons to zone-specific food webs of Chezzetcook and Windsor salt marshes. Niche model results are in parentheses. Bold values are within +/- 1 of niche model error, showing a good fit to the empirical food web property.

	Chezzetcook				Windsor		
	High Marsh	Middle Marsh	Low Marsh	Mudflat	High Marsh	Low Marsh	Mudflat
TS	119	132	134	104	96	119	117
L/S	**14.74** (14.74)	**14.96** (14.95)	**13.54** (13.55)	**14.45** (14.49)	**12.34** (12.36)	**13.48** (13.49)	**17.17** (17.19)
C	**0.12** (0.12)	**0.11** (0.11)	**0.1** (0.10)	**0.14** (0.14)	**0.13** (0.13)	**0.11** (0.11)	**0.15** (0.15)
LinkSD	0.61 (0.50)	0.62 (0.51)	**0.55** (0.51)	**0.48** (0.49)	**0.54** (0.50)	**0.5** (0.48)	**0.43** (0.48)
CC	**0.2** (0.21)	**0.2** (0.19)	**0.16** (0.17)	0.16 (0.23)	**0.19** (0.21)	**0.16** (0.19)	0.17 (0.24)
%Top	**0** (3.4)	**0** (3.5)	**0.75** (3.6)	**4.81** (3.4)	**1.04** (3.75)	**0.84** (3.8)	10.26 (3.0)
%Inter	**79.83** (87.9)	**83.33** (87.9)	**86.57** (87.0)	**83.64** (88.0)	**84.38** (86.5)	**89.08** (86.8)	**82.05** (89.4)
%Omn	55.46 (83.2)	55.3 (83.1)	54.48 (81.6)	61.54 (83.6)	60.42 (80.9)	63.87 (81.9)	69.23 (85.5)
%Basal	20.17 (8.7)	16.67 (8.7)	**12.69** (9.5)	**11.54** (8.6)	**14.58** (9.8)	**10.08** (9.4)	**7.69** (7.6)
%Can	**18.49** (14.1)	**17.42** (12.8)	18.66 (11.1)	**19.23** (16.3)	**13.54** (14.7)	21.01 (12.7)	**20.51** (17.4)
%Herb	28.57 (3.4)	28.79 (3.5)	32.09 (4.0)	30.77 (3.3)	26.04 (2.3)	28.57 (3.6)	24.79 (2.9)
TL Mean	2.33 (3.29)	2.42 (3.29)	*2.42* (3.21)	2.37 (3.34)	**2.59** (3.23)	**2.54** (3.21)	2.55 (3.49)
MeanSim	**0.13** (0.13)	**0.11** (0.12)	**0.1** (0.10)	**0.14** (0.14)	**0.12** (0.13)	**0.11** (0.12)	**0.15** (0.15)
GenSD	**1.16** (1.07)	**1.15** (1.08)	**1.06** (1.10)	**1** (1.05)	**0.92** (1.06)	*0.92* (1.09)	*0.9* (1.03)
VulSD	**0.65** (0.56)	**0.69** (0.56)	**0.66** (0.58)	**0.66** (0.56)	0.77 (0.57)	0.77 (0.57)	0.78 (0.55)

bold = within +/-1 model error; good fit of model to empirical data
italics = marginal model error (between 1 and 1.2); marginal fit of model to empirical data
underlined = large error (>6); severe under/overestimation of model to empirical data

Table 3.7. Niche model comparisons to high-, medium- and low-resolution food webs of Nova Scotia, Windsor and Chezzetcook. Values from preliminary low resolution food webs of Windsor and Chezzetcook are also added to see the pattern of fit of the niche model. Niche model results are in parentheses. Bold values are within +/- 1 of niche model error.

	Nova Scotia			**Windsor**				**Chezzetcook**			
	High	Medium	Low	High	Medium	Low	Old Low	High	Medium	Low	Old Low
TS	271	256	123	182	173	98	71	232	217	105	80
L/S	**20.68** (20.67)	**20.55** (20.57)	**15.05** (15.06)	**18.61** (18.62)	**18.27** (18.30)	**12.61** (12.6)	**6.59** (6.59)	**18.35** (18.37)	**18.22** (18.2)	**14.28** (14.28)	**6.75** (6.77)
C	**0.08** (0.08)	**0.08** (0.08)	**0.12** (0.12)	**0.1** (0.1)	**0.11** (0.11)	**0.13** (0.13)	**0.09** (0.09)	**0.08** (0.08)	**0.08** (0.08)	**0.14** (0.14)	**0.08** (0.08)
LinkSD	*0.59* (0.53)	**0.57** (0.53)	**0.5** (0.5)	**0.5** (0.51)	**0.48** (0.51)	**0.5** (0.50)	**0.52** (0.53)	0.62 (0.53)	0.6 (0.53)	**0.46** (0.49)	**0.49** (0.54)
CC	0.16 (0.14)	**0.17** (0.14)	**0.2** (0.21)	**0.17** (0.18)	**0.17** (0.18)	**0.19** (0.21)	0.06 (0.16)	**0.17** (0.14)	**0.17** (0.15)	**0.21** (0.22)	0.05 (0.15)
%Top	**0.37** (2.7)	**0.39** (2.64)	**0** (3.5)	**0.55** (3.0)	**0.58** (2.9)	**1.02** (3.9)	31 (6.3)	**0.43** (3.13)	**0.46** (3.0)	**0** (3.5)	33.75 (5.9)
%Inter	**85.61** (89.9)	**84.77** (90.0)	**90.24** (87.9)	**90.11** (89.4)	**89.02** (89.3)	**88.78** (86.6)	59.15 (78.4)	**83.62** (88.9)	*82.49* (89.0)	**90.48** (87.9)	56.25 (79.1)
%Omn	58.3 (85.57)	59.38 (85.69)	**76.42** (83.3)	66.45 (85.2)	67.63 (85.0)	**77.55** (81.7)	**64.79** (69.9)	54.74 (84.4)	55.3 (84.4)	72.38 (83.2)	56.25 (70.0)
%Basal	13.65 (7.39)	14.45 (7.36)	**8.94** (8.59)	**9.34** (7.6)	**10.4** (7.8)	**10.2** (9.5)	**9.86** (15.3)	15.95 (8.0)	17.05 (8.0)	**9.52** (8.6)	**10** (15.0)
%Can	17.71 (8.3)	18.75 (8.71)	24.39 (13.78)	19.23 (11.3)	20.23 (11.3)	23.47 (14.7)	0 (9.89)	17.68 (8.71)	18.9 (9.1)	26.67 (15.5)	0 (9.0)
%Herb	29.89 (2.93)	29.69 (2.85)	14.63 (3.57)	25.82 (3.1)	26.59 (3.1)	12.24 (3.9)	25.35 (7.54)	31.47 (3.2)	31.34 (3.1)	18.1 (3.6)	31.25 (7.64)
TL Mean	2.39 (3.33)	2.39 (3.34)	**2.78** (3.31)	2.57 (3.36)	2.53 (3.35)	**2.85** (3.24)	**2.44** (2.77)	2.32 (3.29)	2.32 (3.29)	**2.77** (3.34)	**2.47** (2.77)
Mean Sim	**0.08** (0.08)	**0.08** (0.09)	**0.11** (0.12)	**0.1** (0.11)	**0.1** (0.11)	**0.12** (0.13)	**0.11** (0.1)	**0.09** (0.08)	**0.09** (0.09)	*0.12* (0.14)	**0.09** (0.09)
GenSD	*1.15* (1.15)	**1.14** (1.14)	0.78 (1.07)	**0.98** (1.11)	**0.97** (1.11)	0.7 (1.06)	0.78 (1.12)	**1.21** (1.14)	**1.2** (1.14)	0.82 (1.05)	*0.92* (1.14)
VulSD	*0.72* (0.53)	0.71 (0.57)	0.85 (0.57)	0.74 (0.57)	0.75 (0.57)	0.9 (0.57)	1.19 (0.61)	**0.62** (0.57)	*0.65* (0.53)	*0.72* (0.57)	1.12 (0.61)

bold = within +/-1 model error; good fit of model to empirical data
italics = marginal model error (between 1 and 1.2); marginal fit of model to empirical data
underlined = large error (>6); severe under/overestimation of model to empirical data

Table 3.8. Summary of key results for Nova Scotia salt marshes (Chezzetcook and Windsor) across varying taxonomic resolutions and across tidal zones.

Results	Summary
How much detail is enough?	
Taxonomic Resolution	• Invertebrates represent >50% of taxa in high-resolution webs but c. 25% in low-resolution webs. • Higher *C* in low-resolution webs because aggregated nodes have more realized links per species. • *%Herb* and *%Basal* much lower in low-resolution webs. • *%Omn, %Int* and *%Herb* are much higher in high-resolution webs. Biting flies, mummichogs, and amphipods are the most connected taxa. • Excluding foraminifera does not significantly change food web properties, despite their high abundances.Mean trophic levels do not differ significantly across resolutions for either salt marsh. • Invertebrates have higher connectance and vertebrates have lower connectance in our low-resolution webs. Vertebrates have a lower connectance than invertebrates in low-resolution webs. • Vertebrates have higher trophic levels in low-resolution webs. • All low-resolution marsh webs are clustered in MDS plots.
Spatial Gradient (Tidal Zones)	• Foraminifera have increasing connectance for entire marsh from high marsh through mudflats. • Higher *%Top* in mudflat zones. • Higher *%Basal* in higher marsh zones. • Windsor mudflat has greatest difference between zones; Chezzetcook high and middle marshes group closely; Chezzetcook and Windsor low marshes group closely.
Salt marsh comparisons	
Windsor (young, macrotidal, ice-scoured)	• More fishes and bird taxa. • More *%Top.* • Crustaceans and annelids have higher connectance • Overall, similar food web properties to Chezzetcook.
Chezzetcook (old, mesotidal, thin ice)	• More vascular plants. • Larger spread of values (variability) across resolutions • Insects/spiders, and birds have higher connectance • Resolution is more significant than zones when distinguishing the cause of variability across zones, however, variability across zones is higher here than in Windsor.
Niche model	
	• Does not fit well to functional group properties. • Fits better to low-resolution webs and webs separated by tidal zones. • Underestimates *%Herb* and *%Basal* and overestimates *%Omn* in high- and medium-resolution metawebs.

3.5 Discussion

3.5.1 Taxonomic resolution

We compared two cool temperate salt marshes to answer the question: "How do salt marsh food webs change with different levels of taxonomic resolution?" The taxonomic resolution of a food web dictates the species richness (*S*) and connectance (*C*), and these measures are important in understanding how the food webs work and how complex and stable the ecosystem is (Dunne et al., 2002b, 2004). Taxonomic resolution decreases by about half between the high- and low-resolution Nova Scotia webs. Invertebrates dominate the high-resolution web with 58% of the species richness, and invertebrates, meiofauna and basal taxa richness is significantly less in the low-resolution webs (Table 3.8). The number of vertebrates remains the same. This is a general problem with most published food webs that taxonomic resolution is low at invertebrate and basal levels but high for vertebrates which are represented as species rather than higher categories (e.g., genera, families, orders, classes), imparting bias to the analysis. In fact, vertebrates comprise less than 3% of all known animal species and should not represent the bulk of trophic nodes in an ecologically realistic food web unless weighted by biomass. In salt marshes, where meiofauna, including foraminifera, comprise a major component of the food-web biodiversity, this invertebrate:vertebrate balance is especially problematic.

In the present study, trophic levels of vertebrates and invertebrates do not change significantly with taxonomic resolution, but connectance does. The higher connectance of invertebrates in low-resolution webs indicates a high aggregation of nodes, which affects the interpretation of ecosystem complexity and stability (Dunne et al., 2004). Removing nodes in a food web not only changes overall properties such as connectance and linkage

density but also modifies the trophic distribution (Dunne et al., 2013). In the Nova Scotia webs, aggregating low-trophic level taxa into fewer nodes reduces the importance of any given group. For example, at Windsor, *Corophium volutator* amphipods are the main food source for the semipalmated sandpiper *Calidris pusilla* (Boates and Smith, 1989) and for many fish (Partridge, 2001). If amphipods are amalgamated into one node, the web is unable to model disturbance scenarios involving a single lost species. Similarly, the impact of dieback in a single key plant species such as *Spartina* would not be well-predicted, despite its devastating consequences (e.g McFarlin, 2012).

Comparison of Nova Scotia high- and medium-resolution webs shows that foraminifera do not have significant effects on web properties, despite their role as food source to many highly connected species (e.g., amphipods, midges, polychaetes: Supplement B-3) of great importance to ecosystem structure and energy flow (Lipps, 1983). At Windsor, foraminifera are among the 10 least-connected taxa in the high-resolution web, whereas at Chezzetcook some basal taxa are part of this "top ten", moving most foraminifera to the top 20 least-connected species. Carrion (dead macrofauna) is a food source for many taxa (Supplement B-2) but is among the 10 least-connected taxa (Supplement B-3), reflecting its status as a basal source with links only to consumers.

The low-resolution webs for Windsor and Chezzetcook have higher overall connectivity than the high-resolution webs, probably a reflection of low taxonomic resolution (Dunne et al., 2002b). An example of high connectivity for low taxonomic resolution is the node of phytoplankton, which has a consistently high connectivity in all the food webs because diatoms are assigned as highly aggregated basal nodes that include

multiple species and life forms from benthic to small planktonic taxa. Thus, they have more consumers than other individual prey items and form important connectance points (Wood et al., 2015).

Connectivity values also are significantly higher for invertebrates than vertebrates in low-resolution webs (Table 3.7), which is indicative of taxonomic lumping for omnivorous and intermediate taxa (Wood et al., 2015). In contrast, connectivity is higher for invertebrates in the NS high-resolution metaweb. Thus, interpretation of ecosystem structure and stability is strongly influenced by resolution, especially for webs with high aggregation as evident in stream habitats (Thompson and Townsend, 2005) and intertidal areas (Wood et al., 2015). The Nova Scotia comparisons confirm the general principle (Dunne et al., 2004) that more highly-resolved foodwebs have proportionally lower connectance values.

Individual connectivity values do not fully represent the ecological role of a species because food webs are based on presence or absence and do not account for abundance and biomass. For example, at Chezzetcook, biting midge larvae are among the most abundant epifauna on filamentous algal mats and have a high connectivity in both low- and high- resolution webs (> 2.0; Supplement B-3, B-4). The abundant amphipod *Leptochelia rapax* has a connectivity of 0.96 in high-resolution webs but a much higher value of 1.54 in aggregated low-resolution webs (Supplement B-3, B-4). Thus, two abundant species in the algal mat community have different connectivity depending on the taxonomic resolution. Additionally, conclusions about food webs need better integration of non-trophic interactions, such as soil-binding on mudflats, to improve their explanatory and predictive qualities (van der Zee et al., 2016). Habitat modification can

strongly change food-web structure by increasing or decreasing species richness, and by altering trophic interactions. Invertebrates and sources have more importance in temperate marsh ecosystems, both ecologically and physically. Normally the most connected species in a food web is the main community structural component, but van der Zee at al. (2016) show how temperate Atlantic salt marsh habitat-modifiers like *Spartina alterniflora* have equal importance despite a lower connectivity.

Small macrofauna (especially biting flies, amphipods, and shrimp) are abundant in the marsh and mudflat epibenthos and are important structural elements of Chezzetcook and Windsor webs (Fig. 3.2, Supplement B-3). Sanchez-Hernandez et al. (2015) showed that, in mountain lakes, they extract resources from multiple trophic levels, which promotes food-web stability. For example, biting flies have multiple feeding strategies during their life cycle from deposit-feeding sediment-dwelling invertebrates to sexually dimorphic parasitic or free-living adults, and are highly connected and important trophic species. Meiofauna and small macrofauna occupy the lower trophic levels of a food web and are typically detritivores or herbivores (Miller et al., 1996), yielding high *%Herb* values in all the Nova Scotia food webs (Table 3.4). They represent a large fraction of the biomass and are an important food source for species at higher trophic levels (Schmid-Araya et al., 2002). Being also intermediate and omnivorous taxa, they additionally impact the lowest trophic levels (Miller et al., 1996).

Most webs show high levels of omnivory (Dunne et al., 2004), as noted in the Nova Scotia webs (Table 3.4. *%Omn* = c. 58 to 76). Webs with both high *%Omn* and a high proportion of intermediate feeders *%Inter* (>80%) are expected to have increased linkage density and therefore greater food-web stability (Sanchez-Hernandez et al., 2015).

Omnivorous and intermediate taxa such as foraminifera, midges, amphipods, shrimp and annelids are important vectors for transferring energy through the food web. Additionally, foraminifera, harpacticoid copepods and nematodes can make up 95% of the meiofauna (Chandler, 1989), with thousands of individuals in a 10 ml sample. Foraminifera are a large part of the infaunal and detrital system of salt marshes. Our results show that the medium-resolution NS metawebs, which exclude foraminifera, do not differ significantly from the high-resolution webs. However, in view of the lower resolution of most published food webs, exclusion of foraminifera could make a larger difference in topology, emphasizing their significance in the ecosystem. Binary food webs do not account for abundances and biomass, so stable isotope analysis may help answer the question of foraminiferal food-web importance by quantifying the trophic role of these abundant protists (Chapter 4), and biomass-abundance calculations of Chapter 5 emphasize foraminiferal importance in the small food web.

In the NS webs, the meiofauna are generalist herbivores (eating plankton, algae, plant detritus, particulate organic matter, and bacteria) and are consumed by generalist feeders such as worms, insects, crustaceans and small fishes. Over 50 species (21% of the taxa) in the NS web are in the meiofauna size range for part of their life cycle, comprising over 70% of the total consumers. In temperate benthic freshwater aquatic systems of the UK, meiofauna also represent a high proportion (70%) of the taxa (Schmid-Araya et al., 2002). These generalist omnivores lengthen food chains and increase web complexity and stability as energy is transferred in various pathways to larger consumers (Schmid-Araya et al., 2002). Omitting meiofauna misrepresents web complexity and influences interpretation of food-web patterns. These small omnivores also play a crucial role in

maintaining biodiversity and mediating any cascading ecosystem effects such as extinctions (Bruno and O'Connor, 2005).

Omnivores form crucial links to and from the producer-based "green food webs" and the detritus-based "brown food webs," and so are multichannel feeders that promote ecosystem stability (Wolkovich et al., 2014). These detritus-based systems with abundant and diverse generalist omnivores promote salt-marsh ecological stability, and future food web research should seek to separate and follow the pathways of these "brown-webs" in an ecosystem (Moore et al. 2004). All the Nova Scotia webs have < 10% conversion to trophic species, and zero conversion for some zone-specific webs with no 100% shared predators or prey for nodes. These highly resolved webs suggest a robust response to ecosystem disturbance (Dunne et al., 2002b), whereas the higher individual species connectance and percentage of taxonomic aggregation in the low-resolution webs would suggest less stability and robustness. The higher connectance (*C*) and lower links per species (*L/S*) in low-resolution webs reflect high taxonomic aggregation and an uneven trophic resolution.

As binary food webs increase in quality, models and generalizations become rejected (Akin and Winemiller, 2006). The niche model of Williams and Martinez (2000) shows a good fit to the Nova Scotia webs only at lower resolution. Although the model fits ecological food webs better than random and cascade models, it has limitations for comparison with species-rich webs such as the Nova Scotia datasets. Dunne et al. (2004, 2014) emphasized that increased trophic richness decreases the fit to the model, which often highly underestimates the proportion of herbivores in the system (Table 3.6). This value has the biggest discrepancy in our web-niche model comparisons. In the NS webs,

the herbivore category incorporates all consumers of basal sources (Fig. 3.3; detritus, phytoplankton, bacteria, carrion) and includes detritivores, bacterivores, and scavengers. The high number of species that consume these basal sources and plants explains why the niche model greatly underestimates the high *%Herb* values (Table 3.6). Additionally, Dunne et al. (2004) found that basal groups are the most aggregated even in the most taxonomically uniform webs. In food webs for mountain lakes, more taxa lead to greater change in web properties (Sanchez-Hernandez et al., 2015), regardless of ecological function. In the intertidal webs studied by Wood et al. (2015), five properties did not fit the niche model with $S < 50$, but nine did not fit with $S = 100$. Comparison of the high-resolution NS webs with the niche model emphasizes that the model cannot accommodate empirical food webs with high species richness and low connectivity.

Possibly such high-resolution species-rich webs would follow a nested-hierarchy model (e.g., Cattin et al., 2004) that incorporates phylogenetic constraints instead of body-size constraints in the niche model, better reflecting the complexity and multidimensionality of natural systems. The niche model predicts a *DietDis* of 0 but all food webs examined, including the Nova Scotia webs, have *DietDis* of 0.10 or higher, indicating more dimensionality to the feeding hierarchy than accommodated by the standard niche model (Cattin et al., 2004). However, neither niche nor nested-hierarchy models perfectly match the empirical system.

3.5.2. Chezzetcook and Windsor metawebs

Structurally, Chezzetcook and Windsor have similar food-web properties, with no significant difference in connectance across resolutions between the marshes (see

summary Table 3.8). Both marshes show a similar (albeit not strong) fit with the niche model (Table 3.6), although Windsor fits slightly better, probably due to a lower trophic richness as noted for other marine food webs by Dunne et al. (2004). Chezzetcook has a higher taxonomic diversity in basal species (particularly, vascular plants), resulting in a higher number of herbivores (e.g., insects). Chezzetcook is a more mature salt marsh with a more extensive middle and high marsh and less winter ice influence. Mature marshes such as Chezzetcook appear to have lower primary productivity per unit area than immature marshes, and therefore have an increased importance of detritus as a basal resource (Rooney and McCann, 2012).

At Windsor, crustaceans and annelids have a significantly higher connectance than at Chezzetcook (Windsor: 1.0 and 1.2; Chezzetcook: 0.8 and 0.9; Appendix B-3). The extensive Windsor mudflats support large populations of small macrofauna such as the amphipod *Corophium volutator* and polychaete *Hediste diversicolor*, which are crucial food sources for thousands of shore birds at low tide and many fishes at high tide (Daborn et al., 2003). These small macrofauna play a crucial role in the tide-dominated mudflat system. Though the same tidal feeding structure occurs at Chezzetcook, the more extensive and diverse (in species and structure) vegetation cover leads to higher connectance for insects + spiders, and birds than at Windsor (Chezzetcook: 1.2 and 1.5; Windsor: 0.9 and 1.1; Appendix B-3).

3.5.3. Tidal gradients

In each Nova Scotia marsh, the high and middle marsh zones are more closely related in food-web structural properties than either is to the low marsh or mudflat (Figure 3.8, nMDS plot). This is expected because high and middle marshes have a more “terrestrial”

composition with higher diversity of vascular plants and insects, whereas the low marsh and mudflat have a more marine composition with estuarine fish, crustaceans and annelids. The tidal gradient that determines the marsh zones is a large-scale heterogeneity, similar to the spatial heterogeneity in longitudinal river gradients (e.g., Romanuk et al., 2006) and estuaries with tidal spatial gradients (Wood et al., 2015, Alaska; Coll et al., 2011, Atlantic Canada). In coastal systems such as the Tagus Estuary, Portugal, the salinity gradient is the main reason for significant differences between web properties (Vinagre and Costa, 2014). The percentage of top predators (mostly fish) increases with increasing salinity. In these estuarine systems, fish and birds predatory on fish are at high-trophic levels, but the marine fish cannot tolerate low salinity and the percentage of top predators decreases with marsh elevation (Vinagre and Costa, 2014). In both Nova Scotia marshes, the connectance of foraminifera increases from the high marsh to the mudflat, which accords with previous statements on the important role of sediment meiofauna to the diets of many upper-level consumers in these detritus-based systems.

Salt-marsh conditions are dynamic, and organisms must cope with frequent inundation by sea water, lengthy exposure that increases the risk of desiccation, and an environment of fluctuating anoxia (Bertness, 1991; Scott et al., 2014). Salt-marsh tidal gradients (zonation) must be considered when analyzing ecosystem energy flow. Because the high-resolution, zone-specific webs take this physical heterogeneity into account, they are a more accurate representation of salt-marsh ecology than the high-resolution web for the overall ecosystem. In general, our species composition data (Appendix B-1) show that organisms typical of the mudflat and lower regions of the marsh can cope with or tolerate

frequent and prolonged tidal inundation (see Bertness, 1991; Mitsch and Gosselink, 2008).

3.5.4. Comparison with other food webs

Overall, the Nova Scotia salt-marsh food webs have higher taxonomic resolution than 17 previously published webs for marine, freshwater and terrestrial environments (Table 3.9, Fig. 3.9). The Chezzetcook and Windsor webs are structurally similar to Nova Scotia rockweed and seagrass ecosystems (Schmidt et al., 2011), and on a global scale, to one estuary web, and several lake and grassland webs (reviewed in Dunne et al., 2004; Vinagre et al., 2017). Other estuarine webs and the mediterranean-climate Carpinteria salt marsh in California (Lafferty et al., 2006), with parasites removed from the predator-prey matrices) are less similar. In addition to drastic physical differences between California and Nova Scotian salt marshes, the California webs have more highly-aggregated basal and invertebrate groups and contain more detail for higher trophic levels, with *%Top* much larger (>17) than the Nova Scotia marsh values of <2% (Table 3.9).

Table 3.9. Comparison of eight food web properties for 19 food webs, including three salt marshes (present study, and Lafferty et al. 2006), Nova Scotia rockweed and seagrass (Schmidt et al., 2011), one terrestrial (UK grassland) and several freshwater systems (Dunne et al., 2004) and other marine webs (Dunne et al., 2004; Vinagre et al., 2017). Data are used in multidimensional scaling analysis for Figure 3.9.

	TS	L/S	C	%Top	%Inter	%Omn	%Basal	TL Mean
Windsor Low Resolution*	98	12.61	0.13	1.02	88.78	77.55	10.2	2.85
Chezzetcook Low Resolution*	105	14.28	0.14	0.95	89.52	72.38	9.52	2.77
Carpinteria, California$^{\phi}$	83	5.86	0.07	39.8	50.6	55.4	9.6	2.61
NS Rockweed±	60	12.42	0.21	15	70	83	15	1.94
NS Seagrass±	51	13.65	0.27	22	63	82	16	1.83
UK Grassland$^{\delta}$	61	1.6	0.03	31	56	21	13	2.6
Little Rock Lake $^{\delta}$	92	10.8	0.12	1	86	38	13	2.4
Mirror Lake $^{\delta}$	172	25.1	0.15	1	74	59	25	2.1
Lake Tahoe$^{\delta}$	172	22.6	0.13	9	66	58	28	2.1
Canton Creek$^{\delta}$	102	6.8	0.07	25	22	8	53	1.5
Stony Stream$^{\delta}$	109	7.6	0.07	17	27	10	56	1.5
Chesapeake Bay$^{\delta}$	31	2.2	0.07	32	52	52	16	2.4
St. Mark's Estuary$^{\delta}$	48	4.6	0.1	17	69	71	12	2.5
Ythan Estuary$^{\delta}$	83	4.8	0.06	37	54	54	9	2.6
NE USA Shelf$^{\delta}$	79	17.8	0.22	4	94	78	3	3.1
Small Caribbean Reef$^{\delta}$	50	11.1	0.22	0	94	86	6	2.9
Large Caribbean Reef$^{\delta}$	245	13.8	0.05	0	98	87	2	3.1
Tagus Estuary (Nursery)¥	53	4.7	0.09	28	57	60	15	2.55
Tagus Estuary ¥	90	5.2	0.06	27	63	69	10	2.67

*present study
$^{\phi}$ Lafferty et al., 2006
± Schmidt et al., 2011
$^{\delta}$ Dunne et al., 2004
¥ Vinagre et al., 2017

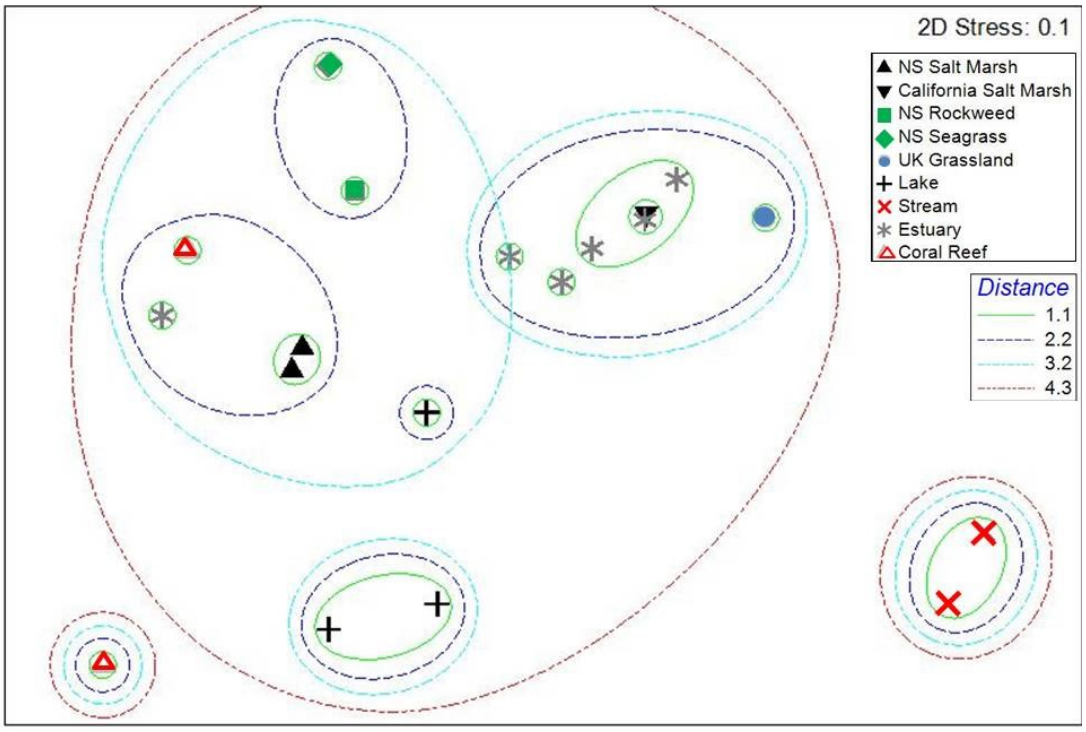

Figure 3.9. Multidimensional scaling analysis overlaid with normalized Euclidean distances from cluster analysis of 8 common food web properties of Chezzetcook and Windsor salt marsh webs with previously published webs (see Table 3.8).

In addition to uneven taxonomic resolution, an increase in species richness will change web structure, regardless of the species interactions (Sanchez-Hernandez et al., 2015). Our lowest resolution webs have more taxonomic resolution than some high-resolution webs in other published studies, making direct comparison difficult. This issue has long been unresolved (Dunne et al., 2004). Recently, more species-rich (S <100) and evenly-distributed fossil lake webs have been analyzed but limitations remain unresolved when comparing to a probabilistic niche model and previously published webs (Dunne et al., 2014).

Food webs reveal general community properties (Vinagre et al., 2017), and neither large samples nor large spatial scales can be informative about local variability and site-specific heterogeneity in salt marsh zones. For the Tagus Estuary, Vinagre et al.

(2017) showed that the extent (size of the study area and salinity range, equivalent to how we interpret the Nova Scotia tidal zones) impacts web structural properties more than the grain (taxonomic resolution). Spatial scale was also examined in the intertidal zone of the Sanak Archipelago in Alaska (Wood et al., 2015), where extending the sampling area increased the taxonomic and link richness but masked heterogeneity and species interactions on a smaller spatial scale.

The coefficient of variation (CV) for food-web properties shows that neither taxonomic resolution (Table 3.4) nor tidal gradient (Table 3.5) has a predominant effect on web differences across resolutions and zones: both play important roles. A CV >10 indicates significant variability between properties (Vinagre et al., 2017). For both Nova Scotia marshes, both taxonomic resolution and tidal gradient have mean CV values >10. Chezzetcook web properties across tidal zones give a larger coefficient of variation than zone variability at Windsor, probably because of the large proportion of middle and high marsh which is ecologically different than the low marsh and mudflat (Figure 3.8). In contrast, the vegetation gradient at Windsor is less pronounced and the difference in web properties across marsh zones is smaller. For the Tagus estuary, extent (equivalent to tidal gradient in the Nova Scotia study) is also the main cause of difference in web properties (Vinagre et al., 2017).

For Chezzetcook and Windsor, the mummichog *Fundulus heteroclitus* has the highest connectance in the low marsh and mudflat zones and the highest connectance overall at Windsor. Similarly, small fish have higher connectance in Argentinian estuarine food webs (Alvarez et al., 2013). Elsewhere, the taxonomic aggregation of lower-level taxa (e.g., diatoms and other basal sources) may lead to a false interpretation

that these nodes have more predators (higher connectance) than other nodes in the web (Wood et al., 2015). For the most part, the low-resolution Nova Scotia webs contain more taxonomic diversity at the lower trophic levels than most previously published webs reported by Dunne et al. (2004).

A salient question is "Do highly resolved webs justify the additional time and effort required for data collection?" Structural food-web properties such as connectance are sensitive to the level of taxonomic inclusiveness, resolution and sampling effort. In a study of freshwater stream webs along a pH gradient, Oleson et al. (2010) found a trade-off between under-sampling and including links that may not be realized locally although common elsewhere (as cited by Layer et al., 2010). Food webs need to be simple enough to be understood without losing the realism that they are intended to represent (Polis, 1991). Dunne et al. (2013) showed that food webs change by simply increasing taxonomic richness (*S*) and connectance (*C*), e.g., when parasites are added. The high-resolution Nova Scotia data indicate that invertebrates, metazoan meiofauna and foraminifera also play specific roles in changing web properties beyond the impacts of increasing *S* and *C*. For example, biting flies are some of the most highly connected species in all webs, with multiple trophic stages of their life cycle and a feeding hierarchy not based on body-size ordering — the basis of the Williams and Martinez (2000) niche model. In part for this reason, the feeding mode of many invertebrates and the high species count (S >100 in Nova Scotia marshes) leads to a poor fit with the traditional niche model. A better fit might result from comparison with the modified niche model of Klecka (2014) that includes predator-prey body mass, or with the nested-hierarchy model which better reflects the complexity and multidimensionality of taxa-rich, complex

systems by using phylogenetic constraints for prediction (Cattin et al., 2004). Rooney and McCann (2012) showed that detrital energy (presumably also including carrion) flows more slowly but includes greater diversity. The benthic ecosystem is more structurally complex and has more diverse communities than the fast chain in a marine pelagic system, and salt marshes typify ecosystems stably anchored by the benthos (Scott et al., 2014).

3.5.5. Implications for conservation

Food webs are powerful tools for examining ecosystem structure and function in terms of species and their energy flow, crucially important for understanding ecological roles and biodiversity mechanisms (Thompson et al., 2012). Much food-web research has focused on ecosystem robustness, stability and ecological complexity in terms of cascading effects and species loss in times of ecological change, for modern data (e.g., Abascal-Monroy et al., 2016, for Terminos Lagoon, Mexico) and fossil assemblages (e.g., Dunne et al., 2014, for diversification following the end-Cretaceous extinction at Messel). Based on their structural properties, Nova Scotia salt-marsh webs are complex not only in terms of links and number of species but also in robustness and stability through the high proportion of omnivorous (>50%) and intermediate (>80%) species (Polis and Strong, 1996). Omnivores have large and possibly mediating effects on ecosystem disturbance because they feed on multiple trophic levels (Marczak et al., 2011). Trophic cascades (secondary extinctions) are less common in complex webs due to a high number of indirect interactions, as provided by the Nova Scotia intermediate and herbivorous taxa (Bruno and O'Connor, 2005).

In terms of overall physical robustness, the high elevation range of *Spartina* grass and high sedimentation rates give Bay of Fundy marshes great resilience and promise for low-maintenance restoration projects (Byers and Chmura, 2007). The macrotidal system and high sedimentation rates are listed as the key factors for such successful tidal-river marsh restoration (Gerwing et al., 2017). At Windsor, a fully-functioning *Spartina* salt marsh ecosystem has developed within 30 years without human mediation following causeway construction. In comparison to other older Bay of Fundy marshes, Windsor apparently has fewer vertical zones and less floral diversity (Byers and Chmura, 2007). However, due to habitat loss over the last 400 years, few pristine reference marshes remain in the Bay of Fundy, comprising <15% (2700 hectares) of the pre-1600 area, and they have more high-marsh vegetation compared to newly-restored sites with higher abundance of *Spartina alterniflora* (Bowron et al., 2009). Mesotidal salt marshes in cool-temperate southeast England can recover quickly (2−107 years) on reclaimed land but the replacement marshes have fewer species and different species compositions, even 100 years later (Garbutt and Wolters, 2008). High-resolution food webs that include meiofauna, small macrofauna and foraminifera can also indicate ecological function and health, as indicated by the structural web similarity for the young Windsor and mature Chezzetcook marshes. Our data suggest that biodiversity and energy flow in a macrotidal marsh may be restored relative to a mature mesotidal marsh in about 50 years.

Barnosky et al. (2017) pointed out that food webs are not only important for ascertaining the structure and robustness of ecosystems but also for conserving and monitoring their health. This requires managing the functional integrity and attributes that characterize the entire ecosystem, rather than solely a few species of interest. The

paleobiology of extinct systems and their food webs provides a baseline for evaluating response to disturbance (Barnosky et al., 2017) and aids in optimizing conservation planning for modern ecosystems at risk. Recently, food webs have been used to look at ancient ecosystems (e.g., the Cambrian Burgess Shale; Dunne et al., 2008) and fossil ecosystem mass extinctions (e.g., the Permian-Triassic and Cretaceous-Paleogene events) to compare with modern analogs. Cambrian Burgess Shale and Chengjiang Fossil Beds food webs use low-resolution, high-uncertainty data that are highly space- and/or time-averaged and show a good fit to the Williams and Martinez niche model (Dunne et al., 2008). For ecosystems following the Permian-Triassic mass extinction in South Africa, Roopnarine and Angielczyk (2015) found that the stability of the community depends more on the functional diversity (e.g., *%Omn, Inter, Herb*) than on high species richness. Dunne et al. (2014) found that lake and forest communities in the Eocene Messel Shale (48 Ma) were species-rich (S >100), with a poor fit to the probabilistic niche model of Williams and Purves (2011). If evaluated only with a model fit, the Messel communities would appear to differ significantly from extant ecosystems, most of which use the niche model when S <100. Dunne et al. (2014) recommended comparing this extinct food web with species-rich webs (such as Nova Scotia salt-marsh webs), rather than simply using a theoretical niche model. Although fossil salt-marsh communities might not survive transgressive erosion, trace fossils in estuarine deposits might constitute proxies for low-resolution food webs to evaluate changing salinity, sedimentation and interstitial oxygen in fossil ecosystems (Hubbard et al., 2004).

3.6. Conclusions

The importance of taxonomic resolution for cool temperate salt marshes in Nova Scotia was analysed to answer the question of how much detail is enough to capture the structure of the salt marsh detritivorous system. Two-hundred and eighty one nodes were compiled from hundreds of samples taken over six years from two marshes for a regional (Nova Scotia) high-resolution metaweb with 5995 feeding links. The larger, mature Chezzetcook marsh has 244 nodes and 4673 links and the smaller, young Windsor marsh has 191 nodes and 3778 links. Medium-resolution webs, excluding only foraminifera species, did not significantly change the food web structures. Low-resolution webs, however, decreased the taxonomic diversity to less than half of that in high-resolution webs, and all aggregated nodes were invertebrates and basal groups, leading to a bias to higher-level vertebrates when interpreting food web properties. The three high-resolution metawebs reveal that invertebrates dominate, with 58% of the species richness. There are slightly more fishes and birds at Windsor, and four times the number of vascular plants at Chezzetcook. The numbers of fishes, birds and mammals are similar across different taxonomic resolutions, but the invertebrate taxa decrease by >50% between high- and low-resolution webs. There are potential negative consequences in neglecting taxonomic details in a detritus-based system where infaunal and epifaunal groups can promote both ecological and physical stability.

When comparing to the niche model, the high species count (S>100) and the underestimation of *%Herb* (e.g., detritivores) are important. Salt marsh systems are dominated by decomposers and detritivores, and including them in food webs emphasizes a bottom-up approach, whereas focusing on higher-level species emphasizes a top-down

approach and a predatory system. High-resolution webs provide a more realistic portrayal of the bottom-up, detritus-based system that characterises tidal salt marshes worldwide.

Overall, the degree of taxonomic resolution is of primary importance in determining the food-web variability of all the NS metawebs. There are few significant differences between the two marshes, despite an 8-fold difference in tidal height and at least a 5-fold difference in marsh age. This implies a high resilience for young marshes along the macrotidal Bay of Fundy that may be important for marsh restoration projects. However, when Chezzetcook and Windsor marshes are examined separately, the difference across tidal zones is greater for Chezzetcook than for Windsor, so food webs for these spatially heterogeneous ecosystems need to be examined separately.

Considerable differences between low- and high-resolution Nova Scotian salt marsh food webs indicate that the degree of taxonomic resolution greatly affects ecosystem interpretation and the representation of the entire community. Within each marsh, however, few significant differences were observed across zones or resolutions in either salt marsh. In contrast, for individual taxa, variability in nodal averages is higher across tidal zones at Chezzetcook where there is a distinct terrestrial-marine gradient. There is also greater variability among individual taxa across taxonomic resolutions at Windsor where the low marsh and mudflat are more extensive and contain diverse infauna. In general, there is enough variability between the marshes to differentiate them by zones and validate the use of a high-resolution database to reveal important differences. This study may also serve as a baseline for global salt marsh food web studies.

CHAPTER 4: USE OF δ^{13}CARBON AND δ^{15}NITROGEN STABLE ISOTOPES WITHIN AND BETWEEN TWO TEMPERATE SALT MARSHES, ATLANTIC CANADA, TO EXAMINE PATTERNS OF FOOD WEB STRUCTURE AND FUNCTION.

4.0 Abstract

Natural stable isotopic tracers $\delta^{13}C$ and $\delta^{15}N$ and ratios of C:N are important tools for understanding the food web dynamics of salt marsh ecosystems, in discerning paleoenvironments, and for monitoring anthropogenic interactions such as restoration projects and pollution. We examined stable isotopes for the three main sources (vascular plants, algae, sediment organic matter) and for consumers (mostly foraminifera, meiofauna, and small invertebrates) of two temperate salt marshes in Nova Scotia: a macrotidal, young marsh at Windsor and a mesotidal, old marsh at Chezzetcook, with mudflat to high marsh zones. Plant $\delta^{13}C$ values distinguish C_3 plants with depleted $\delta^{13}C$ from less-depleted C_4 plants, but plant $\delta^{15}N$ values have greater variability and less clear distribution patterns. Sediment values have relatively consistent $\delta^{13}C$ and $\delta^{15}N$ signatures, regardless of zone or marsh, implying widespread mixing of sources and post-mortem effects. Consumers show variable mean $\delta^{15}N$ values, with meiofauna and foraminifera having the highest variability, highlighting the need for their inclusion in marsh isotope analysis. Trophic positions of consumers are within expected ranges based on other stable isotope analysis studies, and are within predicted values from binary predator-prey food web calculations. Based on stable isotope analysis alone, the two marshes show no major differences overall, but N and $\delta^{15}N$ values tend to be higher at Windsor and $\delta^{13}C$ values

more depleted at Chezzetcook. In contrast, the marsh zones show many significant differences in isotope signatures and C:N values, especially between the high-middle marsh and the low marsh-mudflat, as a consequence of variation in food-web structure along the distinct land-sea transition. The overlapping $\delta^{13}C$ and $\delta^{15}N$ signatures of sources and consumers between marshes and zones emphasize the need for more than one measure of ecosystem structure and function for food-web and paleoenvironmental analysis.

4.1 Introduction

Natural isotopic tracers, primarily $\delta^{13}C$ and $\delta^{15}N$, provide a powerful tool for identifying food-web linkages in aquatic ecosystems, including salt marshes (Currin et al., 1995) and estuaries (Deegan and Garritt, 1997; Cloern et al., 2002). Stable-isotope analysis is a useful tool for investigating trophic interactions of animals and their food sources (Peterson and Fry, 1987; Post, 2002; Claudino et al., 2013), tracing carbon sources (Canuel et al., 1995; Connolly et al., 2005) and determining organic matter (OM=Organic Matter) sources in heterotrophic organisms and sediments (Chmura and Aharon, 1995; Coffin and Cifuentes, 1999; Goñi and Thomas, 2000). Cloern et al. (2002) used stable isotopes to determine OM sources in complex coastal systems where multiple plant communities and diverse exogenous inputs collectively sustain system metabolism, but found the relative contribution of each input difficult to measure.

There are key knowledge gaps related to salt marsh isotopic signatures. In particular, although many studies have since tried to discern the exact contributions and controls of OM, overlapping source signatures, variations in salt marsh age and elevation, and biogeochemical effects such as decomposition lead to inconclusive results (e.g.,

Tanner et al., 2010; Chen et al., 2016). Few assessments have considered all plant communities within a single complex ecosystem to test C and N isotope ratios as source-specific biomarkers of OM origin. For example, some studies of estuaries looked at seagrass and microalgae but not salt marsh plants (Claudino et al., 2013). Regardless of the overlapping isotopic signatures, understanding the trophic dynamics and connectivity of consumers is critical for effective tidal wetland habitat management, restoration and conservation (Kwak and Zedler, 1997) and for refinement of signatures in the geologic record.

These knowledge gaps have led to two main research questions examined in this chapter. The first question is: what are the patterns and magnitudes of variability in the C and N stable-isotopic composition of plants, OM sources, and meiofaunal to small macrofaunal communities in two temperate salt marshes with different tidal regimes? The results aim to clarify the detritus-based food web structure and function of the marshes, below the level of large predators such as mammals, birds and fishes. The second question is: does the importance of "basal" food web components vary in salt marshes with different tidal regimes and across tidal zones? The Nova Scotian marshes differ greatly in tidal amplitude, winter ice cover and geological age, although there is little difference in their food web structures (Chapter 3). Previous work has emphasized the need to examine spatial differences within an ecosystem, especially in heterogeneous estuaries (Nelson et al., 2015), salt marshes (Park et al., 2015) and river networks (Schmid-Araya et al., 2016). The $\delta^{13}C$ and $\delta^{15}N$ values for food web components allow a more refined understanding of food web complexity for the Nova Scotia coastal

ecosystems. Previous studies (Chapter 3) using trophic position, linkage density, and taxonomic group connectance indicate that meiofaunal interactions play a prominent role.

Our study emphasises the importance of including high taxonomic resolution of small macrofauna (<2 cm), meiofauna (63-500 μm) and foraminifera in ecological studies to focus on the stable-isotope composition of small animal tissues and their food sources (Peterson and Fry, 1987; Post, 2002; Claudino et al., 2013). Stable isotope analysis can be used to examine long-term feeding patterns and numerically trace organic matter through a food web. Thus it has an advantage over feeding studies and gut content analyses that give a snapshot of consumer feeding relationships (Schmid-Araya et al., 2016). Furthermore, because small animals are difficult to dissect, much of their food source is too small to identify accurately without use of specialized biomolecular techniques.

To address the research questions, $\delta^{13}C$ and $\delta^{15}N$ values of the vascular plant (macroflora) and meiofaunal communities were measured for each tidal zone of two marshes in Nova Scotia. One is a mesotidal marsh at Chezzetcook Inlet on the Atlantic coast and the other is a macrotidal marsh at Windsor Causeway on the Bay of Fundy (Figure 4.1). This analysis contributes to an ongoing debate (Park et al., 2015) about the trophic role of basal sources and consumers and how their energy production moves to the larger fauna in the ecosystem. These isotope data help to resolve the trophic roles of small macrofaunal and meiofaunal components of the food webs through fingerprinting the source materials that fuel the energy bases of the marshes.

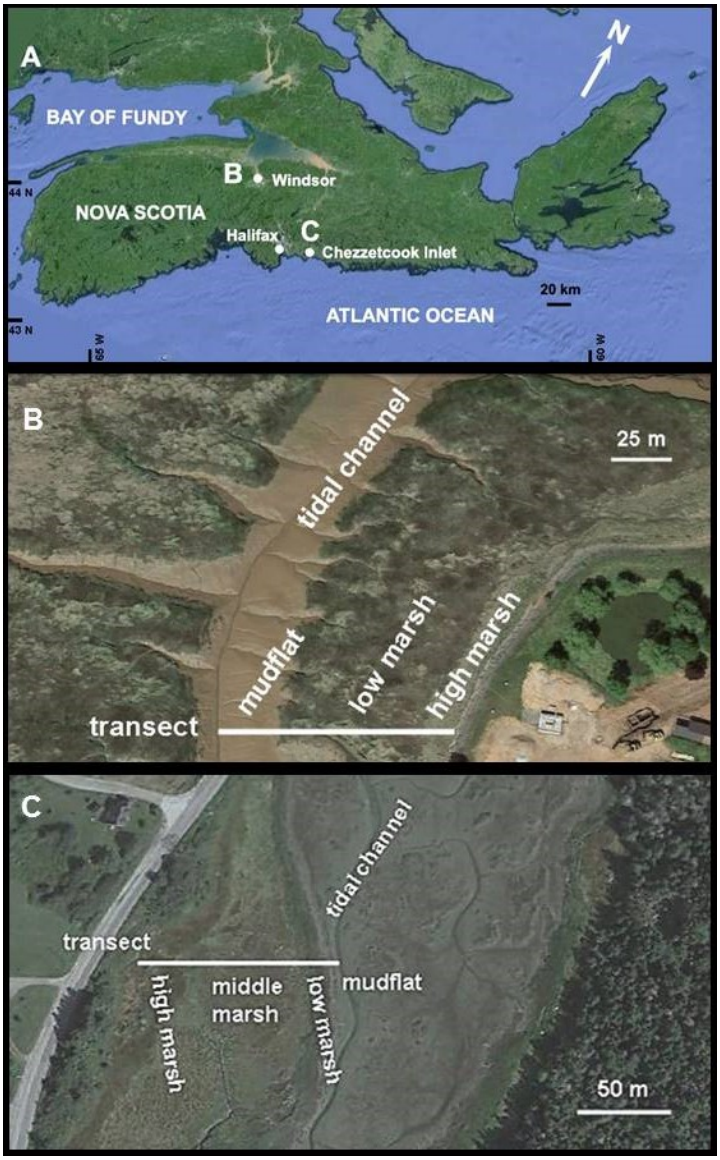

Figure 4.1 (A) Map of Nova Scotia showing locations of Windsor Causeway and Chezzetcook Inlet marshes. (B) Windsor marsh transect in the Minas Basin, Bay of Fundy, north of the constructed causeway. (C) Chezzetcook marsh transect on the Eastern Shore of Nova Scotia, Atlantic Ocean. Long white lines are the locations of the marsh sampling transects.

4.2 Study areas: Nova Scotia marshes

The two contrasting salt marsh ecosystems are from the cool temperate climate region (Dfb Köppen classification) of Nova Scotia, eastern Canada (Figure 4.1). The Chezzetcook marsh is at 44°41’ N, 63°14’ W, and largely fills Chezzetcook Inlet, an

extensive, shallow estuary with winding channels that drain into the Atlantic Ocean and where the tidal heights are between, on average, 0.6 and 1.8 m. This mature marsh began to form between 4,000 and 6,000 years ago. The study site is in a sheltered area midway between the headland and mouth of the inlet, encompassing four tidally regulated marsh zones: mudflat (5 m wide), low marsh (2 m wide), middle marsh (50 m wide) and high marsh (20 m wide). Details of the zones are given in Chapter 3 (Table 3.2). The tidal water salinity increases from 10 –13 psu at the inlet head to 25–31 psu at the mouth. Winter ice cover (from December through March) is thin. Sediment ranges from mud at the protected inlet head to sandy mud at the wind-exposed mouth, and organic carbon content decreases seaward (Scott and Medioli, 1980a). Sedimentation rates are relatively low, about 1–2 mm yr^{-1} higher than the rate of sea-level rise (ca. 3 – 4 mm yr^{-1}) (Chague-Goff et al., 2001), but measurements from Chmura and Hung (2004) give sedimentation estimates of 2.8 mm yr^{-1}.

The salt marsh at Windsor Causeway on the Bay of Fundy (Figure 4.1; (44° 59.75'N, 64° 08.75'W), is located between the causeway and the junction of the Avon and St. Croix rivers. The marsh formed after the causeway was built in 1970. Causeway construction interrupted sediment transport between the Minas Basin and the Avon River, resulting in mud accumulation on the seaward side of the causeway (Daborn et al., 2003). Sedimentation is high, outpacing erosion and resulting in a net gain of about 1.3 cm per year (Daborn et al., 2003). Colonization by isolated patches of salt marsh cordgrass, *Spartina alterniflora,* occurred by the late 1980s, and by the 1990s these patches began to merge, producing the salt marsh and mudflat (van Proosdij et al., 2009).

The marsh experiences extreme tidal heights from 12 to 16 m. A wide mudflat (>20 m from the tidal channel to the lowest *S. alterniflora*) is followed by a 60 m-wide low marsh, and a narrow high marsh (9 m). *Spartina alterniflora* covers about 1 km^2 of the original bare mudflat (estimated from creating polygons in satellite images from Google Earth 2011). Intense winter ice scouring takes place when tides carry pack ice in and out of the marsh (Partridge, 2001), removing large amounts of plant cover. The denuded sediment is re-colonized due to spring seeding and deposition of ice-rafted marsh peat containing grass rhizomes. The marsh has a steep gradient, with the top near the causeway approximately 2 m higher than the low marsh edge adjoining the tidal creeks (Daborn et al., 2003). The overall elevation is 4.70 m above mean sea level. Tidal water salinity varies between 25.6 and 28.0 psu, dominated at all times by Minas Basin tidal inflow with 29.5 psu (Daborn et al., 2003). The water temperature in the marsh averages 19.6°C during summer and autumn and the sediment has on average 68% silt and 23% clay, with minor OM and sand (Daborn et al., 2003)..

4.3 Field and Laboratory Methods

4.3.1 Sample Collection and Preparation

As seasonality was not examined here, samples from both salt marshes were collected during September 2013 during low tide. Additional sampling was required at Chezzetcook in September 2014 Samples of flora, fauna, and sediment were taken from each marsh zone at both sites, as described in Chapter 3. Bird feathers and faeces of unknown species and origin were also collected to give examples of vertebrates that feed in the marsh and to represent possible upper trophic levels. Living vascular plants,

including roots when possible, were removed, and thick (ca. 1 cm) filamentous algal mats were pulled by hand from the sediment surface and stored in plastic bags. For each zone, replicate 1-L bulk sediment samples were collected from the top 5 cm to avoid sampling anoxic subsurface sediment. All faunal and sediment samples were refrigerated until processed, and floral samples were immediately frozen. Micro-habitats such as tidal creeks, tidal channels, and salt pannes were not sampled.

Sediment subsamples of ca.10 ml were rinsed through stacked 250 and 63 μm sieves, and the meiofauna retained on each sieve were rinsed with filtered seawater from the Aquatron facility at Dalhousie University and stored according to size class (>250 μm, 63−250 μm). The meiofauna were hand-picked using a Zeiss Stemi DV4 stereo dissecting microscope (10 – 40x), identified to the lowest taxonomic level possible, and separated accordingly (see species list Appendix B-1). Foraminifera were mainly identified to genus and/or species level using taxonomic information in Scott and Medioli (1980).

4.3.2 Stable Isotope Analysis

Sorted meiofauna and foraminifera were refrigerated for at least 24 hours to allow evacuation of gut contents so that the $\delta^{13}C$ and $\delta^{15}N$ values would reflect tissue rather than digestive tract content. The organisms were fixed in vials of 95% ethanol and frozen until ca. 1.0 mg of each meiofaunal taxonomic and/or functional group was obtained, as needed for analysis.

The frozen plant samples were washed with distilled water to remove residual sediment, separated into roots, stems, leaves, flowers, and seeds, and dried in a Boekol

Model #1078 drying oven at 60°C for 48 hours (as samples continued to lose mass after 24 hours but not after 48 hours). The invertebrate epifauna and meiofauna were rinsed with distilled water and dried at 60°C for 24 hours. Insects, spiders, and small molluscs and crustaceans were dried whole, whereas the larger crustaceans (>5 cm) and the larger molluscs (>2 cm) were dissected and the soft tissue dried. Small gastropods that could not be dissected were soaked in dilute phosphoric acid for 24 hours to try and remove their shell; however, the shells did not fully dissolve. All meiofauna were rinsed thoroughly on a 45 µm sieve to ensure removal of all traces of ethanol.

The filamentous algal mat (probably *Cladophora* and *Chaetomorpha* species, see Table 4.1) from the Chezzetcook mudflat was washed on a 63 µm sieve with distilled water to remove excess sediment and microphytobenthos (diatoms, bacteria) and dried at 60°C for 24 hours. Whole sediment samples (10 ml) from each marsh zone were rinsed with distilled water through stacked 250 µm, 63 µm and 45 µm sieves, and the fractions were dried at 60°C for 24 hours. While many stable isotope studies treat plants, sediments and fauna in 1M HCl to remove inorganic carbonates, we followed Galvan et al. (2008), Bergamino and Richoux (2015), and Nelson et al. (2015) who showed that samples do not necessarily need acidification prior to analysis, and that sample acidification may affect natural isotopic signatures.

The dried plant, invertebrate epifauna, and sediment samples were ground into a fine powder with a mortar and pestle (meiofauna and microalgae samples were not ground due to their small size). The ground samples were weighed into 5 x 9 mm Costech tin capsules using a Sartorius Analytic microbalance (±0.0001 g). Required sample weight ranges for each type were determined from the UC Davis Stable Isotope Facility

guide at http://stableisotopefacility.ucdavis.edu/.The ^{13}C and ^{15}N content of most material was analysed using one sample, with a separate sample for plant stems in view of their low N content. Where possible, three replicates of each sample were analysed. If dry weights for the small meiofauna and foraminifera did not meet the minimum requirement of 0.5 mg (Tables 4.1 and 4.2), the organisms were combined with respect to their closest taxonomic groups (e.g. copepods + amphipods).

Sealed trays of prepared samples were shipped to the UC Davis Stable Isotope Facility in California, USA for analysis using a PDZ Europa ANCA-GSL elemental analyser and a PDZ Europa 20-20 continuous flow isotope ratio mass spectrometer (UC Davis, 2014). The $\delta^{13}C$ and $\delta^{15}N$ values are expressed as ‰ relative to the international standards Pee Dee Belemnite limestone and atmospheric nitrogen, respectively (Vander Zanden and Rasmussen 1999):

$$\delta X\ (‰) = [R_{sample}/R_{standard} - 1]x1000$$

where X = ^{13}C or ^{15}N, and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Instrument precision was 0.1‰ for carbon and 0.3 ‰ for nitrogen.

4.3.3 Data Analysis

Isotopic values of the same taxonomic groups from Chezzetcook 2013 and 2014 samples did not differ significantly and the data were combined (Table 4.1; Supplements C-1 – C-4). The C:N µg total mass ratios, $\delta^{13}C$ and $\delta^{15}N$ were plotted with respect to marsh zones. In some instances, macrofauna were divided into taxonomic groups (e.g., Diptera (flies), crustaceans, molluscs, etc.).

To determine trophic positions of consumers (Supplement C-5), trophic fractionation was corrected by subtracting the δ values from a selected a low trophic level baseline species following the methods of Schmidt et al. (2007) and Kristensen et al. (2016), using the equation:

$$\delta^{15}N_{\text{consumer corrected value}} = \delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline species}}$$

The trophic positions of each taxonomic and/or functional group were then calculated using the generic 3.4‰ trophic enrichment fractionation equation of Vander Zanden and Rasmussen (2001):

$$\text{Trophic position}_{\text{consumer}} = [(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}})/3.4] + 2$$

However, different trophic fractionation values may apply to different consumers (e.g., 2.54‰ $\delta^{15}N$ for many invertebrate detritivores, Vanderklift and Ponsard, 2003).

A Shapiro-Wilk's test showed that the data did not follow a normal distribution. Consequently, non-parametric tests (Mann-Whitney for two samples, Kruskal-Wallis for *k* samples) were employed to examine the differences in $\delta^{13}C$, $\delta^{15}N$, and C:N values for the sources and consumers of marsh zones and marsh sites. The coefficient of variation (CV; standard deviation of the values divided by their mean) was used to calculate variability (Supplement C-7; Kristensen et al., 2016). PRIMER ® v. 6 was used on Euclidean distances of untransformed isotope values to create similarity matrices for nonmetric multidimensional scaling plots and for non-parametric ANOSIM (Analysis of Similarities) calculations. XLSTAT in Microsoft Excel was used for all other data analysis, and all significant values reflect a p-value <0.05.

4.4 Results

A total of 25 taxonomic and/or functional groups from Windsor and 87 from Chezzetcook were identified and analysed for $\delta^{13}C$ and $\delta^{15}N$ (Tables 4.1 and 4.2). The 2013 sediment samples from Chezzetcook high marsh are not included as the values exceeded the limit of measurement in the UC Davis Lab (C > 3000 μg, N > 250 μg). Due to the small size of foraminifera and meiofauna, some samples were pooled with no replicates, and precision was low for some samples with less than 100 μg of carbon and 20 μg of nitrogen (see notes in Tables 4.1 and 4.2).

Table 4.1. $\delta^{13}C$, $\delta^{15}N$, and C:N ratios for producers and consumers of Chezzetcook marsh. Values reported as mean ± standard deviation (SD). Number of sample replicates given in parentheses. * denotes samples with lower precision (<20 µg N or <100 µg C) for N, C or both. Habitat: HM = high marsh, MM = middle marsh, LM = low marsh, MF = mudflat. Plant parts: F = flowers, L = leaves, S = stems, R = roots, AG = above ground (leaves + stems). Common names are listed in Appendix C-1; values in Supplement C-3.

Taxonomic name (or sample name)	Zone	Replicates	$\delta^{13}C$ (‰)	SD $\delta^{13}C$	$\delta^{15}N$ (‰)	SD $\delta^{15}N$	C:N	SD C:N
Vascular plants								
Solidago sempervirens (F)	HM	(3)	-27.40	0.04	1.49	0.21	25.10	0.43
(R)	HM	(3)	-27.19	0.03	1.94	0.02	39.11	1.95
(AG)	HM	(3)	-28.27	0.08	1.76	0.10	34.05	1.41
(S)	MM	(3)	-28.17	0.01	0.51	0.12	14.05	2.69
(F)	MM	(3)	-28.48	0.03	3.58	0.17	19.10	0.56
(L)	MM	(3)	-29.71	0.07	5.08	0.22	33.01	0.22
Cyperaceae (*Carex palaeceae*)	HM	(3)	-18.27	0.25	4.23	0.12	47.41	0.74
Limonium carolinianum (S)	HM	(3)	-26.44	0.31	0.83	0.27	7.97	0.80
(F)	HM	(3)	-27.59	0.18	3.82	0.27	23.69	4.02
(L)	HM	(3)	-27.67	0.05	4.02	0.28	31.87	0.29
Calamagrostis canadensis (S)	HM	(3)	-27.04	0.14	1.52	0.02	6.47	1.01
Juncus sp. (L)	HM	(3)	-28.72	0.12	4.52	0.24	29.85	0.59
(S)	HM	(3)	-28.65	0.15	-0.94	0.38	6.79	1.62
Distichlis spicata (S)	HM	(3)	-12.57	0.05	1.39	0.03	2.76	0.24
(L)	HM	(3)	-12.55	0.09	5.51	0.18	28.34	0.93
Spartina alterniflora (L)	HM	(3)	-12.72	0.05	7.35	0.08	17.29	0.05
(S)	HM	(3)	-12.61	0.12	4.42	0.12	3.88	0.79
Spartina patens (AG)	HM	(3)	-13.33	0.04	6.02	0.19	35.58	1.38
(AG)	MM	(3)	-13.76	0.04	3.33	0.13	51.80	1.86
(L)	HM	(6)	-13.54	0.41	5.25	1.37	42.05	16.25
(L)	MM	(3)	-14.27	0.06	6.75	0.18	25.44	0.18
(S)	HM	(9)	-13.13	0.10	3.91	0.84	16.02	12.52
(S)	MM	(6)	-13.26	0.19	5.96	0.81	15.69	11.26
(R)	HM	(3)	-12.73	0.13	-0.50	0.04	32.74	2.29
(R)	MM	(3)	-13.13	0.06	3.00	0.04	32.03	0.48
Salicornia sp. (AG)	MM	(6)	-27.43	0.52	3.34	1.51	19.72	2.44
(R)	MM	(3)	-21.60	0.30	1.91	0.12	26.87	2.17
Spartina alterniflora (AG)	LM	(3)	-13.38	0.07	1.01	0.04	22.70	0.20
(L)	LM	(3)	-13.82	0.09	6.23	0.29	22.85	1.50
(S)	LM	(6)	-13.11	0.17	4.19	2.65	22.04	13.70
(R)	LM	(3)	-13.31	0.01	0.21	0.09	25.57	0.24
Lichen								
Xanthoria parietina	LM	(3)	-17.44	0.19	8.51	0.46	8.09	0.18
Algae								
Chaetomorpha	LM	(3)	-14.98	0.11	3.81	0.03	16.67	0.07
Lyngbya (?)	LM	(3)	-13.10	0.09	3.75	0.02	9.18	0.11
Cladophora (?) 2014	MF	(3)	-13.60	0.09	5.43	0.14	10.78	0.17

Taxonomic name (or sample name)	Zone	Replicates	$\delta^{13}C$ (‰)	SD $\delta^{13}C$	$\delta^{15}N$ (‰)	SD $\delta^{15}N$	C:N	SD C:N
Cladophora (?) 2013	MF	(3)	-13.69	0.17	4.34	0.04	9.69	0.11
Bulk sieved sediments								
<45µm	HM	(2)	-21.64	0.03	4.02	0.00	11.33	0.00
	MM	(2)	-18.31	0.02	4.27	0.00	8.46	0.51
	LM	(2)	-19.81	0.04	3.79	0.08	7.50	0.04
	MF	(2)	-19.69	0.07	4.67	0.12	6.89	0.02
45µm-63 µm (2014)	HM	(2)	-21.25	0.00	3.66	0.03	13.47	0.07
	MM	(2)	-18.31	0.02	4.27	0.00	9.82	0.04
45µm-63 µm (2013)	MM	(3)	-19.95	0.02	5.04	0.21	7.27	0.06
45µm-63 µm (2014)	LM	(2)	-19.63	0.05	3.70	0.07	7.83	0.02
45µm-63 µm (2013)	LM	(3)	-19.16	0.02	4.33	0.08	8.32	0.05
45µm-63 µm (2014)	MF	(2)	-19.80	0.06	5.00	0.04	7.13	0.03
45µm-63 µm (2013)	MF	(3)	-21.16	0.03	5.53	0.10	7.44	0.01
63µm-125 µm	HM	(2)	-19.29	0.09	3.65	0.07	17.01	0.03
	MM	(2)	-16.89	0.03	4.16	0.05	11.32	0.01
	LM	(2)	-19.01	0.02	3.51	0.05	7.84	0.03
	MF	(2)	-18.67	0.04	5.17	0.01	6.91	0.04
Macrofauna (>2 cm)								
Vertebrates (proxy for)								
Bird Feather A	MM	(3)	-18.06	0.29	10.45	0.22	3.27	0.03
Bird Feather B	MM	(3)	-19.28	0.95	10.98	0.80	3.20	0.01
Bird Faeces A	MM	(2)	-14.29	0.84	4.13	0.08	4.85	0.30
Bird Faeces B	MM	(2)	-14.19	0.02	4.14	0.02	5.42	0.02
Bird Faeces C	MM	(2)	-12.28	0.70	2.95	0.15	5.50	0.50
Bird Faeces D	MM	(2)	-11.11	0.01	3.60	0.07	5.55	0.37
Bird Faeces E	MM	(2)	-13.44	0.36	4.13	0.08	3.85	0.05
Arachnids and Insects								
Grammonata trivitata	HM	(4)	-18.09	0.97	8.53	0.27	4.26	0.48
Araneus diadematus (?)	HM	(3)	-25.56	0.03	6.50	0.07	4.03	0.01
Pardosa littoralis	HM	(1)	-16.85		7.97		5.26	
Doryodes grandipennis	HM	(3)	-26.75	0.04	7.31	0.12	3.75	0.01
Grasshopper (*Dichromorpha viridis*?)	HM	(3)	-20.92	0.04	6.42	0.10	4.07	0.01
Grasshopper (*Paroxya*?)	HM	(3)	-22.04	0.26	6.32	0.17	4.02	0.02
Grasshopper (*Chorthippus curtipennis*?)	MM	(3)	-17.00	0.16	9.12	0.29	4.62	0.02
Coleoptera (Hydrophilidae)	MM	(1)	-20.09		2.69		4.64	
Diptera	MM	(1)	-15.99		8.26		4.52	
	LM	(1)	-21.33		5.09		4.15	
Ephydridae	LM	(2)	-16.96	0.08	9.79	0.17	3.87	0.01
Molluscs								
Melampus bidentatus	HM	(3)	-17.94	0.17	4.95	0.12	10.14	0.22
Gastropod (*Alderia modesta*?)	LM	(1)*	-16.48		7.23		4.36	
Littorina littorea A	LM	(3)	-14.94	0.08	4.19	0.03	4.24	0.05
Littorina littorea B	LM	(3)	-15.09	0.07	4.27	0.06	4.46	0.15
Littorina littorea C	LM	(3)	-14.76	0.09	4.32	0.04	4.87	0.02
Littorina littorea D	LM	(3)	-15.55	0.03	3.82	0.06	4.44	0.01
Littorina littorea E	LM	(1)	-14.66		5.74		3.74	

Taxonomic name (or sample name)	Zone	Replicates	$\delta^{13}C$ (‰)	SD $\delta^{13}C$	$\delta^{15}N$ (‰)	SD $\delta^{15}N$	C:N	SD C:N
Littorina littorea (2014)	LM-MF	(3)	-14.90	0.03	4.96	0.05	4.11	0.03
Littorina littorea (large; 2014)	LM-MF	(3)	-14.38	0.09	4.91	0.03	4.17	0.04
Littorina littorea (2013)	LM-MF	(3)	-13.15	0.02	6.26	0.18	4.25	0.08
Littorina littorea	MF	(3)	-7.07	0.04	5.08	0.05	8.55	0.07
Littorina saxatilis	LM-MF	(3)	-18.33	0.73	11.00	1.39	6.39	0.99
Tritia obsoleta	LM	(3)	-8.62	0.32	3.88	1.08	9.67	1.56
Geukensia demissa	LM-MF	(3)	-18.99	0.16	10.16	0.10	4.92	0.14
Small macrofauna (500 µm – 2 cm)								
Arachnids and Insects								
Unidentified spiders	HM	(3)	-19.06	0.42	7.56	0.20	4.55	0.12
Trombiculidae mites	HM	(1)*	-17.32		5.39		4.39	
Ephydridae larvae	LM	(2)	-15.23	0.90	3.74	0.42	4.73	0.37
Chrysops carbonarius larvae	LM	(3)	-13.04	1.13	6.19	0.50	4.31	0.45
Ceratopogonidae (*Culicoides*)	LM	(3)	-15.86	0.63	7.95	1.16	4.61	0.06
Chironomidae (*Chironomus*)	LM	(3)	-19.85	0.12	3.73	0.33	4.40	0.02
Crustaceans								
Orchestia sp.	HM	(4)	-18.45	0.17	4.45	0.95	5.74	0.59
Leptochelia rapax (2014)	LM	(2)	-15.17	0.21	2.88	0.53	5.06	0.16
Leptochelia rapax (2013)	LM	(3)	-18.02	0.17	4.48	0.29	4.40	0.17
Porcellio scaber	HM	(1)	-15.88		7.54		5.97	
Worms								
Enchytraeidae	HM	(1)*	-17.57	1.69	5.50	2.99	7.41	2.30
	HM-MM	(1)*	-18.77		3.39		4.48	
Tubificidae (red; 2014)	LM	(1)	-17.03	0.05	7.44	0.25	4.73	0.00
Tubificidae (2013)	LM	(3)	-18.56	0.06	6.71	0.10	4.18	0.13
Turbellarians (unidentified)	LM	(1)	-16.41		6.69		4.11	
	MF	(3)	-13.01	0.06	6.86	0.24	5.35	0.03
Molluscs								
Ecrobia trucata (in shell)	LM	(3)	-11.84	2.30	4.42	0.43	5.59	1.38
Ecrobia truncata (on algae)	LM	(3)*N	-3.92	0.12	4.72	0.20	23.55	0.11
Ecrobia truncata (in shell)	MF	(1)*N	-1.66		4.84		4.39	0.45
Littorina littorea	LM-MF	(3)*N	-2.63	0.61	8.22	1.53	17.20	3.78
Meiofauna (63 – 500 µm)								
Arachnids and Insects								
Euzetidae	HM-MM	(1)*	-22.83		2.94		4.28	
	MM	(1)*	-21.40	2.02	4.00	1.50	4.28	0.10
Arrenuridae	LM	(1)	-19.32		5.66		4.16	
Culicoides larvae	LM	(4)	-16.97	0.75	2.00	0.44	4.20	0.20
	MF	(3)	-19.19	0.56	3.17	0.09	4.62	0.07
Culicoides larvae (on algae)	MF	(1)	-13.22		2.16		3.93	
Crustaceans								
Various ostracods	LM	(2)*	-9.43	1.94	4.38	0.51	11.21	6.58
Harpacticoid copepods	LM	(1)*	-18.46		4.42		4.74	

Taxonomic name (or sample name)	Zone	Replicates	$\delta^{13}C$ (‰)	SD $\delta^{13}C$	$\delta^{15}N$ (‰)	SD $\delta^{15}N$	C:N	SD C:N
Mixed crustaceans (copepods, amphipods)	LM	(1)	-15.84		3.88		4.65	
Other								
Nematodes	MM-LM	(1)*	-22.43		6.70		4.18	
Various meiofauna (ostracods, nematodes, copepods)	LM	(1)*	-16.77		4.33		4.56	
	MF	(2) (*1)	-12.42	0.66	4.48	1.52	4.11	0.89
Foraminifera								
Jadammina macrescens	HM	(2)*	-19.21	2.29	5.13	2.16	4.98	0.21
	HM-MM	(3)*	-19.04	2.43	4.75	1.91	4.85	0.30
Miliammina fusca	HM	(1)*	-20.95		3.06		13.07	
	MM	(2)*	-17.71	0.62	5.45	0.99	6.40	0.60
2014	LM	(3)*	-16.65	0.23	4.65	0.20	5.96	0.13
2013	LM	(3)*	-19.87	0.08	4.96	2.91	3.83	0.05
	MF	(3)*	-19.15	0.42	3.48	7.41	1.37	0.42
Tiphotrocha comprimata	HM	(1)*	-18.12		7.86		4.86	
	MM	(1)*	-15.86		8.86		4.86	
Trochammina inflata	MM	(1)*	-15.73		5.62		4.45	
2014	LM	(1)*	-15.29		5.81		4.53	
2013	LM	(3)*	-18.25	0.72	3.44	0.38	4.23	0.39
Trochammina inflata + *Tiphotrocha comprimata*	HM-MM	(1)*	-22.45		4.71		4.47	
Mixed agglutinated	HM-MM	(1)*	-20.52		2.55		4.10	
	LM-MF	(1)*	-14.30		0.59		4.77	
Elphidium sp. (calcareous)	LM	(1)*N	-5.10		0.36		26.91	
	MF	(3)*N	-5.34	0.15	2.22	0.08	16.87	1.17

Table 4.2. $\delta^{13}C$, $\delta^{15}N$, and C:N ratios for producers and consumers of Windsor marsh. Values reported as mean ± standard deviation (SD). Number of sample replicates given in parentheses. * denotes samples with lower precision (<20 µg N or <100 µg C) for N, C, or both. Habitat: HM = high marsh, MM = middle marsh, LM = low marsh, MF = mudflat. Plant parts: F = flowers, L = leaves, S = stems, R = roots, AG = above ground (leaves + stems). Common names are listed in Appendix C-1, values in Supplement C-4.

Taxonomic name (or sample name)	Zone	Replicates	$\delta^{13}C$ (‰)	SD $\delta^{13}C$	$\delta^{15}N$ (‰)	SD $\delta^{15}N$	C:N	SD C:N
Vascular plants								
Spartina patens (L)	HM	(3)	-14.26	0.23	6.38	0.26	13.77	0.00
(S)	HM	(3)	-13.98	0.20	4.65	1.04	3.48	1.42
Spartina alterniflora (L)	HM	(3)	-13.86	0.03	9.26	0.25	3.85	0.53
(S)	HM	(3)	-13.90	0.08	7.31	0.08	6.66	0.00
(L)	LM	(3)	-13.74	0.06	5.95	0.42	7.16	4.20
(S)	LM	(3)	-13.06	0.06	6.34	0.30	3.67	0.00
(S)	LM	(3)	-13.95	0.03	3.45	0.38	5.54	0.00
Bulk sieved sediments								
45µm-63 µm	HM	(3)	-20.69	0.05	5.31	0.21	9.33	0.05
	LM	(3)	-21.57	0.08	5.39	0.24	8.91	0.13
	MF	(3)	-21.57	0.02	5.69	0.30	9.00	0.06
Macrofauna (>2 cm)								
Arachnids and Insects								
Carabidae Coleoptera	HM	(3)	-17.68	0.02	9.13	0.04	5.55	0.03
Coccinellidae Coleoptera	LM	(3)	-14.38	0.15	10.38	0.30	5.59	0.40
Tabanidae Diptera	HM	(3)	-17.65	0.32	9.08	0.26	5.82	0.40
Crustaceans								
Carcinus maenas	HM	(3)	-12.46	0.06	7.40	0.21	7.62	0.10
	LM	(3)	-15.56	0.02	8.57	0.13	4.23	0.07
Molluscs								
Littorina littorea	LM	(2)*	-10.19	0.54	6.26	0.29	7.08	0.12
Tritia obsoleta	LM	(1)	-10.66		6.73		6.66	
Mya arenaria	MF	(3)	-9.88	1.47	5.23	0.21	7.78	2.06
Annelids								
Hediste diversicolor	MF	(3)	-13.87	0.18	7.93	0.24	3.50	0.14
Small macrofauna (500 µm – 2 cm)								
Arachnids and Insects								
Unidentified spiders	HM-LM	(3)	-15.18	0.22	11.73	0.21	5.44	0.12
	LM	(3)	-15.84	0.23	12.08	0.17	4.21	0.09
Ephydridae	HM-LM	(3)	-19.19	0.02	7.98	0.26	7.02	0.17
Unidentified fly larvae	LM	(1)	-15.13		9.03		4.09	
Histeridae Coleoptera	HM-LM	(3)	-18.02	0.06	4.30	0.10	4.98	0.04
Crustaceans								
Talorchestia sp.	HM	(3)	-13.48	0.11	8.14	0.11	5.35	0.11
Corophium volutator	MF	(3)	-14.82	0.12	5.37	0.18	3.85	0.04
Annelids								

Taxonomic name (or sample name)	Zone	Replicates	$\delta^{13}C$ (‰)	SD $\delta^{13}C$	$\delta^{15}N$ (‰)	SD $\delta^{15}N$	C:N	SD C:N
Tubificidae	LM	(1)	-16.03		9.13		4.38	
Molluscs								
Ecrobia truncata139	LM	(3)	-9.68	0.06	6.71	0.13	6.70	0.34
Meiofauna (63 -500 µm)								
Various meiofauna	LM	(1)*	-13.94		4.88		4.56	
	MF	(1)	-14.07		8.83		4.11	
Foraminifera								
Haplophragmoides manilianensis	LM	(1)*	-16.73		7.39		2.35	
Trochammina inflata	LM	(2) 1*	-14.97	0.36	5.81	0.35	4.89	0.00
Helenina anderseni (Calcareous)	LM	(2)*	-5.99	0.22	6.55	4.09	17.64	4.85
Haynesina orbiculare (Calcareous)	LM-MF	(1)*	-7.17		8.72		13.77	
Mixed foraminifera	All zones	(1)*	-11.33		14.78		5.54	

4.4.1 Overall patterns of $\delta^{13}C$, $\delta^{15}N$ and C:N within and between marsh sites

The $\delta^{13}C$ and $\delta^{15}N$ values for salt marsh taxonomic or functional groups (Fig. 4.2) comprise seven categories: vascular plants, bulk sieved sediments (= Sediment Organic Matter, or SOM; includes both organic and inorganic matter), algae (filamentous algal mats), macrofauna (> 2 cm), small macrofauna (500 µm – 2 cm), meiofauna (63 – 500 µm), and foraminifera.

The source materials (C_3 and C_4 vascular plants, filamentous algae, and sediment) form clusters on a biplot of $\delta^{13}C$ against $\delta^{15}N$, whereas the macrofauna, meiofauna, and foraminifera have more scattered distributions. At Chezzetcook, macrofauna have a higher $\delta^{15}N$ than other consumers, whereas at Windsor, small macrofauna have higher values. Foraminifera and meiofauna values cluster around microalgae and SOM values for both $\delta^{15}N$ and $\delta^{13}C$, but foraminifera have a higher variability in mean values and large standard deviations. The less depleted (ca. -5‰) $\delta^{13}C$ consumer values are from calcareous foraminifera and small gastropods that could not be dissected prior to analysis.

Vascular plants cluster between -25 and -30 ‰ δ^{13} at Chezzetcook and between -12 and -15‰ $\delta^{13}C$ at both marshes (Figs. 4.2 and 4.3); $\delta^{15}N$ values are much more variable (c. -1 – 8 at Chezzetcook, 3 – 9 at Windsor) . Sediments cluster at approximately -20‰ $\delta^{13}C$ in both marshes, with modest variation in $\delta^{15}N$ (4 – 6‰). At Chezzetcook, algae cluster between -13 and -15 ‰ $\delta^{13}C$, with $\delta^{15}N$ between c. 3 and 6‰.

Considering all samples from both marshes, $\delta^{15}N$ has more variability than $\delta^{13}C$. Values of $\delta^{15}N$ averages ±0.45 and 0.40 ‰ whereas $\delta^{13}C$ averages ±0.31 and 0.19 ‰ for Chezzetcook and Windsor, respectively.

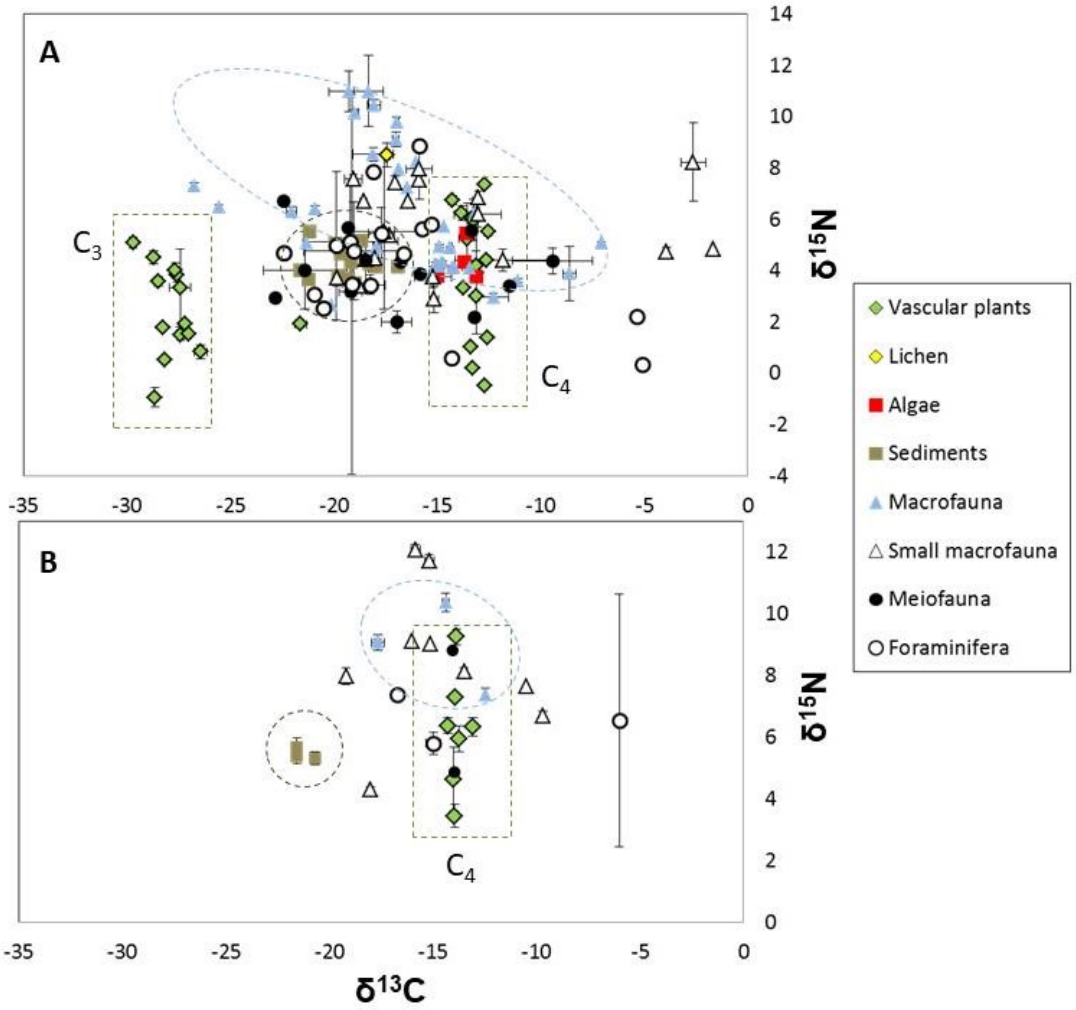

Figure 4.2: Mean $\delta^{13}C$ and $\delta^{15}N$ (‰) biplots of the source material (salt marsh plants, algal mats, and sediment) and consumers (macrofauna, small macrofauna, meiofauna, and foraminifera) from the Chezzetcook salt marsh (A) and the Windsor salt marsh (B). Error bars show standard deviations.

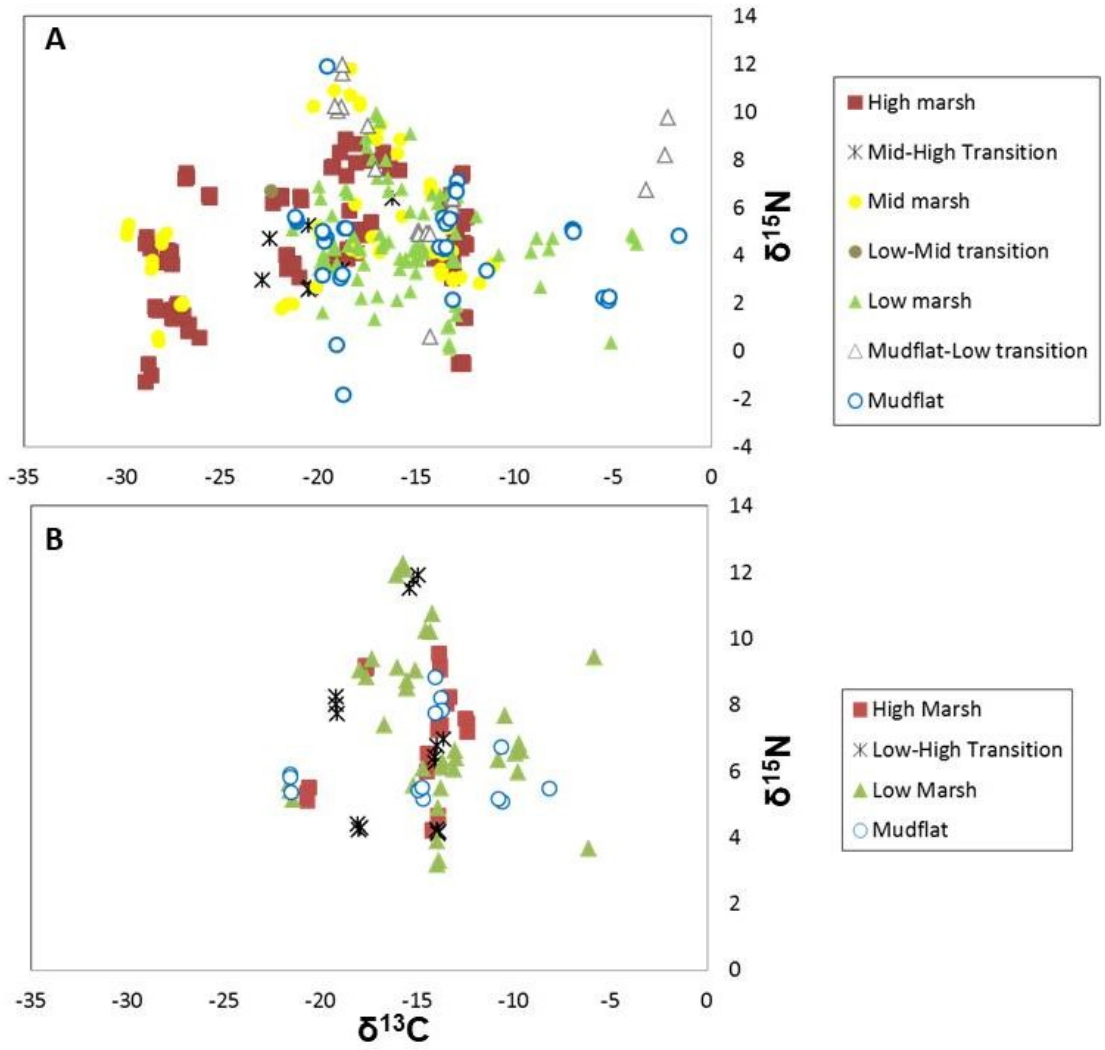

Figure 4.3: $\delta^{13}C$ and $\delta^{15}N$ (‰) biplots of all samples within each salt marsh zone (see index) at Chezzetcook (A, four zones and three transitions) and at Windsor (B, three zones, one transition).

When constituents are considered by zone, no distinct clustering is observed, although Chezzetcook high and mid marsh zones are more depleted in $\delta^{13}C$ than low marsh and some mudflat and mudflat-low marsh transition zones (Fig. 4.3). There is a notable difference in the $\delta^{13}C$ spread between the two marshes, while $\delta^{15}N$ values appear equally scattered for each zone in both marshes.

Examination of the spread of data using Euclidean distance matrices, nMDS plots and ANOSIM (Fig. 4.4) shows similar patterns to the raw data (Fig. 4.3). Chezzetcook

shows a greater horizontal and vertical extent on the plots than Windsor where values cluster in the upper left (Figure 4.4A). High and middle marsh zones tend to be separated from lower zones in Chezzetcook (4.4E), but no major patterns are seen in Windsor (4.4F). In both marshes, plants, sediments and gastropods form clusters (Fig. 4.4C, D). Results from ANOSIM show no statistical difference between Windsor and Chezzetcook overall ($R = 0.048$, $p = 0.149$; Appendix C-2), but marsh zones are a significant variable ($R = 0.091$, $p = 0.005$; Appendix C-2), with the high and mid marsh zones being distinct from the low marsh and mudflat. Taxonomic groups are also a significant variable ($R = 0.096$, $p = 0.001$; Appendix C-2), and plants and sediment account for much of the significant pairwise comparisons. Considering the marshes separately, these patterns emerge strongly for Chezzetcook (Fig. 4.4E), but Windsor zones to do not show significant variability across the marsh zones (Fig. 4.4F; $R = 0.014$, $p = 0.389$; Appendix C-2).

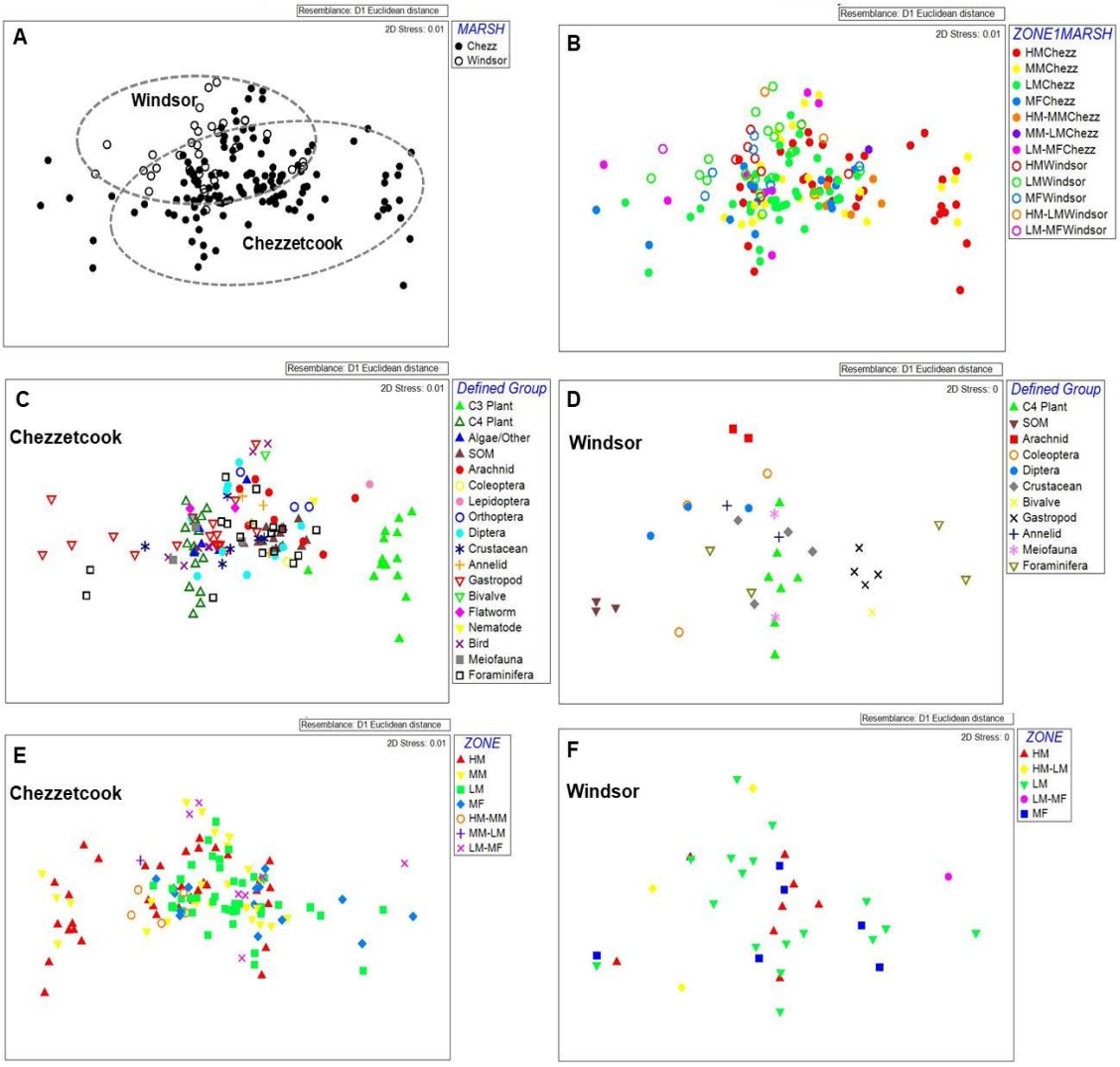

Figure 4.4. Non-metric MDS plots of Euclidean distances of $\delta^{13}C$ and $\delta^{15}N$ values of each sample from Chezzetcook and Windsor. (A) All samples from Chezzetcook and Windsor. (B) Samples from Chezzetcook and Windsor separated by salt marsh zones. Samples from Chezzetcook (C) and Windsor (D) by major taxonomic groups. Samples from Chezzetcook I and Windsor (F) by salt marsh zones.

Based on the coefficient of variation (CV), Chezzetcook shows more isotopic variability than Windsor ($\delta^{13}C$ = -0.02 vs -0.01, $\delta^{15}N$ = 0.08 vs 0.05). The C:N ratio shows high variability for both marshes (CV = 0.19). Comparing zones between the two marshes, CV for $\delta^{13}C$ shows no statistical difference ($p = 0.24$; Appendix C-4, Supplement C-7) but $\delta^{15}N$ is slightly more variable across zones at Chezzetcook (CV = 0.08) than at Windsor (CV = 0.04; $p = 0.07$). Comparing taxonomic groups, the two

marshes are not distinct in $\delta^{13}C$, $\delta^{15}N$, or C:N ($p = 0.42$, 0.87 and 0.75, respectively; Appendix C-4, Supplement C-7).

Figure 4.5 plots isotopic values of taxonomic groups by zone. Overall, there is a slight shift from more depleted $\delta^{13}C$ in the high marsh to less depletion in the low marsh. No major trends are visible in $\delta^{15}N$, although Windsor shows higher $\delta^{15}N$ values. Most taxonomic groups show higher variability in $\delta^{15}N$ than $\delta^{13}C$.

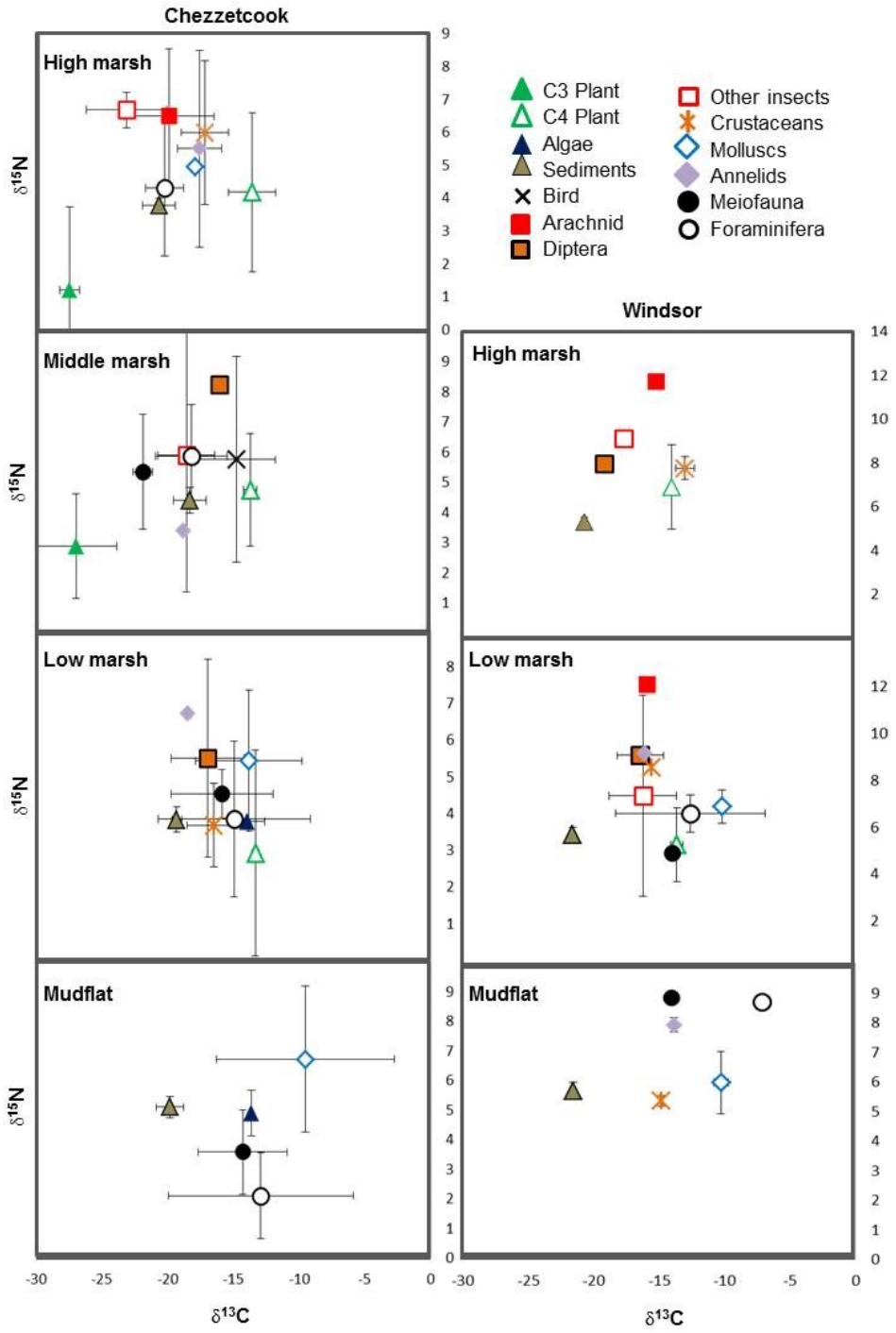

Figure 4.5. Chezzetcook and Windsor salt marsh biplots of mean ±SD $\delta^{13}C$ and $\delta^{15}N$ values (in ‰) of source materials (plants, algae (algal mats), and sediment) and consumers (various macrofauna and small macrofauna, meiofauna, and foraminifera) from the mudflat, low marsh, middle marsh and high marsh zones. Note that $\delta^{15}N$ axes scales differ in some panels.

4.4.2 Isotopic composition of sources

Comparing averages of source samples, Chezzetcook $\delta^{13}C$ values are significantly different across zones ($p = <0.001$); with high marsh (HM) -20.3, middle marsh (MM) -18.8, low marsh (LM) -15.4, mudflat (MF) -13.9‰ (Appendix C-3, Supplement C-6), with the greatest depletion in the high marsh. Neither $\delta^{15}N$ nor C:N are significantly different across zones, although $\delta^{15}N$ is slightly higher in the mudflat at 5.1‰. Windsor zones show no significant differences for $\delta^{13}C$, $\delta^{15}N$ or C:N. The $\delta^{13}C$ and $\delta^{15}N$ values differ significantly between the marshes. Mean $\delta^{13}C$ is -14.3‰ for Windsor and -17.4‰ for Chezzetcook ($p = 0.001$), and mean $\delta^{15}N$ is 7.5‰ for Windsor and 4.7‰ for Chezzetcook ($p <0.0001$). The C:N values are not significantly different, but the mean is higher at Chezzetcook (10.6) than at Windsor (8.2).

Plants and microalgae show no large differences from the high marsh through the mudflat (Fig. 4.6), other than the well-known $\delta^{13}C$ distinctions between plants with a C_3 pathway (more depleted) and a C_4 pathway (less depleted). At Chezzetcook, algae show a significant zonal difference only in $\delta^{15}N$ ($p = 0.002$; MF 4.9, LM 3.8‰; Appendix C-3, Supplement C-6). Plants in the high and middle marsh are significantly more depleted in $\delta^{13}C$ than in the low marsh ($p = 0.008$, HM -19.5, MM -21, LM -13.4‰), but show no significant zonal differences for $\delta^{15}N$ or C:N, despite the visual trend of high C:N in high marsh. At Windsor, plants in the high marsh are slightly more depleted in $\delta^{13}C$ than in the low marsh ($p = 0.047$, HM -14, LM -13.7‰), but show no significant zonal differences for $\delta^{15}N$ or C:N, although the high marsh shows higher $\delta^{15}N$ (6.3‰) than the low marsh (5.4‰). Comparing plants between the two marshes, all three isotopic parameters differ. For $\delta^{13}C$, the mean values differ (Chezzetcook -19.1, Windsor -13.9‰) but not

significantly (p =0.8) due to high standard deviations of the means. For $\delta^{15}N$, values are significantly higher at Windsor (5.9‰) than at Chezzetcook (3.2‰, p <0.001). For C:N, values are significantly higher at Chezzetcook (24.1) than at Windsor (16, p=0.003), linked to higher nitrogen at Windsor.

Sediment organic matter shows more similarity from high marsh to mudflat than plants, although C:N for SOM is higher in the high marsh (Figure 4.6). At Chezzetcook, all parameters show some significant zonal differences. For $\delta^{13}C$ between zones (p = 0.017), the high marsh is more depleted (-20.7‰) than other zones. For $\delta^{15}N$ between zones (p <0.001), the mudflat (5.1‰) has higher values than the high marsh (3.8‰). For C:N, the most significant difference is between the high and middle marsh (p < 0.001, HM 13.9, MM 9, LM 7.9, MF 7.1; Appendix C-3, Supplement C-6). At Windsor, no parameters show significant zonal differences, though C:N is slightly higher in the high marsh than the mudflat (p = 0.051; HM 9.3, LM 8.9, MF 9.0; Appendix C-3, Supplement C-6). Comparing sediment values between the two marshes, the isotopic parameters shows significant differences. For $\delta^{13}C$, Windsor (-21.2‰) is more depleted than Chezzetcook (-19.5‰; p =0.0001). For $\delta^{15}N$, Windsor (5.5‰) is higher than Chezzetcook (4.4‰; p=0.000). For C:N, values show no significant difference (p=0.08, both 9.1).

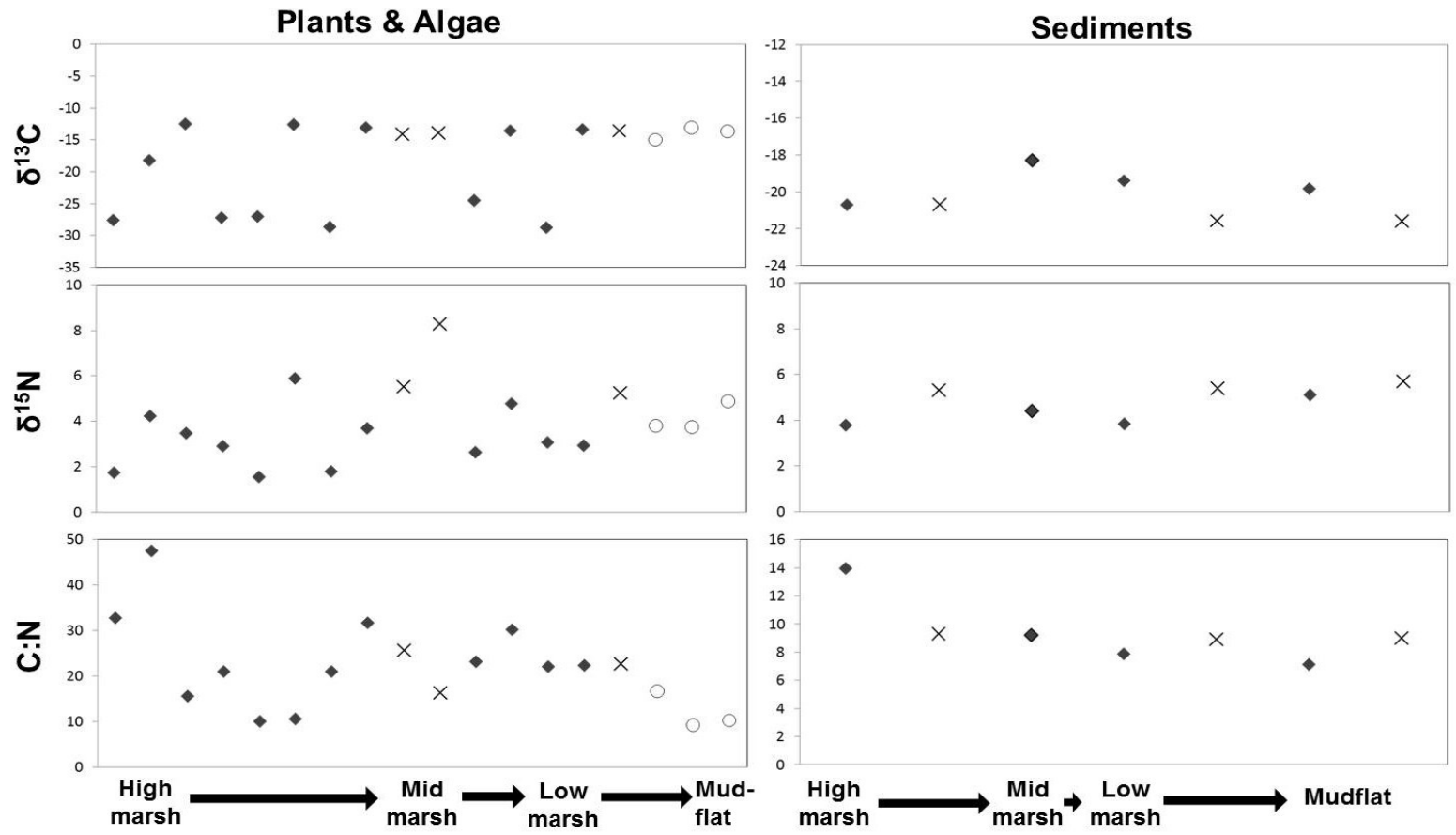

Figure 4.6. $\delta^{13}C$ and $\delta^{15}N$ values (expressed as ‰) and C:N ratio of flowering plants and sediments (SOM) from Chezzetcook (**black diamonds**) and Windsor (**X's**) salt marshes, in order of high marsh through the mudflat. **Open circles** are algae samples from Chezzetcook. Data points represent the sample means from Tables 4.1 and 4.2. Note that Y axes for $\delta^{13}C$, $\delta^{15}N$ and C: N between plants and sediments are not necessarily the same scale.

4.4.3 Isotopic composition of consumers

Consumers show enriched $\delta^{13}C$ in the lower marsh zones (Figure 4.7). The $\delta^{15}N$ values and C:N ratios are relatively consistent for small macrofauna and meiofauna from the high marsh to the low marsh. Foraminifera show the biggest spread of values.

Considering all data for consumers by marsh and zone, Chezzetcook zones show a significant difference for $\delta^{13}C$ ($p < 0.001$; Appendix C-3, Supplement C-6), with more depletion in the high marsh than in lower zones (HM -20.2, MM -17.1, LM -15, MF -13.1‰). Neither $\delta^{15}N$ nor C:N show significant zonal differences, but $\delta^{15}N$ is slightly higher in the mudflat (7.1‰) than in the upper zones. At Windsor, there is a similar significant zonal difference for $\delta^{13}C$ ($p = 0.01$), with more depletion in the high marsh than in lower zones (HM -15.7, LM -14.3, MF -12‰). Neither $\delta^{15}N$ nor C:N show significant zonal differences. Comparing all consumers between the two marshes, $\delta^{13}C$ is more depleted at Chezzetcook (-16.3) than at Windsor (-13.6‰, $p = 0.001$), $\delta^{15}N$ is higher at Windsor (8.1) than at Chezzetcook (5.3‰, $p < 0.0001$), and C:N shows no significant difference (Appendix C-3, Supplement C-6).

At Chezzetcook, macrofauna show significantly more $\delta^{13}C$ depletion in the high marsh than in lower zones (HM -21.4‰ to MF -14.5‰, $p < 0.001$; Appendix C-3, Supplement C-6). Neither $\delta^{15}N$ nor C:N show significant zonal differences. At Windsor, macrofauna also show significantly more $\delta^{13}C$ depletion in the high marsh than in lower zones (HM -15.7‰ to MF -11.7‰, $p = 0.031$), and $\delta^{15}N$ is more depleted in the mudflat than the high marsh (HM 8.2‰, MF 6.6‰, $p = 0.015$). Overall, macrofauna are significantly more depleted in $\delta^{13}C$ at Chezzetcook (-16.6‰) than at Windsor (-4.3‰, $p = 0.007$), and are also more depleted in $\delta^{15}N$ at Chezzetcook (6.4‰) than at Windsor

(8.0‰, p =0.001). The C:N ratios are significantly higher at Windsor (5.9) than at Chezzetcook (5.0, p = 0.00).

At Chezzetcook, small macrofauna show significantly less $\delta^{13}C$ depletion towards the mudflat (p = 0.001, HM -18.1, MM -18.8, LM -13.7, MF -8.2‰). The $\delta^{15}N$ values show some zonal differences that are not statistically significant (HM 5.9, MM 3.9, LM 5.6, MF 7.2‰, p =0.071). The C:N ratios show significant zonal differences (p = 0.044, with MF significantly higher at 12.1 compared with HM 5.4, MM 4.5, and LM 7.6). At Windsor, the only statistically significant parameter across zones is C:N (p = 0.023, MF 3.85 compared with 5.2 for LM and HM; Appendix C-2, Supplement C-6).

Because of the few meiofauna samples at Windsor, all the small macrofauna and meiofauna were combined to allow statistical comparison between the two marshes. Only $\delta^{15}N$ differs significantly (Windsor 8.0, Chezzetcook 5.1‰; p = 0.00). Chezzetcook $\delta^{13}C$ (-15.2) is slightly but not significantly more depleted than Windsor (-14.7‰, p = 0.09; Appendix C-3, Supplement C-6). At Chezzetcook, meiofauna values show no statistically significant zonal differences, although $\delta^{13}C$ is more depleted in the high marsh (-21.4‰) than in the low marsh (-16.3‰) and mudflat (-15.9‰). Meiofauna $\delta^{15}N$ values range from 3.4‰ in the mudflat to 4.0‰ in high and middle marsh.

Foraminifera have mean isotopic values with large standard deviations, so the Kruskal-Wallis and Mann-Whitney tests have a high probability of incorrect p-values. At Chezzetcook, $\delta^{13}C$ is more depleted (-19.1‰) in the high marsh than in the mid marsh (-18.6‰), low marsh (-16.8‰), and mudflat (-12.5‰). The $\delta^{15}N$ values decrease from high marsh (5.7‰) to mudflat (2.5‰), and C:N is higher in the mudflat (8.5) than the rest of the marsh. There were not enough samples in each zone at Windsor to compare zones.

Comparison of foraminifera between the marshes shows that both $\delta^{13}C$ and $\delta^{15}N$ are significantly more depleted at Chezzetcook than at Windsor ($\delta^{13}C$ -16.7‰ and -11.0‰, $p = 0.008$; $\delta^{15}N$ 4.3‰ and 7.9‰, $p = 0.013$; Appendix C-3, Supplement C-6). The C:N ratios are not significantly different ($p = 0.164$), but Chezzetcook (9.5) has lower values than Windsor (6.6).

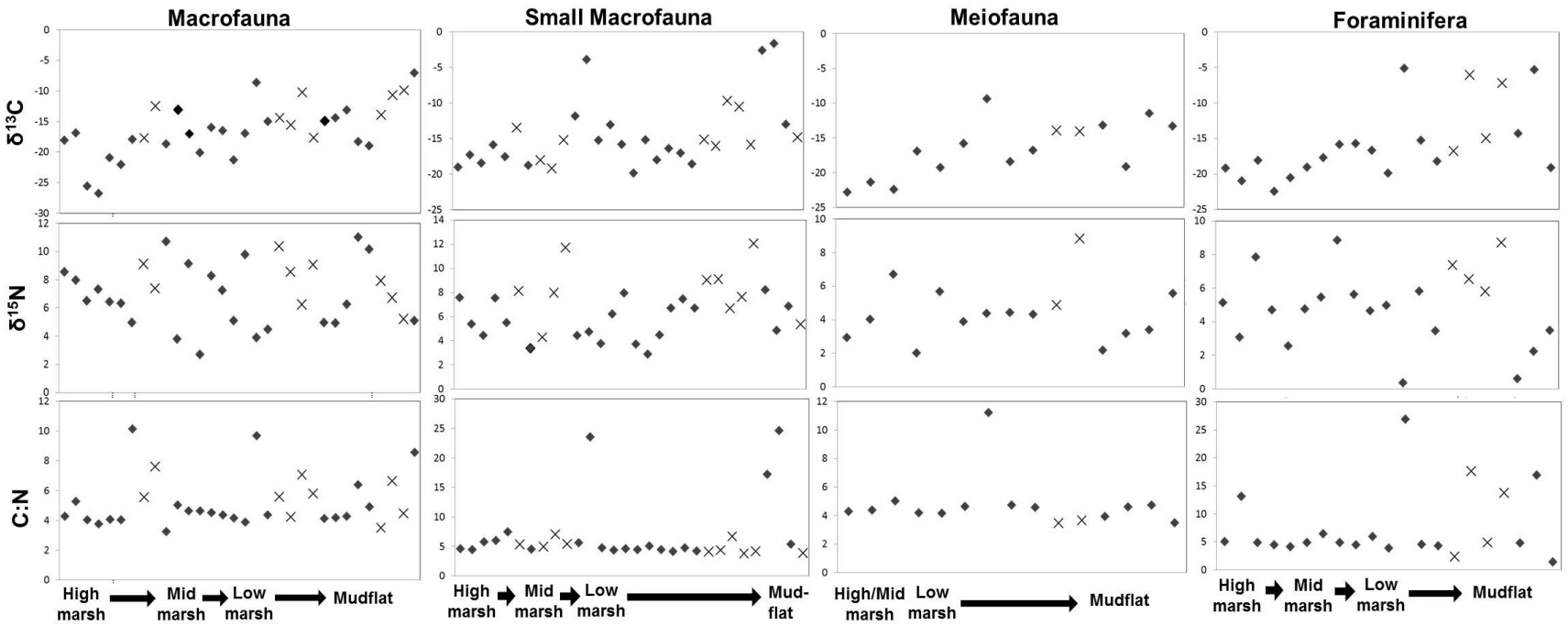

Figure 4.7. $\delta^{13}C$ and $\delta^{15}N$ (expressed as ‰) and C: N ratio of consumers Chezzetcook (**black diamonds**) and Windsor (**X's**) salt marshes, in order of high marsh through the mudflat. Data points represent the sample means from Tables 4.1 and 4.2. Note that Y axes for each of $\delta^{13}C$, $\delta^{15}N$ and C: N between consumers are not always the same scale.

4.4.4 Trophic positions of consumers

To determine the trophic positions of consumers, the approach of Anderson and Cabana (2007) and Kristensen et al. (2016) was followed in choosing primary baseline consumers that are most common throughout each marsh. The biting midge larva, *Culicoides* sp., which often feeds on microalgae, was selected for Chezzetcook. The abundant amphipod, *Corophium volutator,* a sediment scraper and suspension feeder of diatoms and detritus, was selected for Windsor. Following Kristensen et al. (2016), the mean of all $\delta^{15}N$ values was used as a baseline correction (*Culicoides* = 2.46, *Corophium* = 5.36), allowing calculation of the trophic positions of Chezzetcook and Windsor consumers (Tables 4.3 and 4.4; Supplements C-5, C-8), assuming a trophic level of 1 for the source materials.

At Chezzetcook (Table 4.3), the highest calculated trophic position in the mudflat is occupied by flatworms (3.29), in the mudflat-low marsh by the rough periwinkle (*Littorina saxatilis*; 4.51), in the low marsh by shore flies (4.16), in the middle marsh by birds (using feathers as proxies; 4.5) and a grasshopper (3.96), and in the high marsh by spiders (*Grammonata trivitata*; 3.79). Foraminifera mostly occupy low trophic levels but have higher values in the middle marsh (3.88). Meiofauna also occupy a variety of trophic positions. Overall, trophic positions show a general decrease from the high marsh through the mudflat (HM 3.13, MM 2.82, LM 2.71, MF 2.8; Figure 4.8A) but do not differ significantly ($p = 0.07$; Appendix C-5; Supplement C-8). Major groups of consumers (macrofauna, small macrofauna, meiofauna and foraminifera) show no significant differences from each other (Figure 4.8B), though foraminifera have the largest variability.

At Windsor (Table 4.4), the attribution of highest trophic position is to foraminifera (4.77) is likely due to the small sample size giving low precision. Other than this outlier, carabid beetles (3.11) and spiders (3.87) occupy the highest trophic positions in the high marsh, spiders in the low marsh (3.98), and mixed meiofauna (3.02) and the ragworm *Hediste diversicolor* (2.75) in the mudflat. The lowest trophic positions are occupied by hister beetles in the high marsh (1.69), foraminifera (2.13) and meiofauna (1.86) in the low marsh, and soft-shelled clams (*Mya arenaria*; 1.96) in the mudflat. As at Chezzetcook, the trophic positions of foraminifera and meiofauna vary by zone, and the mean trophic positions tend to decrease from the high marsh (2.81) through the mudflat (2.52), although the differences are not significant ($p = 0.642$, Figure 4.8C). None of the consumer groups show significant differences between each other, though arachnids have higher trophic positions (Figure 4.8D; Appendix C-5, Supplement C-8).

Between the marshes, overall mean trophic levels show no significant differences (Chezzetcook= 2.84, Windsor =2.80, $p =0.814$; Appendix C-5, Supplement C-8), nor between the same zones of each marsh. Trophic positions for consumer groups show no significant differences between the two marshes.

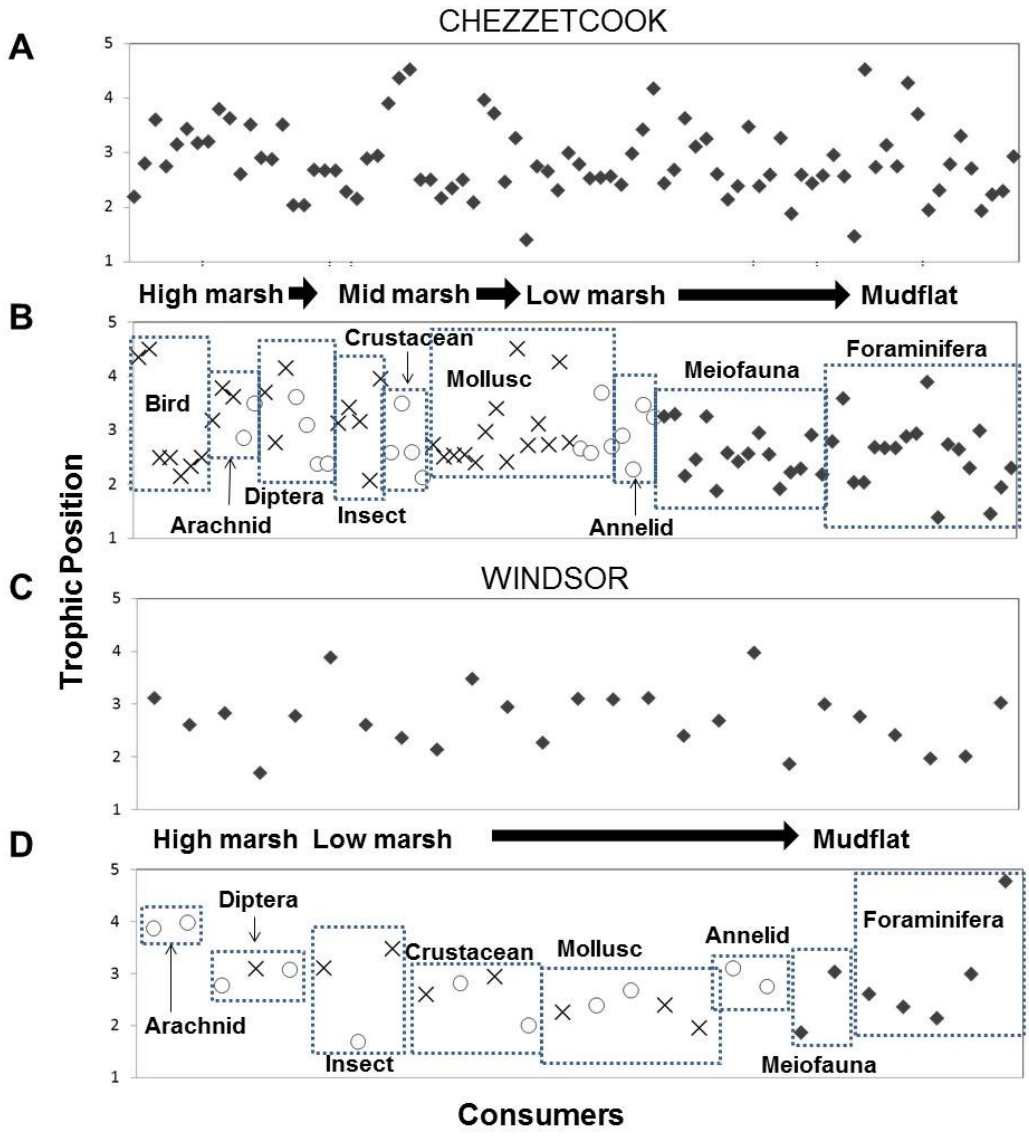

Figure 4.8. Calculated trophic positions of consumers in Chezzetcook (A, B) and Windsor (C, D) salt marshes. A and C: Trophic positions of all consumers ordered by zone, from high marsh through to the mudflat. B and D: Trophic positions of all consumers ordered by major taxonomic/functional groups and not organized by zone (**X** = macrofauna, **O** = small macrofauna, **diamonds** = meiofauna and foraminifera).

Table 4.3: Calculated trophic positions of consumers from the Chezzetcook marsh, ordered from highest to lowest trophic position value in each zone. Baseline $\delta^{15}N$ for biting midge larvae = 2.46.

Zone	Consumer	Corrected $\delta^{15}N$ (‰)	Trophic Position
High marsh	Spider (*Grammonata trivitata*)	6.07	3.79
	Spider (*Pardosa littoralis*)	5.51	3.62
	Foraminifera (*Tiphotrocha comprimata*)	5.40	3.59
	Various small spiders	5.10	3.50
	Isopod (*Porcellio scaber*)	5.08	3.49
	Moth (*Doryodes grandipennis*)	4.85	3.43
	Spider (*Araneus diadematus*?)	4.04	3.19
	Small grasshopper (*Dichromorpha viridis*?)	3.96	3.16
	Large grasshopper (*Paroxya*?)	3.86	3.14
	Oligochaetes (Enchytraeidae)	3.04	2.90
	Red Mites (Trombiculidae)	2.93	2.86
	Foraminifera (*Jadammina macrescens*)	2.67	2.79
	Coffee bean snail (*Melampus bidentatus*)	2.49	2.73
	Amphipods (*Orchestia* sp.)	1.99	2.59
	Foraminifera (*Miliammina fusca*)	0.60	2.18
High-Mid	Foraminifera (*J. macrescens*)	2.29	2.67
	Foraminifera (*T. comprimata* + *Trochammina inflata*)	2.25	2.66
	Oligochaetes (Enchytraeidae)	0.93	2.27
	Soil mites (Euzetidae)	0.48	2.14
	Foraminifera mixed	0.09	2.03
Mid marsh	Bird Feather B	8.52	4.50
	Bird Feather A	7.99	4.35
	Grasshopper (*Chorthippus* sp.?)	6.66	3.96
	Foraminifera (*T. comprimata*)	6.40	3.88
	Large fly larvae	5.80	3.71
	Foraminifera (*T.inflata*)	3.16	2.93
	Foraminifera (*M. fusca*)	2.99	2.88
	Bird Faeces B	1.68	2.49
	Bird Faeces A	1.67	2.49
	Bird Faeces E	1.67	2.49
	Soil mites (Euzetidae)	1.54	2.45
	Bird Faeces D	1.14	2.34
	Bird Faeces C	0.49	2.15
	Water beetle (Hydrophilidae)	0.23	2.07
Mid-Low	Nematodes	4.24	3.25
Low marsh	Shore fly adults (Ephydridae)	7.33	4.16
	Biting midges (*Culicoides*)	5.49	3.62
	Red oligochaete (Tubificidae) 2014	4.98	3.46
	Sacoglossan sea slug (*Alderia modesta*?)	4.77	3.40
	Oligochaetes (Tubificidae) 2013	4.25	3.25
	Flatworms (Turbellaria) 2014	4.23	3.24
	Deerfly larvae (Chrysops carbonarius)	3.73	3.10
	Foraminifera (*T.inflata*) 2014	3.35	2.99
	Common periwinkle (*Littorina littorea* E)	3.28	2.97
	Unknown water mites	3.20	2.94
	Large fly larvae 2013	2.63	2.77
	Foraminifera (*M. fusca*) 2013	2.50	2.74

	Salt marsh snail (*Ecrobia truncata*)	2.26	2.66
	Foraminifera (*M. fusca*) 2014	2.19	2.64
	Amphipod (*Leptochelia rapax*) 2013	2.02	2.59
	Copepods (Harpacticoid)	1.96	2.58
	Salt marsh snail (*Ecrobia truncata*)	1.96	2.58
	Ostracods	1.92	2.56
	Various meiofauna	1.87	2.55
	Common periwinkle (*Littorina littorea* C)	1.86	2.55
	Common periwinkle (*Littorina littorea* B)	1.81	2.53
	Common periwinkle (*Littorina littorea* A)	1.73	2.51
	Crustaceans (copepods, amphipods)	1.42	2.42
	Mudsnail (*Tritia obseleta)*	1.42	2.42
	Common periwinkle (*Littorina littorea* D)	1.36	2.40
	Shore fly larvae (Ephydridae)	1.28	2.38
	Non-biting midge (*Chironomus*)	1.27	2.37
	Foraminifera (*T. inflata*) 2013	0.98	2.29
	Amphipod (*Leptochelia rapax*) 2014	0.42	2.12
	Biting midge (*Culicoides)* larvae	-0.46	1.86
	Foraminifera (*Elphidium* sp.)	-2.10	1.38
Low-Mudflat	Rough periwinkle (*Littorina saxatilis*)	8.54	4.51
	Ribbed mussel (*Geukensia demissa*)	7.70	4.26
	Common periwinkle (*Littorina littorea*) in shell	5.76	3.69
	Common periwinkle (*Littorina littorea*) 2013	3.80	3.12
	Common periwinkle (*Littorina littorea*) 2014	2.50	2.74
	Common periwinkle (*Littorina littorea*) (large)	2.45	2.72
	Foraminifera mixed	-1.87	1.45
Mudflat	Flatworms (Turbellaria) 2013	4.40	3.29
	Mixed meiofauna 2013	3.09	2.91
	Common periwinkle (*Littorina littorea*)	2.62	2.77
	Salt marsh snail (*Ecrobia truncata*)	2.38	2.70
	Foraminifera (*M. fusca*)	1.02	2.30
	Mixed meiofauna 2013	0.94	2.28
	Biting midge (*Culicoides)* larvae 2013	0.71	2.21
	Foraminifera (*Elphidium* sp.) 2014	-0.24	1.93
	Biting midge (*Culicoides)* larvae (on algae)	-0.30	1.91

Table 4.4: Trophic positions of consumers from the Windsor marsh, ordered from highest to lowest trophic position value in each zone. Baseline $\delta^{15}N$ for *Corophium* amphipod = 5.36.

Zone	Consumer	Corrected $\delta^{15}N$ (‰)	Trophic Position
ALL	Mixed foraminifera	9.42	4.77
High	Beetle (Carabidae)	3.77	3.11
	Amphipod (*Talorchestia* sp.)	2.78	2.82
	Green crab (*Carcinus maenas*)	2.04	2.60
High-Low	Small spiders	6.37	3.87
	Shore fly (Ephydridae)	2.62	2.77
	Beetle (Histeridae)	-1.06	1.69
Low marsh	Small spiders	6.72	3.98
	Beetle (Coccinellidae)	5.02	3.48
	Oligochaetes	3.77	3.11
	Fly (Tabanidae)	3.72	3.09
	Fly larvae (unknown)	3.67	3.08
	Green crab (*Carcinus maenas*)	3.21	2.94
	Salt marsh snail (*Ecrobia truncata*)	2.29	2.67
	Foraminifera (*Haplophragmoides manilianensis*)	2.03	2.60
	Salt marsh snail (*Ecrobia truncata*)	1.35	2.40
	Foraminifera (*Helenina anderseni*)	1.19	2.35
	Common periwinkle (*Littorina littorea*)	0.90	2.27
	Foraminifera (*Trochammina inflata*)	0.45	2.13
	Mixed meiofauna	-0.48	1.86
L-MF	Foraminifera (*Haynesina orbiculare*)	3.36	2.99
Mudflat	Mixed meiofauna	3.47	3.02
	Ragworm (*Hediste diversicolor*)	2.57	2.75
	Mudsnail (*Tritia obseleta*)	1.37	2.40
	Amphipod (*Corophium volutator*)	0.01	2.00
	Soft-shelled clam (*Mya arenaria*)	-0.13	1.96

4.4.5 Salient features of the results.

1) At Chezzetcook, there is a clear clustering of $\delta^{13}C$ between vascular plants with C_3 (ca. -28‰) and C_4 (ca. -13‰) photosynthetic pathways, but at both marshes, the $\delta^{15}N$ plant values are variable (Figures 4.5 – 4.6).

2) Sediment organic matter, with $\delta^{13}C$ (average of -20‰) and $\delta^{15}N$ signatures (average of -5‰), has narrow ranges regardless of zone or marsh (Figures 4.5 – 4.6).

3) Consumer mean $\delta^{15}N$ values are variable, with meiofauna and foraminifera having the highest variability. There are no significant differences between marshes, though $\delta^{15}N$ values tend to be higher at Windsor and $\delta^{13}C$ signatures more depleted at Chezzetcook (Figures 4.5 and 4.7).

4) The coefficient of variation (CV) indicates more variability at Chezzetcook than at Windsor, overall and by marsh zones. However, among the major taxonomic groups (plants, sediments, macrofauna, small macrofauna, meiofauna, foraminifera), there are no significant differences in variability between the two marshes.

5) The marsh zones show many significant differences in isotope signatures. The Euclidean matrices show fewer differences and patterns than the raw data, but various salt marsh zones and taxonomic groups show clusters, especially for Chezzetcook (Figure 4.4).

6) At both marshes and in individual zones, higher trophic positions are occupied by predatory insects and spiders, whereas lower trophic positions are occupied by foraminifera and meiofauna, though with highly variable trophic positions (Tables 4.3 – 4.4 and Figure 4.8).

4.5 Discussion

4.5.1 Comparison of Chezzetcook and Windsor marshes

Source isotopic signatures and C:N content

Overall, the marsh sources show two clusters of $\delta^{13}C$ for vascular plants but variable $\delta^{15}N$ values (Figure 4.2). The pronounced differences between Windsor and Chezzetcook plant $\delta^{13}C$ are due primarily to the presence of two isotopic groups at Chezzetcook at -25 to -30‰ and -10 to -15‰ (Table 4.1). These groups correspond to plants with C_3 or CAM and C_4 photosynthetic pathways and are consistent with reported mean $\delta^{13}C$ values of ~-28‰ and ~-13‰, respectively (Peterson and Fry, 1987; Cloern et al., 2002). Chezzetcook mudflat microalgae are relatively enriched in $\delta^{13}C$, with an average value of -13.6‰, close to C_4 plants. Similar microalgal values were reported for an estuarine mudflat in Brazil (Claudino et al., 2013) and other salt marshes (Currin et al., 1995), although algal sources have a much wider $\delta^{13}C$ range from -5 to -20‰ (Wozniak et al., 2006).

At Chezzetcook, three of nine vascular plants have the C_4 photosynthetic pathway (Table 4.2), including the grasses *Spartina alterniflora* and *patens* and *Distichlis.* The C_3 taxa, including *Solidago*, *Juncus* and *Limonium*, tend to be confined to the middle and high marsh zones, as reported by Chmura and Aharon (1995) for various marshes in the United States, but the succulent *Salicornia* (C_3 photosynthesis) can colonise open low marsh mudflats. At Windsor, all $\delta^{13}C$ plant values reflect the dominance throughout of the C_4 grasses but $\delta^{15}N$ does not distinguish taxa. The mean $\delta^{15}N$ of vascular plant taxa differ widely, ranging from -1 to 8‰ at Chezzetcook and 3 to 9‰ at Windsor (Tables 4.1 and 4.2) as observed elsewhere (Kwak and Zedler, 1997).

Plant $\delta^{15}N$ can be used to determine the source of nitrogen (Peterson and Fry, 1987). Atmospheric N_2 has a $\delta^{15}N$ value of 0‰, and plants that fix and use atmospheric N_2 include legumes with N-fixing bacteria and values of ~-2 to 2‰. Other plants have nitrogen values that reflect more varied soil values (Peterson and Fry, 1987), and sea

water has high and variable $\delta^{15}N$. The wide $\delta^{15}N$ range for vascular plants from both Nova Scotian marshes suggests a primarily soil- and seawater-based rather than an atmospheric N_2 source. Variability in $\delta^{15}N$ also reflects the part of the plant being sampled, as roots and stems have much lower $\delta^{15}N$ than leaves and flowers of the same plant (we included samples of most plant parts; see Table 4.1 – 4.2). Currin et al. (1995) and Cloern et al. (2002) also reported higher $\delta^{15}N$ for *Spartina* litter and standing dead plant than for living parts, and sediment organic matter in the two marshes may reflect this additional source of variation. Blue-green algae are also N_2 fixers with a wide range of $\delta^{15}N$ values, but most reports are closer to zero because of fractionation during ammonium uptake or use of depleted dissolved inorganic N (Currin et al., 1995, and references therein). Additionally, higher $\delta^{15}N$ values at Windsor may also be indicative of sewage and agricultural runoff, as there is a nearby storm culvert at the area of the tidal channel sampled.

At Chezzetcook, plant diversity (9 species) and isotopic range is higher than what we sampled at Windsor (2 species), and taxa are segregated according to marsh zone as defined by inundation duration and salinity (cf. Chmura and Aharon, 1995). These differences in species composition and distribution are probably due to the difference in NS marsh ages, as also determined by Redfield (1972) for New England marshes. Zonal differentiation in the young Windsor marsh is at an early stage, whereas the Chezzetcook marsh has been well-established for millennia. Elsewhere in the Bay of Fundy, mature marshes have 3–4 zones and high plant species diversity (Bowron et al., 2009).

Sediment organic matter has a narrow range of values, with $\delta^{13}C$ (ca. -20‰) and $\delta^{15}N$ (ca. -5‰), regardless of zone or marsh. The significant isotopic differences between

the marshes (Tables 4.1 and 4.2) reflect the site-specific sediment composition. Both marshes have highly organic sediments, but locally low OM concentrations (0.7 – 2.4 organic carbon %) are present in the Bay of Fundy marshes (MacKinnon and Walker, 1979) whereas peats at Chezzetcook have average OM concentrations of 44% in the vegetated zones above the mudflats (Chague-Goff et al., 2001). In general, organic matter content (in sediment) increases with marsh age (Howe and Simenstad, 2015a; Chen et al., 2016).

Mudflats in the Minas Basin adjoining the Windsor marsh have % organic content of 0.8 – 2.3 % dry weight (Amos et al., 1988). Though a smaller sample size, sediments from the Windsor high marsh have a $\delta^{13}C$ value of ~-20‰, whereas the low marsh and mudflat values are slightly more depleted at ~-21‰ (Table 4.2). This trend is opposite to that in the mature Great Marshes of Barnstable, Massachusetts where $\delta^{13}C$ values decrease at higher elevation due to the relative increase in C_3 plants that also grow in supratidal settings (Middelburg et al., 1997). Similarly, the mature Chezzetcook marsh has more depleted high marsh sediment values (~-21‰) (Figure 4.6).

The high overall mean C:N values of the Chezzetcook high marsh (~ 14) in comparison to Windsor (<10) also may reflect maturity, although the difference is not significant. Sediment C:N (mostly <10; Tables 4.1 and 4.2; Figure 4.6) is lower than C:N for above-ground vegetation (>20), and sediment C:N decreases from the high marsh (>10) to the mudflat (<10). Such patterns are typical of marsh SOM (Lamb et al., 2006). In the high marsh, large changes of sediment C:N can occur, from values of ~ 50 in the vegetation to 14-18 in the sediments (Lamb et al., 2006).

For both Nova Scotian marshes, sediment $\delta^{13}C$ is intermediate between the values of C_3 and C_4 plants, as noted elsewhere (Ember et al., 1987), and is also slightly more depleted than algal values (Tables 4.1 and 4.2; Figure 4.6). Thus, SOM values may represent a triad of potential sources (microalgae, C_3 and C_4 plants), regardless of marsh zone or location relative to tidal channels (Chen et al., 2016). In San Francisco Bay, isotopic variation within each plant group was large enough to mask any major patterns of sediment organic matter, due to differences in living and dead plant biomass, interannual variability, differences between species, and microhabitats (Cloern et al., 2002). Additionally, decomposing plant matter in *Spartina* marshes has a fractionation of ca. -5 ‰ due to bacterial transformation and increase in refractory lignin depleted in $\delta^{13}C$, producing bulk values of -17 to -22 ‰ (Ember et al., 1987; Boschker et al., 1999). This decomposing *Spartina* within the sediments may keep the SOM values within a narrow range throughout the Nova Scotia marshes.

Sediment $\delta^{15}N$ differs significantly between the young macrotidal and mature mesotidal marshes (Windsor $\delta^{15}N = 5.1 – 5.9‰$; Chezzetcook $\delta^{15}N = 3.5 – 5.6‰$). Nitrogen fractionation occurs during organic matter decomposition in sediment, influencing $\delta^{15}N$ (Peterson and Fry, 1987). Decomposing *Spartina* grass has increased $\delta^{15}N$ compared to living leaves (Middelburg et al., 1997; Cloern et al., 2002; Connolly et al., 2005). At Chezzetcook, the slower sedimentation rate, longer history of peat formation, lower tidal range and less flushing, less winter ice scour, and higher biological oxygen demand (see Weigert and Pomeroy, 1981) may all contribute to the difference between the two sites. More importantly, agricultural runoff into the Minas Basin (Daborn et al., 2003) and sewage influx (e.g., Carlier et al., 2007) may contribute to the

overall higher $\delta^{15}N$ values at Windsor; agricultural runoff may increase $\delta^{15}N$ by up to 15‰ compared to pristine areas (Kristensen et al., 2016). Strong tidal flushing and high sedimentation rates at Windsor (e.g., Andrews et al., 1998) may keep $\delta^{15}N$ values lower than this extreme, but they are still higher than at Chezzetcook. The role of ice-scour is uncertain but presumably retards the stabilization of low marsh sediments and formation of salt marsh peat.

Overall, sources in complex, heterogeneous systems such as salt marshes cannot be fully determined using stable isotope analysis alone (Cloern et al., 2002). The differences between Chezzetcook and Windsor probably reflect multiple factors. The dominance of C_4 plants (*Spartina* species) explains the slightly less-depleted $\delta^{13}C$ in Windsor macrotidal sediment. Importantly, we have shown that differences between high – middle marsh zones and low marsh – mudflat zones emphasize the need to examine salt marshes as spatially-distinct zones and not as entire entities when considering energy flow through food webs.

Consumer isotopic signatures

Consumer mean $\delta^{15}N$ values are variable, with meiofauna and foraminifera having the highest variability and there are no significant differences between marshes. For both marshes, $\delta^{13}C$ values become significantly more depleted from the mudflat to the high marsh, probably reflecting habitat-specific dietary sources. More depleted values may indicate terrestrial sources (Ha et al., 2014), especially for the high marsh. The greater overall depletion at Chezzetcook (-16.3‰) than at Windsor (-13.6%) reflects differences in source material and the closer terrestrial fringe at Chezzetcook (as described in Chapter 3, Tables 3.1 – 3.2).

In general, the $\delta^{13}C$ of macrofauna (including small macrofauna) and meiofauna is intermediate between plant and sediment (Figure 4.2). Generalist and omnivorous taxa may display variable values with respect to source material because they may consume food from more than one basal source and trophic level (Peterson and Fry, 1987; Post, 2002; Schratzberger and Ingels, 2017). The large isotopic variability within one species or taxonomic group reflects variability in feeding modes (e.g., suspension feeding, deposit feeding) and food sources, including vascular plants, detritus and algae (Galvan et al., 2008; Nordstrom et al., 2009, 2015). In salt marshes, the detritus contains plant and animal remains (Teal, 1962), explaining consumer taxa variable $\delta^{13}C$ (Peterson and Fry, 1987). Studies of Brazilian and New Zealand estuaries show that three to five different sources, including plant matter, particulate organic matter, algae and biofilms, may contribute to consumer $\delta^{13}C$ values (Claudino et al., 2013; Leduc et al., 2009). Isotopic fractionation within consumer tissue may yield a change of ~0.8‰ in $\delta^{13}C$ per trophic level (Post, 2002; Vander Zanden and Rasmussen, 2001), but this change is masked by the great variability induced by the factors noted above.

The undissected snails (e.g., *L. littorea*) and calcareous foraminifera (e.g., *Elphidium*) display higher $\delta^{13}C$ values than other consumers (Figure 4.2). These values probably reflect contributions from inorganic carbon in the $CaCO_3$ shells. Inorganic carbon does not undergo the same degree of fractionation as organic carbon (Peterson and Fry, 1987; Post, 2002), and although the shells are precipitated from biological activity, their $\delta^{13}C$ values largely represent the inorganic environment (Post, 2002), excluding the innermost organic lining.

Although $\delta^{15}N$ values overlap for macrofauna, small macrofauna, and meiofauna in the Nova Scotian marshes, macrofauna $\delta^{15}N$ often exceeds that of the small macrofauna and meiofauna (Figures 4.2, 4.5, 4.7). The macrofauna tend to occupy higher trophic levels in both marshes and in most zones (Tables 4.3, 4.4), except on the Windsor mudflat where the functional group 'small meiofauna' dominates, followed by the foraminiferan *H. orbiculare* (Table 4.4). Experimental studies in a high marsh in South Carolina show that the macro-epifauna prey upon members of the meiofauna (Bell, 1980), in accord with the higher $\delta^{15}N$ values and calculated trophic positions of Nova Scotia macrofaunal taxa.

In both marshes, predatory insects and spiders occupy higher trophic positions and foraminifera and meiofauna have variable trophic positions. However, Claudino et al., (2013) cautioned about interpreting consumer $\delta^{15}N$ in terms of trophic position, as $\delta^{15}N$ also may reflect specific inputs. For example, molluscs and crustaceans normally have lower ^{15}N enrichment than would be expected from their trophic position due to excretion of ammonia, and spiders may store ^{15}N in their opistosoma (Vanderklift and Ponsard, 2003). The $\delta^{15}N$ variability in the two marshes, especially for the within-taxonomic groups, is indicative of generalist omnivorous feeding modes which are common in salt marsh systems (Anderson and Cabana, 2007).

The isotopic variability of meiofauna and foraminifera in all zones and both marshes validates their generalist, omnivorous feeding interactions. Opportunistic foraminifera, such as those in the two marshes, often have a higher $\delta^{15}N$ (4 to 8‰) and more depleted $\delta^{13}C$ (-16 to -25‰) than other foraminifera, such as mudflat algal feeders in the study area (Figure 4.7; Mateu-Vicens et al., 2016).

At Chezzetcook, the macrofaunal species shift from marine-based in the lower marsh to terrestrial-based in the higher marsh zones (Figure 4.5). Marine gastropods dominate the mudflat and low-marsh macrofauna, and insects and arachnids dominate the middle and high marsh. This change correlates with increased elevation. The Windsor marsh, however, does not display zonal changes in the distribution of the macrofauna taxa (Figure 4.5), likely due to the lower complexity of the flora.

4.5.2 $\delta^{13}C$ and $\delta^{15}N$ values and species assemblages in cool temperate marshes

Many consumer taxa show no significant differences in $\delta^{13}C$ or $\delta^{15}N$ despite variation in isotopic content of basal sources. This homogenization within the consumers is partly due to the importance of detrital sources and detrital-consumer interactions in salt-marsh ecosystems (Schrama et al., 2012) and, as documented here, large differences in potential detrital sources (marsh plants, algae, bacteria and decaying animal matter).

The trophic position quantifies how much biomass is metabolically processed within the food chain, as determined from the amount accumulated in the consumer (Vander Zanden et al., 1997). Because sources are considered trophic level 1, many primary consumers are close to values of 2, secondary consumers at values of 3, and so on. In many estuarine and salt marsh systems, reported trophic positions of consumers are between 1.8 and 4 (Claudino et al., 2013) and in zoobenthic and plankton freshwater systems between 2 and 3 (Vander Zanden et al. 1997). The trophic positions of Chezzetcook and Windsor salt marsh consumers cluster between 2 and 4 (mean 2.8 for both marshes) using the 3.4‰ trophic enrichment factor of Vander Zanden et al. 1997), showing that they are primary and secondary – tertiary consumers. Calculated trophic positions from binary food webs for these systems (Chapter 3) follow these patterns,

although they are slightly lower overall than indicated by stable isotopes (2.3 for Chezzetcook and 2.6 for Windsor). Carscallen et al. (2012) also noted trophic position from marine polar food-web analysis was not significantly different from those calculated by $\delta^{15}N$ (the trophic positions only differed by 0.2 – 0.5). Expected basal consumers (e.g., *Corophium* and *Culicoides*) represent primary trophic positions in binary food webs, validating their use as baseline consumers for calculating trophic position based on stable isotopes. The overall low trophic level for consumers in the present study accords with other studies with a similar fauna of zoobenthos and small invertebrates (Schwarmborn and Giarrizzo, 2015).

Differences between trophic positions based on binary food webs and stable isotopes reflect the variability in $\delta^{15}N$, especially in the baseline consumer $\delta^{15}N$ within the ecosystem. Individuals of the same expected trophic position within an ecosystem can have $\delta^{15}N$ values that reflect a difference of >1 trophic position (e.g., freshwater fishes in Ontario and Quebec, Canada, Vander Zanden et al., 1997). In the Curuca Estuary of Brazil, prediction of trophic level using $\delta^{15}N$ explains 75% of the variability in $\delta^{15}N$, but source signatures, differences in trophic fractionation, and the biochemical composition of consumers also influence the final $\delta^{15}N$ values of consumers (Schwamborn and Giarrizzo, 2015). The salt marsh consumers from our Nova Scotia marshes also show this variability. Where isotopic variation in baseline consumers is large across time and/or space, a bulk estimate of the trophic enrichment fractionation is better than choosing one species to calculate trophic position, especially in these omnivorous systems (Kristensen et al., 2016). There are numerous approaches for calculating trophic position in these detritivorous, generalist and omnivorous systems, and the assembly of binary food webs

(Chapter 3) has as many problems as using $\delta^{15}N$, gut content analyses, or other approaches (as discussed in Carscallen et al., 2012 for polar marine food webs). Based on comparisons to trophic positions of Chapter 3, stable isotope analysis provides a useful albeit imperfect estimate of consumer trophic positions within the examined food web.

Measurement of $\delta^{13}C$ and $\delta^{15}N$ in the Nova Scotia salt marshes provides an initial characterization of meiofaunal communities, their predators, and their basal energy sources. The meiofauna are important food-web components of the intermediate taxa, facilitating transfer between the source material and consumers at higher trophic levels (Tables 4.3, 4.4). Meiofauna consume a wide spectrum of food sources (Schratzberger and Ingels, 2017), leading to a higher variability in isotopic signatures and calculated trophic positions than those of herbivores, carnivores and filter feeders. Their small size often leads to the assumption that they are primary consumers with low trophic levels, but because many feed generalistically and opportunistically, they may have a higher trophic position than expected (Schmid-Araya et al., 2016). Excluding small consumers such as meiofauna and foraminifera reduces the reliability of conclusions about ecosystem energy transfer (Schmid-Araya et al., 2016), especially in the detritally-dominated salt marsh.

Isotopic mixing models help in determining the proportion of each carbon source (plants, animals, microalgae, and particulate organic matter) to the diet of the meiofauna and invertebrate epifauna (e.g., Riera et al., 1999; Galvan et al., 2008; Park et al., 2015). Mixing models also account for error in the stable isotope data due to isotopic fractionation (Erhardt and Bedrick, 2013). However, the challenges of using mixing models may outweigh the benefits for assessing meiofaunal diet in detrital systems

(Kristensen et al., 2016). Model outputs are highly sensitive to input data, and due to the overlapping signatures that characterize salt marshes, may bias interpretation of the food sources (Kristensen et al., 2016).

In studies such as the present analysis of cool-temperate salt marshes with a large involvement of small detrivorous consumers, the use of mixing models is nearly impossible due to the large uncertainty in percent source contributions, as found for harpacticoid copepods by Cnudde et al. (2015). At Chezzetcook, the large standard deviations associated with the mean $\delta^{13}C$ and $\delta^{15}N$ values of the small meiofauna functional groups also point to the need for more highly-resolved food webs in which all taxa are examined individually (Chapter 3). In general, binary food webs are time-consuming, their taxonomic resolution is subjective, and the trophic links all have the same weighted level of importance (Post, 2002). Therefore, using isotopic analysis provides a useful validation for binary food webs, and subsequently vice versa, to examine the structure and function of energy flow (through feeding links) in a system.

4.5.3 Implications of the salt marsh stable isotope studies

Interest in salt marsh conservation is high, but the number of well-studied marshes is low. Stable-isotope analysis provides a quantitative map of food-web trophic interactions. Kwak and Zedler (1997) characterized an estuarine ecosystem in California using ^{13}C, ^{15}N, and ^{34}S isotopes. In addition to isolating the source materials of the food web and determining the number of trophic levels, they found that the salt marsh was trophically linked with tidal channels, revealing the need to manage them as one inter-related ecosystem. The study also challenged the notion that vascular plants contributed the most

to the food web via detrital inputs, and indicated that the marsh and lagoon food webs did not conform to salt marshes along other North American coastlines. Thus, stable-isotope analyses from our study can provide key input for conservation recommendations.

For the two marshes, the ^{13}C and ^{15}N results assist in defining food-web trophic interactions and trophic positions of the zoobenthic community (see also Currin et al., 2011), and consumer signatures are useful in monitoring ecological succession and ecosystem recovery during salt marsh restoration (Nordstrom et al., 2015). For example, created salt marsh sites at Venice Lagoon in Italy have dominant microalgivores such as insect larvae feeding at the surface, leading to a succession of subsurface oligochaetes feeding on detritus (Nordstrom et al., 2015). In addition to their use in monitoring salt marsh restoration areas such as those of the Bay of Fundy, such observations can also be used to monitor salt-marsh succession from an immature mudflat to a mature middle- and high-marsh. Chezzetcook has dominant algivores in the low marsh and mudflat (*Culicoides*) and more oligochaetes and detrital feeders in the middle and high marsh zones.

This restoration pattern of dominant algal production and consumption followed by the dominance of subsurface detritivores is also seen at recovering marshes along the Skokomish River Estuary, Washington, USA (Howe and Simenstad, 2015a). Although food sources vary in time and space, there is a general trend from a microalgal-production food web towards a detritus-based food web, supporting previous conclusions on the dominance of detrital sources rather than microalgal production (e.g., Galvan et al., 2008). Significant isotopic differences may not be apparent between “restored” or “created” marshes such as Windsor and older reference marshes such as Chezzetcook

because food webs may converge to a natural state in little more than 10 years (Nordstrom et al., 2015). The Windsor marsh is over 40 years old, and may already have reached full functionality, although the extremely low taxonomic diversity of macrophytes in the three-zone system points to a current state of marsh immaturity and disequilibrium.

4.5.4 Implications for geological interpretation of salt marsh sediments

Carbon isotopes and C:N ratios are important for dating and interpreting paleoenvironments and correlating ancient strata (Byrne et al., 2001; Canfield et al., 2010). In particular, excursions of $\delta^{13}C$ can be used as a "gold standard" for correlating some geological time intervals like the Ypresian Stage in the Paleogene (Aubrey et al., 2007) and C:N is an index of land:sea nitrogen portioning from Archaen to Anthropogenic time (Canfield et al., 2010). Sediment organic matter signatures are especially useful in the absence of microfossils such as foraminifera (Lamb et al., 2006) and for evaluating the presence of old marine carbon in shells (e.g., Mudie and Lelièvre, 2013). Situated at the land-sea transition, salt marshes are used for reconstructing former sea levels. Salt marsh plants (both C_3 and C_4) dominate the bulk of sediment carbon signatures, but bulk sediments may include a variety of sources and it may be hard to determine the exact plant composition (Tanner et al., 2010). Diagenetic effects such as decomposition also influence isotopic values. Chmura and Aharon (1995) noted that C_4-dominated sediments have $\delta^{13}C$ values of about -15‰ in the low marsh and that sediments with mixed C_3-C_4 sources have values of -17 to -24‰ in the mid to high marsh. From the present study, sediment (SOM) values from Chezzetcook and Windsor, regardless of zone, are within these values. Sediments from freshwater areas have $\delta^{13}C$

values of -27.8‰, sediments from brackish marshes have -16.9‰ $\delta^{13}C$, and sediments from salt marshes have -16.2‰ $\delta^{13}C$ (Chmura et al., 1987). Although the depletion in $\delta^{13}C$ from C_4 plants (*Spartina alterniflora*) to sediments can come from bacteria, benthic algae, and transported organic matter, decomposition probably plays the biggest role in terms of the negative shift in $\delta^{13}C$ in sediments.

On some coastlines, sea-level trends for ancient salt marsh sediments can be reliably determined using the shift from less-depleted sediment signatures from C_4-dominated low marsh areas to more-depleted signatures from C_3-dominated higher marsh areas (Byrne et al., 2001). Lamb et al. (2006) also emphasized the direction of sediment isotopic change (relative rather than absolute values) in interpreting paleoclimate and sea level and distinguishing freshwater from marine sediments. The complexity of detritus-based food chains requires caution when using stable isotopes to interpret coastal paleoenvironments by small isotope excursions, where, in the geologic record, excursions of as small as ± 2 ‰ are correlated to events such as mass extinctions.

Geological applications of stable isotope analyses are also important when examining microfossils such as foraminifera. For example, *Miliammina fusca* is indicative of low marsh sediments with SOM between -20 and -22‰ $\delta^{13}C$, and *Trochammina inflata* is indicative of middle- and high marsh sediments with SOM between -22 and -28‰ $\delta^{13}C$ (Milker et al., 2015). The present analysis displays this distinction between the high-middle marsh cluster and the low-mudflat cluster in sources and consumers. Combining stable isotopes with microfossils (e.g., Milker et al., 2015; Kemp et al., 2017; Sen and Bhadury, 2017), pollen signatures and diatom salinity indices

(Byrne et al., 2001; Mudie et al., 2013) provides a more accurate, multiproxy approach to paleo-sealevel reconstruction.

4.6 Conclusions

Patterns of $\delta^{13}C$ and $\delta^{15}N$ of two temperate salt marshes are not significantly different, despite very large differences in age, tidal regime, sedimentation rate, ice scour and possibly anthropogenic nitrogen loads. However, marsh zones that reflect a land-sea gradient in physical and biological factors show many significant isotopic differences, with some strong clustering of isotopic values for individual zones and taxonomic groups, especially at Chezzetcook. At both mesotidal and macrotidal marshes, higher trophic positions are occupied by predatory insects and spiders whereas foraminifera and meiofauna have variable trophic positions between the marshes and among the marsh zones.

At both marshes, sediment organic matter has a relative consistency that indicates the pervading dominance of multiple sources, processes that mix detritus, and post-depositional changes, regardless of tidal regime and difference in sediment stability due to ice and plant cover. Mean $\delta^{15}N$ values are variable for consumers, with meiofauna and foraminifera having the highest variability. The isotopic distinction between salt marsh zones at Chezzetcook is sufficient to warrant individual examination of trophic structure by zone, as indicated also by food web studies of the marshes (Chapter 3).

CHAPTER 5: MESOCOSM AND MICROCOSM EXPERIMENTS ON THE FEEDING OF TEMPERATE SALT MARSH FORAMINIFERA.

Protist Protest

Little protists of the sea
How do we treat thee?
As foraminifers, Oh wee beasties of the sea?
Or, shall it be, foraminifera,
for the plural or the singular?
Perhaps we can float the word ''foraminiferan''
but then again,
it still would mean a single cell,
but how in hell
can foraminifera be for one and two,
when so many live in the ocean blue?
Please, please tell me Dr. Foram Man or M'am,
Is it –minifer, -minifera, or –miniferan?

---- by Sally E. Walker, in Lipps et al. (2011), p.309.

5.0 Abstract

Agglutinated foraminifera dominate most zones of temperate salt marshes, making them key indicators for monitoring sea level and environmental changes. Little is known about the biology of these benthic foraminifera because of difficulty in distinguishing live from dead specimens, given their cryptic motility and semi-opaque tests. We present data from 10 years of biological experiments using the trochamminoid species, *Trochammina inflata* and *Jadammina macrescens*, and the milioid agglutinant *Miliammina fusca*, compared to two rotalid calcareous species *Helenina anderseni* and *Elphidium williamsoni.* All experiments used specimens from a laboratory mesocosm representing Chezzetcook Inlet salt marsh, a type locality for Holocene studies on the east coast of Canada. To study the biology of the most common and abundant agglutinated salt marsh

foraminifera, culture requirements were determined for maintenance in small petri dishes over periods of 10 – 12 weeks. Nine simple, non-terminal ways of identifying live organisms were developed. The live criteria include (1) lateral and vertical movement; (2) detritus-gathering (entire and/or apertural); (3) attachment; (4) clustering of individuals; and (5) opaque areas within the test. Comparison with Rose Bengal for living-to-dead observations showed <10% diversion for calcareous species and *Trochammina inflata,* whereas *Miliammina fusca* was over-counted by >30%. *Trochammina inflata* was used to examine food consumption in transmission electron microscopy studies of the terminal chambers and to identify food in digestive vacuoles of specimens from the mesocosm marsh (*in vivo*) and from starved and bacteria-fed *in vitro* individuals. Bacteria and unidentified detrital pieces were the dominant material in the vacuoles, establishing for the first time that this agglutinated species is a saprophagous and bacterivorous detritivore. Observations of movement and feeding orientation in the agglutinants suggest links between form and function that underscore their value as ultra-high resolution sea level proxies. Feeding trials *in vitro* between foraminifera and similar-sized meiofauna were done to examine inter-specific predator-prey feeding interactions, as determined by disappearance of specimens over 48 hours. The trials revealed no direct predation, by or of foraminifera. Mesocosm biomass and abundance counts of foraminifera and associated meiofauna show that foraminifera occur in high abundances (>50% of foraminifera + meiofauna), and represent a large percentage of the meiofaunal biomass, emphasizing their importance in the food web and energy-flow dynamics of temperate salt marsh systems.

5.1 Introduction

Foraminifera are protists that have been extensively studied for over 150 years (Myers, 1943; Arnold, 1974; Loeblich and Tappan, 1988; Sen Gupta, 1999; Murray, 2006; Kitazato and Bernhard, 2014). Most studies focus on their taxonomy, assemblages and distributions in marine and brackish environments around the world and throughout geologic history since the Cambrian because they are important biostratigraphic tools and key proxies for interpreting the paleoecology of ancient seas and fluctuations in relative sea level (RSL). Recently, the complex ecology of modern foraminifera has been the subject of several major texts (Lee and Anderson, 1991; Murray, 2006). These monographs reveal that many basic questions about feeding, growth and reproduction remain unresolved since the earlier work of Arnold (1974), particularly for agglutinated marsh species and other benthic foraminifera (Kitazato and Bernhard, 2014). In effect, most environmental interpretations based simply on relating generalized modern distributions to abiotic conditions remain circumstantial until the biological factors that constrain foraminiferal occurrences are understood, including their complex feeding habits (Goldstein, 1999; Mojtahid et al., 2011). For example, the notoriously high patchiness of foraminifera (Lee, 1974) may be governed by food availability, feeding methods, competition with meiofauna, commonly-cited abiotic factors (salinity, elevation; see Chapter 2), or a combination of all and some of these.

A key objective of this thesis is to expand knowledge of trophic niches that control the spatial and temporal population dynamics of temperate salt marsh foraminifera as shown by pioneering Quaternary paleo-sea level studies (Scott et al., 2001 and references therein; Kemp et al., 2011, 2013). Within the suite of salt marsh

marker species, agglutinated taxa such as *Jadammina macrescens, Miliammina fusca,* and *Trochammina inflata* are the main tools for paleoenvironmental work in coastal environments because of their better preservation potential in acidic salt marsh sediments compared to calcareous taxa. Most past studies, however, have focused on calcareous taxa common on mudflats or in deeper coastal water, including *Ammonia beccari/tepida*, *Haynesina germanica*, and *Elphidium* spp. (Dupuy et al., 2010; Jauffrais et al., 2016; Seuront and Bouchet, 2015). Thus, previous conclusions on behavioural, feeding, and biotic interactions of "salt marsh benthic foraminifera" are based on a restricted part of the total assemblage and fail to consider the agglutinated species that are widespread throughout the entire salt marsh, often in extremely high abundances.

Direct observation of feeding and behavioural habits in these dominant salt marsh taxa is crucial for inferring their role in the ecosystem, but few studies have previously examined these species in incubator (microcosm) cultures (Goldstein and Alve, 2011; Weinmann and Goldstein, 2016; LeKieffre et al., 2017; van Dijk et al., 2017). Past observations and/or feeding experiments (e.g., Lee and Anderson, 1991; Bernhard and Bowser, 1992; Sen Gupta, 1999; Suhr et al., 2003; Mojtahid et al., 2011; Jauffrais et al., 2016) have shown that benthic foraminifera can be photosynthetic (hosting diatoms), chemosynthetic (hosting bacteria), herbivorous (grazing on diatom mats), detritivorous, carnivorous or parasitic. Moreover, in deep waters in the Arctic (Sea of Okhotsk), and in mudflats along the North Sea coast, benthic foraminifera constitute over 50% of meiofaunal (63 – 500 μm) biomass and abundance in small-scale (<5 cm^3) patches, and have a wide range of production, between 90 to over 5000 mg C m^{-2} yr^{-1} (Chandler, 1989), showing that they can be vital parts of the benthic ecosystem.

The primary objective of this study is to examine the feeding and behaviour of the dominant salt marsh taxa used in the RSL studies of Scott and Medioli (1980). The selected species are two agglutinants in the Class Globothalamea, Subclass Textulariia (*Trochammina inflata* and *Jadammina macrescens*), one agglutinant in Class Tubothalamea, Order Milioda (*Miliammina fusca*), and two calcareous species in Class Globothalamea, Order Rotaliida (*Elphidium williamsoni* and *Helenina anderseni*). To perform these studies, there is need for developing new methods for non-harmful examination of living populations using a list of criteria to distinguish living agglutinated benthic foraminifera from dead specimens, such as the six criteria described in Arnold (1974), which were based on thin-walled calcareous taxa. Most previous studies that have investigated ways to distinguish between living and dead assemblages of foraminifera in surface sediments (Murray and Bowser, 2000) involve killing the specimens by fixing and staining with Rose Bengal or Sudan Black, or examining cellular material using transmission electron microscopy (TEM) and scanning electron microscopy (SEM) methods. A non-terminal method using fluorescent dye CellTracker™ Green (CTG) is very expensive and also requires specialised fluorescence research microscopes for time-consuming stain-reaction studies that are difficult to quantify (Figueira et al., 2012). In this study, new methods are developed for non-harmful examination of living populations of agglutinated foraminifera with thick, opaque chambers, using a list of criteria to distinguish living benthic foraminifera from dead specimens.

The cool temperate salt marsh mesocosm in the Dalhousie Aquatron (Chapter 2) allowed implementation of feeding trials with foraminifera and meiofauna from a temperate environment, on a year-round basis. Additionally, new observations could be

made on the key agglutinated and calcareous salt marsh paleo-sealevel proxies that have been overlooked in past biological studies of marshes in warmer regions (e.g., California: Bradshaw, 1968; Georgia and Florida, USA: Weinmann and Goldstein, 2016). The feeding habits of the mesocosm temperate climate salt marsh foraminifera will be assessed by direct observation and by indirect criteria such as accumulation of detritus at the terminal chamber aperture (Goldstein, 1999), or around the whole specimen (Arnold, 1974), which have been previously called "feeding cysts" (Heinz et al., 2005). Transmission electron microscopy (TEM) of the feeding vacuoles in the agglutinant *Trochammina inflata* are used to develop novel information on feeding mechanisms in selected individuals fed with unaltered marsh mud or marsh bacteria isolates. Biomass is also determined to show how much benthic foraminifera contribute to the organic matter (OM) and carbon budgets of the salt marsh sediment.

The objectives of this study are three-fold: 1) to identify low-maintenance, non-terminal methods for distinguishing three agglutinated and two calcareous salt marsh foraminifera in a mesocosm culture setting; 2) to identify feeding modes in *Trochammina inflata* using TEM; 3) to validate feeding habits of salt marsh foraminifera and to determine their biomass in culture experiments. This set of observations will contribute to new understanding of agglutinated and key calcareous salt marsh foraminiferal responses within their ecological niches, how they might respond to environmental changes affecting their food sources, and how their biomass contributes to carbon budgets and sediment energy fluxes.

5.2 Methods

5.2.1 Sediment sampling, foraminifera acquisition and observation of live specimens

Surface sediment samples with living foraminifera and potential food came from the mesocosm marsh developed in the Aquatron facility at Dalhousie University using slabs of sediment originally from Chezzetcook Inlet, Nova Scotia (Chapter 2). The size of samples removed for cultures varied from 2 cm^3 to 10 cm^3, depending on the amount of foraminifera needed, with a surface scraping less than 0.5 cm thick. The samples were taken from the mesocosm marsh elevational zone likely to provide maximum numbers of the selected foraminifera needed for detailed study, based on their known relative abundances (Chapter 2, Table 2.4).

Samples were gently washed through nested 500 and 63 µm sieves (Figure 5.1), using filtered seawater adjusted with distilled water to keep salinity at 15 psu. The 500 µm mesh removed large debris. The >63 to 500 µm sediment fraction was poured into petri dishes, and 2 µm-filtered sea water + distilled water was added to reach approximate salinity from the corresponding salt marsh zone. Petri dishes were covered to slow evaporation. Dishes were left at room temperature (22°C).

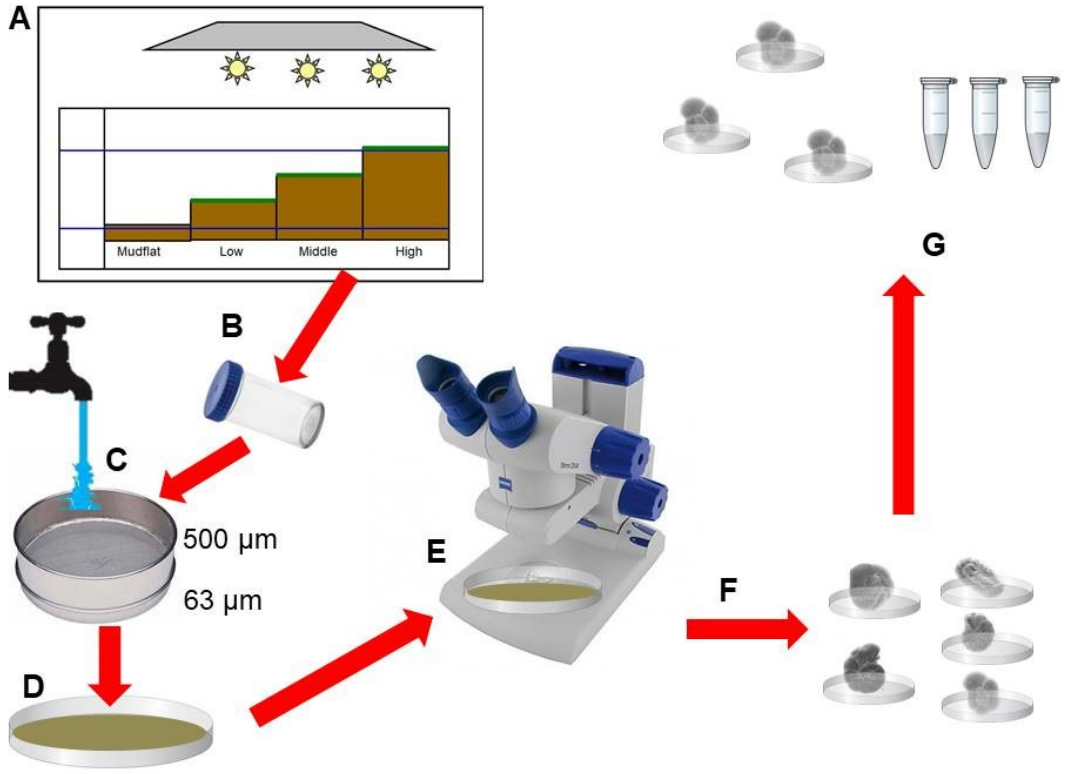

Figure 5.1. Diagram of sampling protocol. Samples (B) were scraped from marsh surface from the mesocosm (A), washed through stacked sieves (C), with the sieved residue stored in 15 psu water in 10-cm petri dishes (D). Living foraminifera were picked from dishes (E) and placed in separate 5-cm dishes per species (F), to explore a variety of feeding conditions as explained in the text, and used for a variety of experiments, including TEM (G).

Dishes were examined under the Zeiss stereomicroscope (10 – 40 x) using an adjustable fibre optic light which does not heat the sample but provides brighter than normal light. Living individuals 150 and 300 µm in size, generally recognized by movement or chambers containing cytoplasm, were transferred by fine brush or pipette from the 10 cm Petri dish to a smaller (5 cm) Petri dish. The smaller dishes contained a few millimeters of water with salinity adjusted for the corresponding marsh zone. The dishes were left for 24 hours and foraminifera were reevaluated the following day to remove dead individuals that were previously thought to be living. For dishes containing

calcareous species, 0.2 µl of calcium (Hagen® Fluval® Sea Calcium) and alkaline (Hagen® Fluval® Sea Alkalinity) solutions were added to give sufficient calcium carbonate for test maintenance, growth and/or sexual or asexual reproduction of specimens. All dishes were left at ambient room temperature (c. 22°C) and light. The length of time for the experiments/observations ranged from days to weeks.

5.2.2 Preparation of food

Because many benthic agglutinated foraminifera are assumed to be detrital and bacterial feeders, the stocks of food used for maintenance and experimentation were 1) unaltered mesocosm salt marsh mud; 2) filtered detritus; and 3) cultured salt marsh bacteria. For the first "field" mud food source, a small amount of salt marsh sediment was scraped from the mesocosm high-salinity middle marsh (T2-M; Chapter 2) and placed in a dish with ambient water. Sediment was stirred to separate large particles and disperse the material. One or two pipette drops of this stirred mud were then added to culture dishes of foraminifera.

Secondly, to prepare filtered detritus, marsh sediment samples (2 cm^3) were washed over stacked 45 and 63 µm sieves. The remnant 45–63 µm detrital food material contained no meiofauna, macrofauna, and few foraminifera but included particulate and dissolved organic matter, bacteria and non-filamentous micro-algae. The detrital food source was maintained in a loosely-capped vial with filtered seawater adjusted to the source marsh zone, and it was replenished on a weekly basis during the experiments.

Thirdly, for cultured bacteria, new and/or sterile equipment was used, work stations were thoroughly sterilized, and transfers occurred in a fume hood. All bacteria

were grown on Tryptic Soy Agar (TSA) plates. Small (<1 ml) samples of marsh water and sediment were taken from the mesocosm with pipettes and placed in Petri dishes. A sterile inoculating loop transferred 0.1 ml of samples to agar plates, smearing the loop over the entire plate. Two plates were smeared for each sample of marsh water or sediment, totaling eight plates. They were covered and placed upside down in a sterile plastic box for four days at room temperature. After five days, individual bacterial colonies were removed and smeared on new plates. A sterilized inoculating loop removed the center from each culture and smeared it on to a new TSA plate. Five colonies of visibly different bacteria were smeared, and these five plates were covered and stored upside down for three days.

The five covered plates were examined daily under a dissecting microscope to make sure the smears contained only one "species" (same colony) of marsh bacteria. The colonies were re-smeared weekly for the first month, and subsequently once a month to maintain the cultures. These bacterial cultures were used as food sources for both general feeding experiments and for the TEM work.

5.2.3 Foraminiferal feeding observations

General methods

Feeding culture experiments were performed using the five dominant species of foraminifera found in certain zones of the mesocosm marsh. These species included three agglutinated species *Miliammina fusca*, *Jadammina macrescens*, *Trochammina inflata*, and two calcareous species *Helenina anderseni* and *Elphidium williamsoni* (Figure 5.2).

Most of the experiments used *T. inflata* because of the need for data on agglutinated species, and because of its relatively large size, and conspicuous motility.

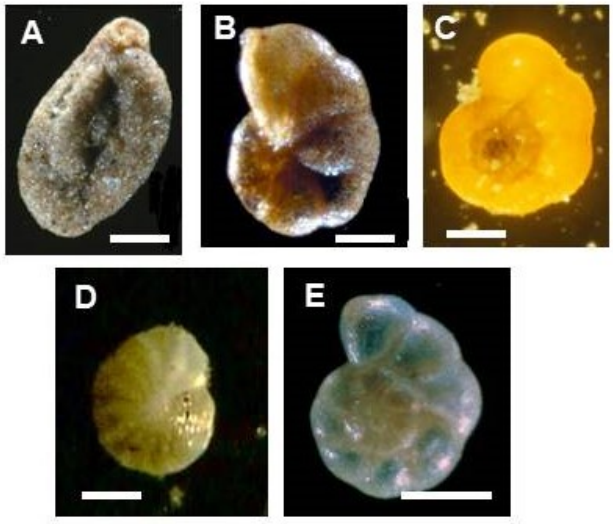

Figure 5.2 Five species used for culturing and feeding experiments. Top row: agglutinants (A) *Miliammina fusca*, derived from calcareous species (Habura et al., 2006); (B) *Jadammina macrescens*, with arenaceous test; (C) *Trochammina inflata*, with arenaceous test covered by outer organic veneer. Bottow row calcareous: (D) *Elphidium williamsoni*, and (E) *Helenina anderseni*. Scale bar = 100 µm. Images A, B, E from D.B. Scott.

To prepare cultures for feeding experiments, live foraminifera were taken from the stock culture dishes (Figure 5.1), after removing any attached detritus with a fine brush. Five individuals of the same species were placed in a 5 cm petri dish with ~5 ml of filtered seawater and distilled water (30 psu for calcareous species, and 15-20 psu for agglutinated species). The water was about 3-4 mm deep. The dishes were kept at room temperature (22°C) and natural ambient light from windows and overhead fluorescent lights (8 am – 5 pm). If the foraminifera were being fed bacteria, the salt water was further filtered through a 0.45 µm syringe filter to remove any bacteria in the water before being added to the dish. Food types used in various feeding observation experiments included 1) control (no added food; for meiofaunal feeding studies); 2) two

drops of marsh mud + water (for general foraminifera feeding observations); 3) two drops of filtered detritus (for a 12-week culture experiment); and 4) a loop (0.01 ml) of cultured marsh bacteria (for one TEM experiment). Dishes were examined every day or two for activity (e.g., foraminiferal movement, whether direct or cryptic, accumulation of detritus around entire individuals or apertures), and water levels and salinity were adjusted and fresh food was added weekly for experiments longer than one week.

Bacteria-fed trials for TEM work

Five living *T.inflata* were placed in five separate 5-cm petri dishes, one dish for each of five colonies of bacteria. Foraminiferal specimens were left overnight to allow feeding vacuoles to empty. The foraminifera were then placed in new dishes with 0.02 ml of one of the five bacterial cultures, and left for two days. Overall feeding observations were made by examining dishes under the stereomicroscope before preparing them for TEM study of the chamber contents.

5.2.4 Transmission electron microscopy (TEM) for *Trochammina inflata*

Protocols of Goldstein and colleagues (Goldstein and Barker, 1988; Goldstein and Moodley, 1993; Goldstein, 1997) and Bowser and colleagues (Bowser et al., 1995) were used in conjunction with those of the Simpson laboratory at Dalhousie University. *Trochammina inflata* was chosen for TEM work because of its large, round chambers compared to the narrow chambers of *Jadammina macresens*, which would be difficult to thin-section. Also, *T. inflata* also has a fine-grained test whereas the test of *M. fusca* incorporates larger sediment grains that might damage the glass and diamond knives (A. Simpson, pers. Comm.; Bernhard and Richardson, 2014). Interpretations of TEM photos

were validated by Alastair Simpson (Dalhousie University), Susan Goldstein (University of Georgia) and Emmanuelle Geslin (Université Angers), as well as by comparison with images of Anderson and Lee (1991) and Goldstein and Corliss (1994).

Foraminifera fixation and embedding

To examine "field-fed" foraminifera, live *Trochammina inflata* specimens were processed immediately after taking samples from the mesocosm middle marsh (T2-M; see Chapter 2) and six specimens were placed in each of two Epindorf tubes. The foraminifera were then killed and fixed with 0.1 ml 2.5% glutaraldehyde and 0.9 ml of sugar buffer (0.5 g sucrose and 5 ml. 0.1 cacodylate in 5 ml distilled water) for 90 minutes, then rinsed three times with buffer. After the last rinse, the foraminifera were soaked for 90 minutes in buffered 0.5 ml 1% osmium tetraoxide (OsO_4) solution (0.125 ml 4% OsO_4 plus 0.375 ml buffer), followed by six rinses with distilled water.

The tests of the fixed foraminifera were punctured with a fine needle to make at least two holes for penetration of resin into the cytoplasm. The punctured specimens were then dehydrated with 30% ethanol (30 mins) followed by 50% ethanol for c. 24 hrs, then further dehydrated with 70%, 90%, 95% ethanol and 100% anhydrous ethyl alcohol. The foraminifera were then placed for 1 hour each in a graded series of Spurr's resin dilutions with 100% ethanol, (30%, 60%, 100% resin). Four 100% resin coatings were the applied over 48 hours. The coated foraminifera were embedded in wells with partially polymerized resin to prevent their sinking, then polymerized by heating overnight in an oven at 60ºC.

Thin section preparation and examination

Embedded foraminifera were sliced using a Leica EM UC6 microtome microscope after removing excess resin with a razor blade (Figure 5.3). The agglutinated tests were sectioned with a glass knife to ~1 µm thickness. The outermost chamber with cytoplasm (terminal or penultimate chamber) was sectioned to examine the intra-shell cytoplasm closest to the apertural pseudopodia used in food collection. A diamond knife was then used to cut through the 1 µm-thick sections of cytoplasm, at 100 nm-thickness (Figure 5.3).

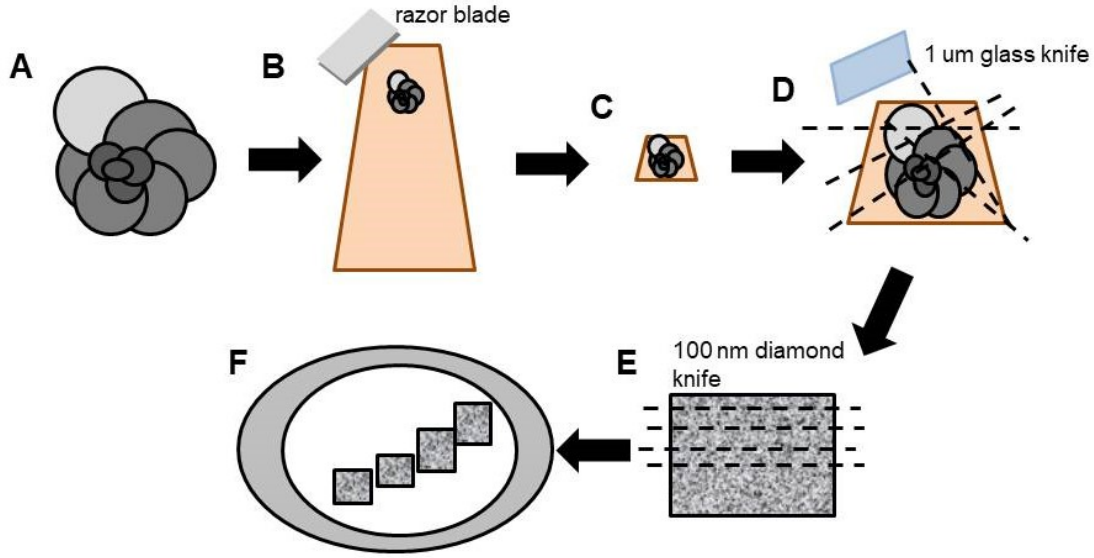

Figure 5.3. Schematic of thin-sectioning used on polymerized resin-embedded individuals of *Trochammina inflata* for TEM. Fixed individuals (A) were polymerized in Spurr's resin (B) and a razor blade removed the excess resin (C), then a glass knife was used to make 1 µm slices of the outermost chamber with cytoplasm, removing all the test wall (D). The trimmed slices were then cut to 100 nm thickness with a diamond knife (E) and the slice were mounted on a Formvar-coated slot grid (F) to stain and prepare for TEM.

The sections were stained with uranyl acetate (Uac) and lead citrate by immersing holding grids (Figure 5.3) in 2% Uac + 50% ethanol for 10 minutes. After three rinses in distilled water, the samples were dried and the grid was immersed in Reynold's lead

citrate for five minutes, followed by three rinses in degassed distilled water. Dried sections were examined individually using a FEI Tecnai-12 transmission electron microscope and images were captured using Analysis software.

5.2.5 Culturing experiments to validate live specimens

To determine the best way to recognise live foraminifera without use of stains, foraminiferal petri dish cultures maintained for 12 weeks were examined and counted weekly. A total of 90 5-cm diameter petri dish microcosms were used with three species (*Trochammina inflata, Miliammina fusca, Helenina anderseni*), providing 30 microcosms for each species. Each microcosm contained 10 living individuals in 5 ml of 20 psu filtered seawater to which a drop of filtered detritus was added weekly. Salinity and water levels were also adjusted weekly. The dishes were kept in ambient light and a constant temperature.

Every week, each dish was examined with a Zeiss stereomicroscope (10 – 40 x) and all living foraminifera were counted and dead individuals were removed. For species with translucent shells, arenaceous *Trochammina inflata* and calcareous *Haynesina anderseni,* living foraminifera were identified by presence of protoplasm and by sediment aggregated around the entire individual and/or the aperture. For the opaque arenaceous species *Milliammina fusca*, sediment accumulation around the test, especially at the aperture, and re-orientation of the specimen aperture-side down were the main criteria used.

At the end of the 12 weeks, all samples were stained with 2-3 drops of Rose Bengal, and 0.5 ml ethanol was added to each dish to confirm the assessment of live

condition. After 24 hours, any foraminifera with living protoplasm at the time of application should be stained a bright rose pink (Walton 1952). The final count of pink specimens was used to assess that all foraminifera remaining at the end of the feeding study were correctly classified as living (Supplement D-1).

5.2.6. Feeding trials with associated invertebrate meiofauna

To examine potential invertebrate meiofauna-foraminifera interactions, separate cultures were made that used foraminifera combined with meiofauna or small macrofaunal species. Petri dishes were prepared from mesocosm samples (Figure 5.1), and foraminifera and meiofauna were combined as shown in Table 5.1. Samples for this experiment were taken from selected elevational zones of the marsh mesocosm once in October, and once in February. Cultures were observed microscopically after 24 hours and 48 hours, including counts of individuals and notes on interactions between them, such as direct feeding or items in guts.

Table 5.1. Groups of feeding trials with paired foraminifera and meiofauna/small macrofauna at the start of the feeding experiments. Each petri dish contained foraminifera and a meiofaunal group (13 dishes with oligochaetes, 3 with polychaetes, 2 with gastropods, 4 with ostracods, 4 with soil mites). A schematic example of a petri dish (not to scale) with foraminifera and oligochaetes is shown to the left of the table.

# Oligochaetes	# Foraminifera
1	5
3	5
2	3
1	5
1	5
15	10
5	5
5	5
5	1
2	10
1	5
1	5
1	5
# Gastropods	**# Foraminifera**
10	8
1	1

# Polychaetes	# Foraminifera
1	5
1	5
1	5
# Ostracods	**# Foraminifera**
3	5
1	3
3	3
1	5
# Soil mites	**# Foraminifera**
1	1
1	5
1	10
1	5
# *T. inflata*	**# *M. fusca***
10	10

5.2.7 Biomass and abundance calculations of foraminifera and meiofauna

For background information on the biomass of foraminifera and associated meiofauna (defined here as animals of size 63 – 500 µm) within the sediment community of salt marshes, multiple 2.5 ml samples of salt marsh mud from Chezzetcook Inlet and each of the four high-salinity mesocosm zones were washed over 63 – 500 µm sieves. The sieved samples were fixed with ethanol and stained with 2 ml Rose Bengal solution, and then re-washed over a 63 µm sieve to remove residual Rose Bengal and ethanol after 24 hours. Individuals were counted and sorted into major taxonomic groups: foraminifera, nematodes, polychaetes, oligochaetes, ostracods, copepods, amphipods, isopods, fly larvae, and mites. The wet and dry weights were then recorded for each group of taxa

within each sample. The wet weights were measured after evaporation of excess water; dry weights were obtained after oven-drying at 65˚C overnight.

5.2.8. Data analysis

Results from feeding trials and culturing experiments are presented as qualitative observations. TEM work is also interpreted from images. Quantitative analyses (descriptive mean and standard deviation statistics) compared in-culture living counts to the final counts of those stained with Rose Bengal. Meiofaunal feeding trials are presented in table form. Biomass (mg) and abundance calculations are based on the mean and standard deviations of the *n* samples per zone (see Supplement D-2). Percents of biomass and abundances are based on the total of meiofauna plus foraminifera.

5.3 Results

5.3.1 General feeding observations and identifying living specimens

Of the agglutinated salt marsh foraminifera in this study, *Trochammina inflata* was the only species seen with an extended pseudopodial (rhizopodial) network that provided motility. Movement of the living specimens could be observed with a stereomicroscope, or inverted compound light microscope. *T. inflata* moved by orienting the aperture-side ventrally and pulling the test along the petri dish with extended pseudopodia at a unidirectional speed of up to 2 mm hr^{-1}. After one day, individuals were often up the sides of the 1-cm tall petri dish, or on the opposite side (50 mm). No lateral movement was seen in *Miliammina fusc*a or *Jadammina macrescens* but individuals were also commonly found congregated in pairs or small clusters (Figure 5.4), whether single or

multiple species were present (Figure 5.5A,B), indicating that slow, cryptic movement occurred. *Miliammina fusca* also displayed cryptic movement in re-orienting its test from horizontal to vertical (aperture-side down) position.

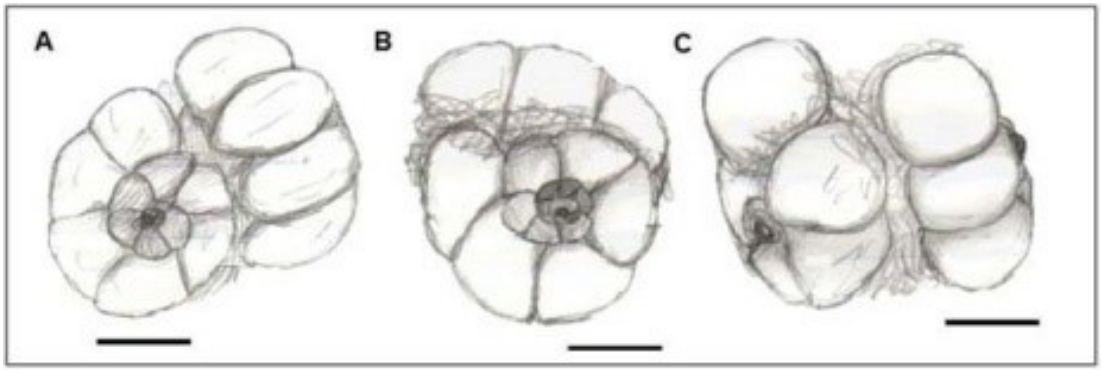

Figure 5.4. Sketches of the same two *Trochammina inflata* individuals in a petri-dish with filtered-detritus over a period of 6 hours. Detritus is common between the individuals and at the apertures. Scale bar = 100 μm.

Regardless of motility, a good indicator of living specimens with extended pseudopodia/cytoplasm was the anchoring of the foraminifera to the bottom of the petri dish. A gentle swirl of the dish revealed those "attached" to the bottom (living) and those that free-floated (dead). Another common indicator of live specimens was the presence of detritus at the aperture (Figure 5.2C; 5.5C) or covering the individual. After adding detritus to the living cultures, individuals covered themselves in sediment (becoming "feeding cysts") within 24 hours (Figure 5.5A, D, E). *M. fusca* often oriented itself aperture-side down (vertically) on the petri dish, with a bolus of detritus around the apertural opening. Clean specimens of *J. macrescens* became surrounded in a thin layer of detritus (Figure 5.5C) within 24 hours, with most particles concentrated at its aperture. When detritus-free agglutinated specimens of *T. inflata* were fed bacteria cultures, thin,

translucent whitish “clouds” would surround the entire test of the living foraminifera within 24 hours.

Calcareous species (e.g., *Elphidium williamsoni* and *Helenina anderseni*) have thin, shiny white, translucent tests and they were the easiest of the experimental taxa to distinguish as being alive. In large dishes of unwashed, unsieved mud, both species would be found attached to filamentous algae. Detritus-free specimens had alga-filled cytoplasm in many chambers except the terminal chamber. The cytoplasm was orange-brown in *H. anderseni* and greenish-brown in *E. williamsoni* (Figure 5.5 E – G). Test and organic linings of agglutinated species, especially *M. fusca,* were less transparent than the calcareous species. However, their cytoplasm-filled inner chambers were consistently darker than tests without cytoplasm viewed either under inverted light or direct light. The three agglutinated species had viscous, opaque white cytoplasm regardless of food source. Some living specimens that were damaged when moved by brush or pick showed this living cytoplasm oozing out of the cracks or holes.

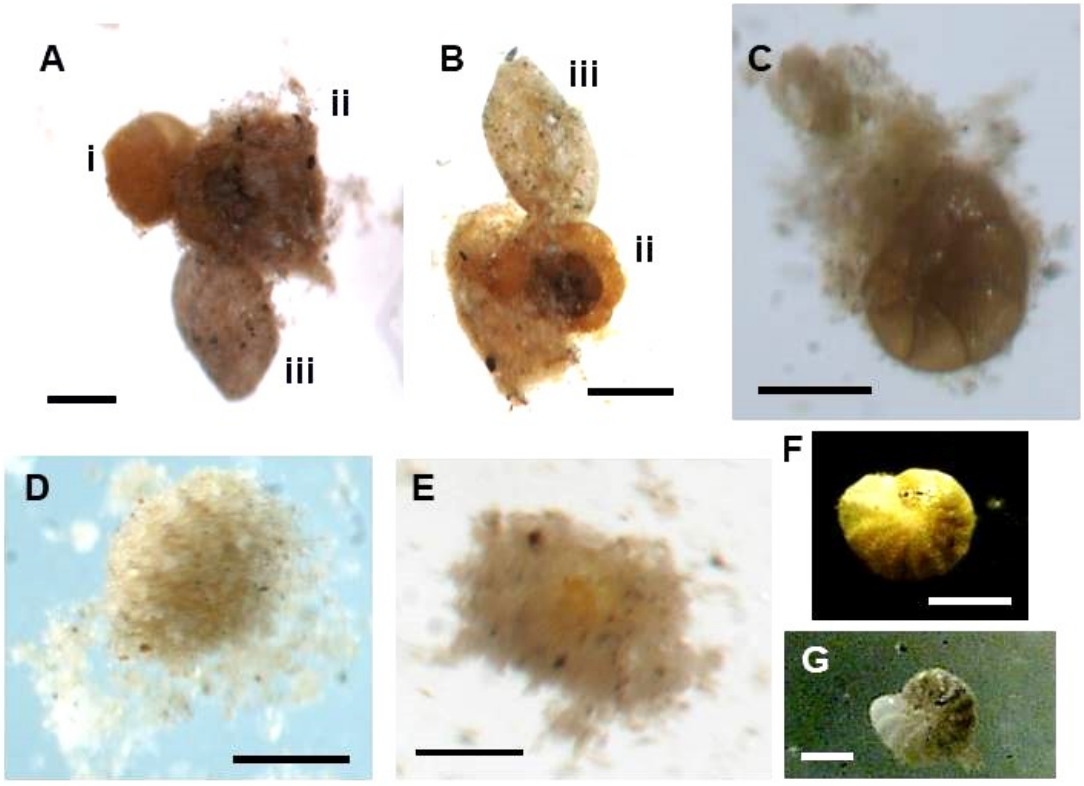

Figure 5.5. Stereomicroscope photos of living salt marsh foraminifera. (A) clumped *Helenina anderseni* (i), detritus-covered *Trochammina inflata* (ii), and *Miliammina fusca* (iii); (B) *M. fusca* top) and *T. inflata*, with detritus; (C) *Jadammina macrescens* with detritus concentrated around aperture opening; (D, E) *Helenina anderseni* covered in gathered detritus; (F, G) living *Elphidium williamsoni* with alga-filled yellow (F) or green (F) cytoplasm in all but terminal chambers. Scale bar = 100 μm.

Images of corresponding organic linings from the mesocosm foraminifera after removal of the test with acids (Frail-Gauthier and Mudie, 2014) show further details of fine structure and sometimes organic exudate from outer chambers (Figure 5.6).

Figure 5.6. Organic linings of foraminifera from T1-M (middle marsh). Top panel, Left: mid- focus showing mostly cytoplasm-filled chambers; Right: high-focus showing remnant external organic membrane, possibly part of a sticky mucous-like feeding network that assists in detritus gathering. Middle panel: Two dead specimens of *T. inflata* showing the organic lining structure and differences in micropore-structures in the chamber walls between terminal and inner chambers. Bottom panel: *M. fusca* with stained cytoplasm in chambers surrounded by a yellowish organic layer.

5.3.2 Transmission Electron Microscopy

TEM images of *Trochammina inflata* taken directly from the mesocosm show a variety of items in the food vacuoles including many bacteria in various stages of degradation, small detrital particles and degraded cellular material (Figures 5.7, 5.8). Not all thin slices showed cellular materials but digestive vacuoles were recognised as relatively large, light-coloured structures surrounded by a single membrane, whereas mitochondria and the nucleus are darker (denser contents) and have double membranes (e.g., Figure 5.7). Food vacuoles are surrounded by denser cytoplasm with blobs of unknown light and dark material (possibly perioxisomes or smaller vacuoles not used for digestion), and they often contain a mixture of items of various shapes and sizes (Figure 5.8).

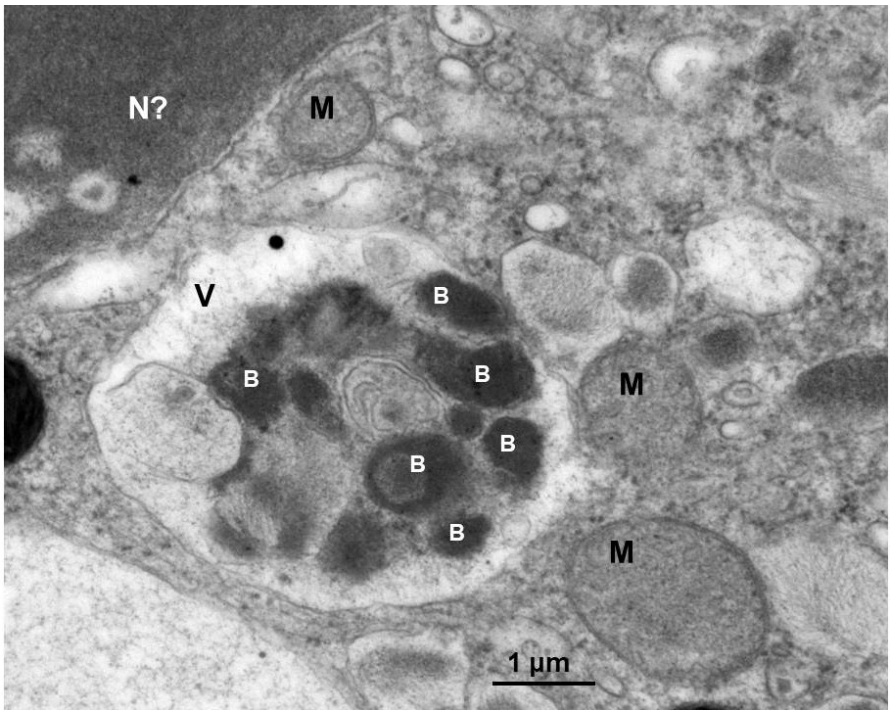

Figure 5.7. Section of direct-from-mesocosm *Trochammina inflata,* showing degraded bacteria (B) in a food vacuole (V). (M) – mitochondria, (N) – probable nucleus due to dense material and wide double membrane.

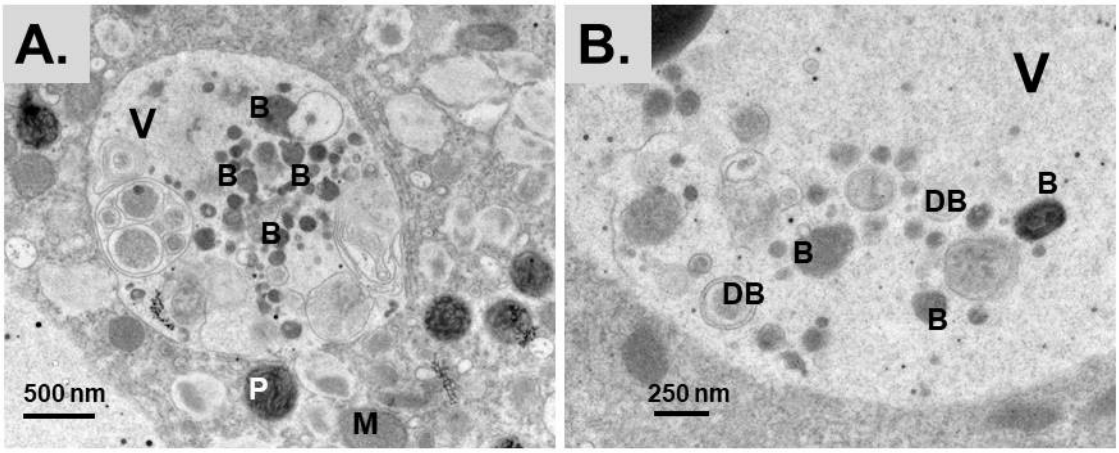

Figure 5.8. Sections of two different *T. inflata* food vacuoles (V), showing bacteria in various stages of degradation (B and DB). Perioxisomes (P) and mitochondria (M) also visible in A. A = 16,500 x magnification of one vacuole, B = 26, 500 x magnification of another vacuole.

These images confirm that the bacteria fed to the foraminifera were being drawn towards the test for possible consumption (Figure 5.9B). Specimens fed bacteria type 4 had vacuoles and intracellular material with well-preserved bacterial cells (Figure 5.10). Bacteria tend to lose their rod-shaped structure when they begin to degrade, giving rounded or asymmetrical shapes (Simpson, pers. comm.; Figure 5.11).

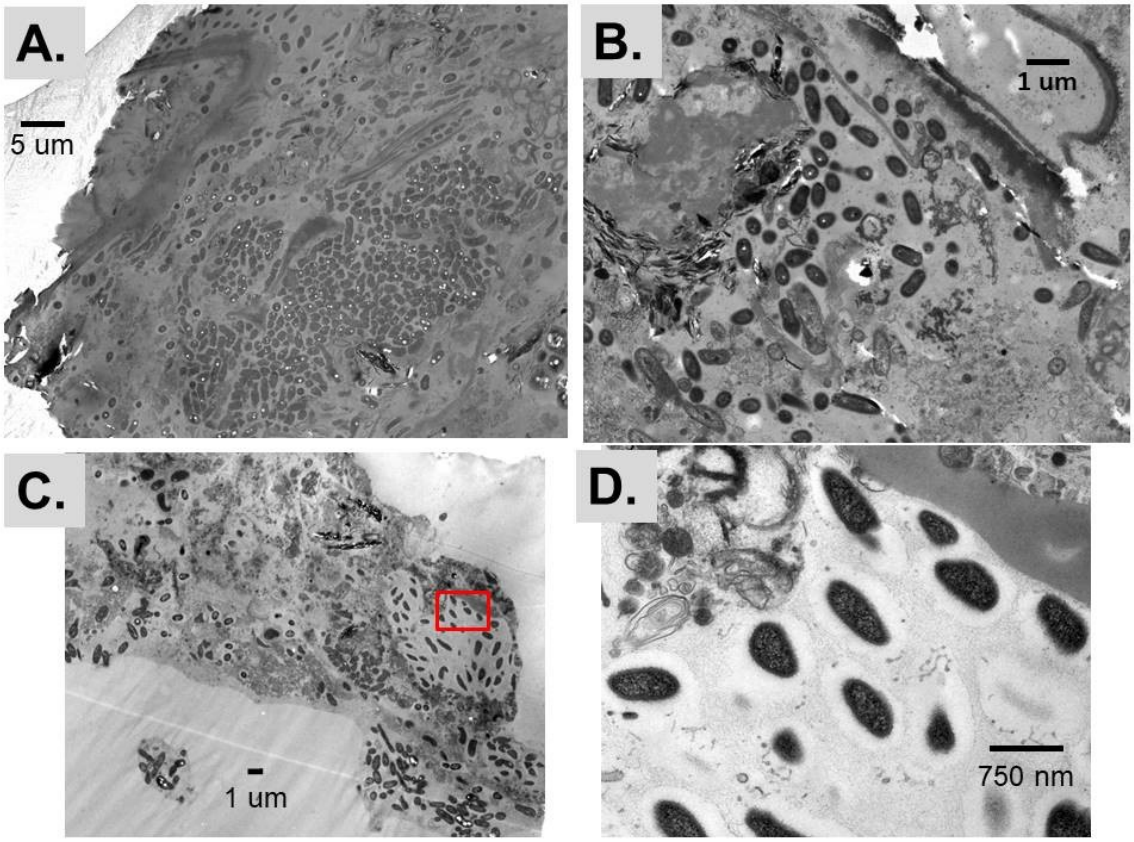

Figure 5.9. Intra-shell material of bacteria-fed *T. inflata* individuals. All bacteria are rod-shaped bacilla species. (A) Bacteria 1-fed foraminiferal slice. (B) Bacteria 3-fed foraminifera and extracellular material. (C) Bacteria-1 fed slice, with the red square expanded in (D) to show details of intact bacteria.

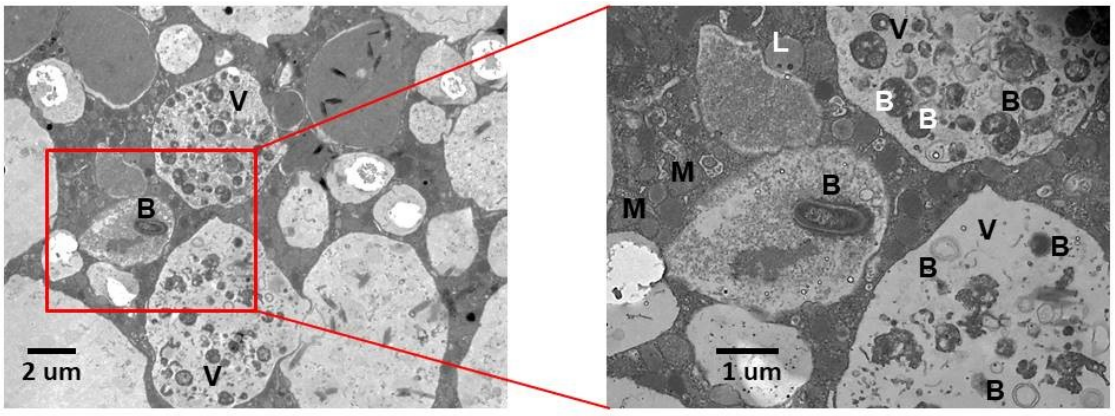

Figure 5.10. Vacuoles (V) in a bacteria-4 fed individual, showing undigested bacteria (B). Enlarged image shows details of the vacuole contents and bacteria, including a fully-digested state where only the linings remain (bottom right vacuole). The enlarged images also show mitochondria (M) and lipid droplets (L; used for energy storage).

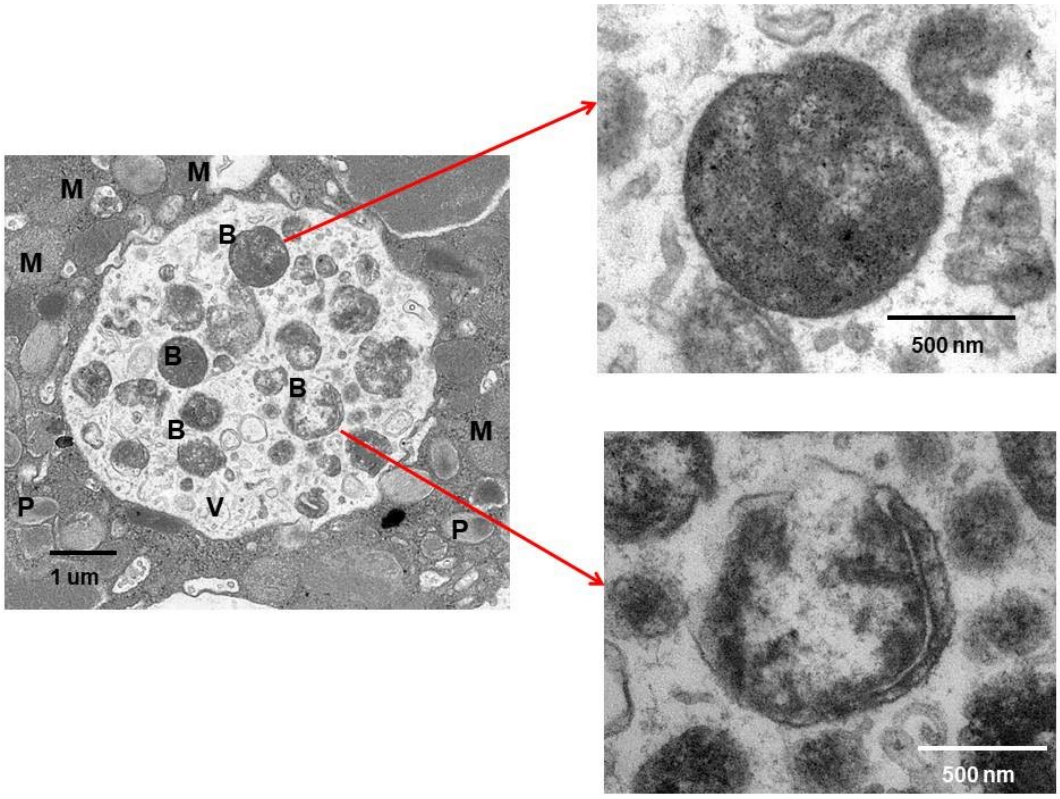

Figure 5.11. Left: Food vacuole (V) from a bacteria 4-fed individual, showing many bacteria (B). (M) – mitochondria; (P) – perioxisomes. Enlarged images show a non-degraded bacterium in cross-section (top center) and partially degraded bacterium (bottom center).

In general, the TEM images show definitive cellular material, with feeding vacuoles dominated by bacteria in bacteria-fed trials, and a mixture of bacteria and unidentifiable detritus in direct-from-mesocosm samples.

5.3.3. Determining living foraminifera in culture

After 12-week culturing experiments of observing multiple living foraminiferal species fed with filtered detritus, Rose Bengal was used to quantifiably evaluate the counts of living foraminifera in cultures of *T. inflata*, *M. fusca* and *H. anderseni*. Results of culture-determinant *in vitro* counts versus Rose Bengal-determinant living (*in vivo)* counts are given in Table 5.2.

Table 5.2. Counts of observed living foraminifera after a 12-week culturing experiment compared to counts after staining with Rose Bengal. In the "Count error" column, a negative number means **fewer** foraminifera were stained with Rose Bengal than originally counted in culture; a positive number means that the stained count gave **more** living foraminifera than originally counted in culture. SD = standard deviation. See Supplement D-1 for all numbers used to calculate values here.

Species	Live Count (original count)	Rose Bengal Stained Count	Count error per dish	Average Percent Difference	Conclusion
Helenima anderseni	130 total (4.48 per dish; SD 1.98)	131 total (4.52 per dish; SD 1.88)	-1 to +3; SD +0.03 per dish	2.97% more living; SD 0.31	Rose Bengal shows more living than counted.
Trochammina inflata	141 total (4.7 per dish; SD 1.78)	128 total (4.27 per dish; SD 1.6)	-2 to 0; SD -0.43 per dish	8.27% fewer living; SD 0.13	Rose Bengal shows fewer living than counted.
Miliammina fusca	182 total (6.1 per dish; SD 1.66)	123 total (4.1 per dish; SD 2.48)	-6 to +1; SD -1.97 per dish	33.9% fewer living; SD 0.35	Rose Bengal shows far fewer living than counted.

Overall, Rose Bengal correctly estimated living counts in calcareous individuals with 130 of 131 individuals being correctly identified as living using Rose Bengal (Table 5.2). For agglutinated species, counts based on *in vitro* observations showed more living individuals than stained; and *M. fusca* were the least successfully identified, with *in vitro* observations over-estimating living specimens by over 30%. Key determinants for identifying living foraminifera in cultures, without disturbing or killing them, are listed in Table 5.3.

Table 5.3. Summary of non-terminal ways for identifying living foraminifera in cultures based on all feeding and culturing experiments performed over the course of this study.

Non-terminal methods for determining living agglutinated foraminifera include:
1. presence of detritus or sediment balls sustained by living streams of cytoplasm and/or pseudopodia 2. detritus or sediment at the aperture opening 3. adherence to the bottom/sides of the petri dish 4. movement over a short period of time (<24 hours) 5. presence of visible pseudopodial networks seen stereomicroscope 6. "fuzzy" appearance because of small amounts of cytoplasm leaking from micropores 7. opaque appearance in contrast to translucent tests as seen in inverted light 8. orange-brown or greenish-brown-filled tests of calcareous species 9. congregation of individuals (Figure 5.4, 5.5 A,B).

5.3.4. Meiofaunal feeding trials

The 48-hour feeding experiments with meiofauna were less successful than the feeding trials with detritus and bacteria. No direct feeding observations were noted in the meiofauna experiments, but 6 of 27 petri dishes had missing individuals (Figure 5.12; foraminifera, ostracods, oligochaetes), which could indicate that some cannibalistic or inter-species feeding took place.

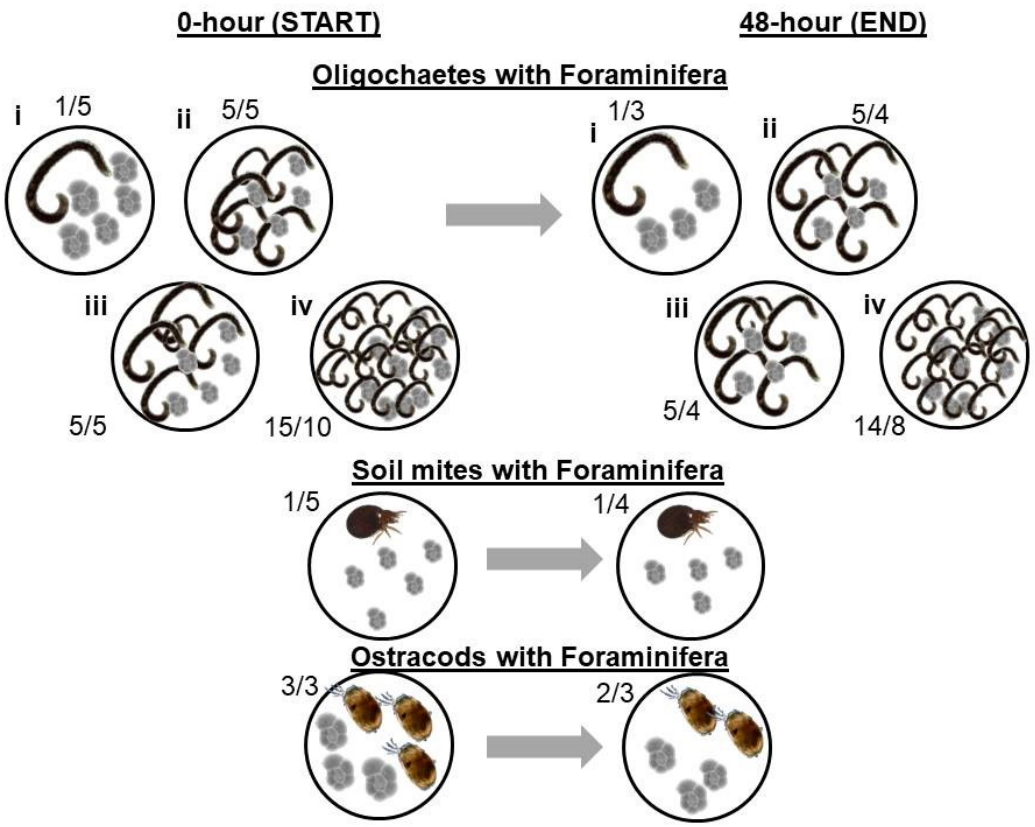

Figure 5.12. Results after 48 hours of meiofauna/foraminifera feeding trials for top: oligochaetes (4 dishes: i to iv); middle: soil mites, and bottom: ostracods. Number of meiofauna and foraminiferal specimens at the start (0-hr), and end (48 hours) are depicted for each dish and count proportions are enumerated by fractions.

5.3.5 Biomass and abundance calculations

Multiple 2.5 ml samples of 63 – 500 μm were counted from each zone of the mesocosm (Table 5.4). Foraminifera are not only the most abundant, but also contribute to the most biomass of total meiofaunal organisms. In the mudflat, foraminifera account for almost half of the meiofaunal abundance (49%) and almost one quarter of the meiofaunal biomass in the sediment (23.7%). The dominance of foraminifera increases throughout the higher elevations of the marsh, exceeding an average of 75% in both abundance and biomass in the middle and high zones (Table 5.4). After foraminifera, nematodes dominate meiofaunal abundance in the mudflat (20%) and low marsh (11%), and soil

mites dominate in the middle (14.2%) and high marsh zones (7.5%). Flatworms (39%) and oligochaetes (28%) have the highest biomass after foraminifera in the mudflat and low marsh, respectively. Soil mites have the biggest weights of the meiofauna in the middle (9.3%) and high marsh zones (10.1%; Table 5.4).

Table 5.4. Mean abundance and biomass values for multiple 2.5 ml 63 – 500 μm samples of marsh sediments from each zone (mudflat through high marsh) of the high-salinity (T2) mesocosm marsh, from mudflat through the high marsh. The number of replicates for each zone is given in parentheses for each zone. Standard deviation values are given as ±. Average percentages of foraminifera for each zone are shown in the bottom row. See Supplement D-2 for all data.

	Abundance	Dry weight (mg)	Abundance	Dry weight (mg)	Abundance	Dry weight (mg)	Abundance	Dry weight (mg)
Marsh Zone	**Mudflat (6)**	**Mudflat (6)**	**Low (7)**	**Low (7)**	**Mid (5)**	**Mid (5)**	**High (4)**	**High (4)**
Foraminifera	157.2 ±67.4	3.8 ± 3.1	657.9 ± 194.4	12.8 ± 4.9	624 ± 216	6. 2 ± 2.5	477.5 ± 103.1	4.7 ± 2.1
nematodes	64.3±55.6	0.7 ± 0.4	96.1 ± 67.5	1.8 ± 3.6	29.4 ± 33.4	0.4 ± 0.3	20.8 ± 18.7	0.3 ± 0.5
ostracods	42 ± 28.4	1.3 ± 1.5	5.9 ± 4.5	0.2 ± 0.2			1	0
polychaetes	5 ± 6.7	0.3 ± 0.4	9 ± 6.9	0.2 ± 0.2	7.5 ± 5.4	0.3 ± 0.3	7.7 ± 4	0.2 ± 0.1
oligochaetes	6 ± 4	0.03 ± 0.06	13.9 ± 8.2	6.2 ± 14.8	6.4 ± 4.6	0.06 ± 0.05	15.7 ± 9.3	0.2 ± 0.2
copepods	23.2 ± 15.5	2.2 ± 3.4	62.4 ± 43.2	0.5 ± 0.4	9.8 ± 6.1	0.3 ± 0.5	13.7 ± 12.4	0.07 ± 0.1
midge larvae	19.3 ± 15.6	0.97 ± 0.8	5.3 ± 4.4	0.3 ± 0.3	3	0.2	1	0
soil mites	2 ± 1	0.4 ± 0.4	11.5 ± 4.3	0.2 ± 0.1	113 ± 50.9	0.8 ± 0.7	43.3 ± 29.6	0.6 ± 0.5
flatworms	2	0	1	0				
amphipods			2	0				
% foraminifera	**49%**	**23.7%**	**76%**	**57.6%**	**78.7%**	**75.8%**	**82.3%**	**76%**

5.3.6. Summary of Results

Overall, we use nine non-terminal methods to help validate living specimens of three agglutinated and two calcareous species of salt marsh foraminifera. The best method is directly seeing millimetre-scale movement or pseudopodial networks, but those were only observed in *T. inflata*. In *J. macrescens* and *M. fusca*, aperture-down orientation and accumulation of detritus around the aperture or all over the test on clean specimens were used. In all species except *M. fusca*, the presence of opaque cytoplasm within the test was also a good indicator of living specimens, especially for the calcareous species that had colourful (green, orange-yellow) cytoplasm in comparison to the test. TEM feeding experiments with *T. inflata* show no preference for food type, though bacteria are the most common item in food vacuoles of *T. inflata*. In culture dishes, there is no preference for the food type offered, and no petri dish had reproductive events, or significant chamber additions (growth) over the 12-week periods. Meiofaunal feeding experiments also had no direct observation of feeding, though the loss of specimens in the dish is an indirect conclusion that feeding did take place. In salt marsh samples, foraminifera make up almost half of the meiofaunal abundance in the mudflat, but more than 75% in the low, middle, and high marsh zones. They account for less than 25% of the biomass of this size fraction in the mudflat, and over 50% of the biomass in the other zones.

5.4 Discussion

To reiterate, the three main objectives of this study are interconnected, but primary goals are as follows: 1) to find low-maintenance, inexpensive, non-terminal methods for distinguishing living salt marsh foraminifera in a microcosm culture setting; 2) to use

Transmission Electron Microscopy (TEM) to investigate digestion in the agglutinated foraminifera, *Trochammina inflata*; and 3) to investigate feeding habits of key salt marsh foraminifera and associated meiofauna using microcosm culture experiments.

5.4.1 Non-terminal criteria distinguishing living foraminifera

There is a large literature on criteria for distinguishing living foraminifera using non-terminal methods (Arnold, 1974; Bernhard, 2000) but information on the agglutinated species that characterise elevational zones of salt marshes is sparse. The possibility of sampling from a salt marsh mesocosm allowed weekly monitoring of feeding trials and examination of the feeding habits of two agglutinating and one calcareous marker species over a period of 12 weeks. This time-series study depended on establishing non-destructive methods to distinguish living from dead foraminifera for feeding trials of the marker species in microcosm cultures after removal from the marsh mesocosm. Finding quick and effective ways for picking out living foraminiferal individuals from stock samples (Figure 5.1) is also important for the feeding experiments used in TEM work.. Previous studies have primarily employed cytoplasm colour and bolus formation as living criteria. However, cytoplasm colour only works for calcareous species which have translucent tests (Bernhard, 2000), and often cannot be seen within agglutinated salt marsh species. An apertural bolus can persist long after death (Arnold, 1974) or be a post-mortem release of sticky cellular material, not a feeding structure (Langer and Gehring, 1993). However, for salt marsh agglutinants in 12-week microcosm experiments, we find the apertural bolus to be one of several valid criteria for determining live specimens. We determined that after gently removing the bolus every week, it would re-form in living specimens within 24 hours.

We have established nine criteria for distinguishing living specimens of five key salt marsh indicator foraminifera species, giving most attention to three agglutinated species not previously studied (Table 5.3). The applicability of individual criteria varies among the species. Our study shows that the key marsh foraminifera are not highly mobile, with the largest species, *Trochammina* moving fastest, at a rate of c. 2 mm/hr (50 mm/d). Cryptic movement expressed as clumping and test re-orientation over a period of 24 hours was observed in the other marsh agglutinants. The faster movement of *T. inflata* may be related to the fact that it is wider across the umbilical-spiral plane compared to *J. macrescens* (Figures 5.4 and 5.5), so aperture-side-down orientation and movement by pseudopodial traction would be easier. The much larger apertural opening in *T. inflata*, compared to the small pore-like aperture openings in *J. macrescens* may also explain the faster movement (Loeblich and Tappan, 1988 – *T. inflata*: pl. 129, figs. 20–23; *J. macrescens*: pl. 133, figs. 7–13). Other foraminifera, such as infaunal *Pseudorotalia gaimardii* and epifaunal *Quinqueloculina lamarckiana* have been recorded moving at rates of less than 50 μm min^{-1} (0.3 mm $hour^{-1}$) in or on sediments, but move twice as fast on smooth surfaces as in petri dishes (Kitazato, 1988; Travis and Bowser, 1991). This extrapolates to less than 10 mm day^{-1} (20 mm day^{-1} on smooth surfaces) but recent studies of calcareous estuarine forms (e.g., *Ammonia tepida* and *Haynesina germanica*) show faster movements of 2 – 8 mm hr^{-1} (Seuront and Bouchet, 2015). A form and function relationship between activity and test shape and size could help explain why some species move more readily and more quickly than others. For example, the larger apertural opening and higher number of pseudopodia in *T. inflata* show that even though it is a wider, more bulbous specimen than *J. macrescens*, it is able to pull itself on the

sediment surface much faster than expected for its test shape and size. This theory was validated in other species by Kitazato (1988), where having more and/or larger pseudopodia gives faster movement than expected in large species. For *T. inflata*, the movement in culture dishes is therefore probably faster than would be expected in loose, fine sediments in the salt marsh, but it is nevertheless likely to be much faster than for the other agglutinants studied here. Visible motility alone cannot be used as the only factor for distinguishing living from dead foraminifera in cultures. Temporary dormancy can also terminate movement (Arnold, 1974), so the other non-terminal methods have to be used to distinguish living specimens.

Other practical criteria for two species studied — *T. inflata,* and *J. macrescens*— are presence of thick, healthy tests containing visible protoplasm within one or more chambers. Transmitted light microscopy can be used to confirm this interpretation by examination of the organic lining contents after acid removal of the agglutinated test (Figure 5.6 A,B). The miliolid *M. fusca*, however, has a test made of much larger sediment grains than the other two trochamminid agglutinated species, and with inverted light microscopy, we determined that light only penetrates the tests of small (<100 μm) specimens. Most specimens of *M. fusca* taken from the Chezzetcook marsh mesocosm were over 200 μm in length; therefore, seeing cytoplasm within the test was not a practical method of determining life status for this taxon.

For species with only cryptic movement, such as *M. fusca*, the best living indications are the rapid attachment (<1 hour) to the bottom of the dish or to algal strands and other large detritus particles, and/or the presence of a detrital bolus at the aperture. In experimentally-grown cultures of *M. fusca* by Goldstein and Alve (2011), a “rough”

granular appearance was noted in fine-grained (<53 μm) sediment. Stereomicroscope examination revealed the grains to be detrital "feeding cysts". These easily detachable, sticky envelopes are a mixture of detritus, foraminiferal cytoplasmic material, and microbiota to help the foraminifera obtain food (Heinz et al., 2005). These "feeding cyst" structures are normally found at the aperture but can cover the entire organism and have been observed in deep sea unilocular species and in the estuarine calcareous *Ammonia beccarii* (Goldstein and Corliss, 1994). According to Heinz et al. (2005), these "cysts", made through pseudopodial collections of surrounding detritus, are for food gathering, but in some cases, they may have reproductive importance or be a normal part of test building. Regardless, detritus around the specimen or at the aperture was the main determinant of vitality for *M. fusca* and is also applicable for specimens of the other four salt marsh species in this study (see sticky detrital envelopes in Figure 5.5).

Because most individuals of species other than *T. inflata* did not visibly move in the petri dish, the orientation of a specimen was also used as a living determinant. Most individuals orient themselves aperture-side-down on sediment or aperture-side-at-food-source for detached surfaces such as plant fragments or algal filaments. As a result, specimens were oriented at an angle, and not lying flat in the dish. This ventral apertural orientation was also noted in Travis and Bowser (1991) with unilocular *Allogromia* sp. In *M. fusca*, the aperture is located on one end of the oblong organism (Loeblich and Tappan, 1988, pl. 40, figs. 4–7) which may necessitate living specimens often being oriented "downward". The aperture in this species is small for the size of the specimen, possibly accounting for cryptic movements using pseudopodia extruded from the opening. Langer and Gehring (1993) studied positioning of *Textularia bocki* on seagrass

and concluded that glycosaminoglycan secreted by pseudopodia was used for bacterial farming, forming networks to collect detritus and associated microbiota. Our new experiments show for the first time that agglutinated salt marsh species also secrete adhesive cellular material around the tests, probably for gathering (and farming) food particles while relatively immobile in the salt marsh sediment.

5.4.2. Using Rose Bengal to Validate Live Foraminifera

Most previous studies of modern foraminifera use specimens from surface scrapings where samples are sieved then stained to determine the proportion of living specimens in assemblages as described in Chapter 2. These studies most commonly use Rose Bengal cytoplasm stain after fixing with formalin and/or ethanol (Walton, 1952). However, Rose Bengal staining is known to over-estimate living foraminifera. Bernhard (2000) gives an extensive review of all known terminal and non-terminal methods for determining live foraminifera, including the debatable use of Rose Bengal, and later (Bernhard et al., 2006) concludes that the clearest non-terminal methods are those that use fluorogenic probes.

Comparison of the living counts using one more of the nine criteria (Table 5.3) versus Rose Bengal stain counts shows variable results among three temperate salt marsh taxa. The stain overestimates living specimens for the calcareous species *Helenina andersoni* by only 3%, underestimates living numbers for the agglutinant *T. inflata* by c. 8%, and *M. fusca* by up to c. 34%. The large discrepancy for *M. fusca*, however, possibly includes errors in determining living specimens for cultures of these large, thick-walled, slow moving, detritus-covered foraminifera where cytoplasm content could not be

gauged. Although *M. fusca* has a thicker test, Rose Bengal absorbs easily into live cytoplasm not just inside the chambers, but over the outside of the test, making the entire specimen bright pink. This may be because of the "fuzzy" organic linings seen in Figure 5.6 (bottom panel), which allows cytoplasm to come out of micropores over the entire body. This also may help with the specimen-covered detritus "glue" previously discussed and forms the "feeding cyst" structure.

5.4.3. Results of Feeding Trials and TEM

Feeding of two agglutinated and one calcareous salt marsh species was assessed for the first time by observing direct feeding and by indirect observations of common feeding modes, and by using TEM to determine the contents of digestive vacuoles in *T. inflata* after feeding trials. Feeding trials conducted over 12 weeks showed no difference in terms of growth, death, or reproductive events between cultures that were fed filtered detritus, cultured salt marsh bacteria, or unaltered mesocosm mud. The detritus itself may or may not be consumed, as many particles in the food vacuoles could not be explicitly identified. Bacteria, in various stages of degradation, were the most common particles in vacuoles observed with TEM. Therefore, we conclude that detritus primarily gives a physical medium to help grow and gather bacteria on the surface of the foraminiferan's sticky, energy-rich adhesive (Langer, 1992), from which particles are taken into the shell chamber cytoplasm via the extended pseudopodial nets. According to Bowser et al. (1985), vacuoles in pseudopodial/reticular networks outside the shell lack digestive enzymes, so digestion of the particles only begins once inside the terminal chamber. Anderson and Lee (1991), however, suggest that digestion can begin before material even enters the shell, which would make TEM analyses of intra-shell material dependent on

the process of digestion. Our TEM images of *T. inflata* show that bacteria are present inside the first chamber but outside the cytoplasm (Figure 5.9), and that bacteria are present inside food vacuoles (Figures 5.10–5.11), indicating that most digestion in this agglutinant species occurs inside the test.

Other cytological studies of foraminifera have not examined agglutinated species, except for unilocular *Allogromia* sp. (Bowser et al., 1985). In multi-chambered species examined, the terminal chamber and pseudopodial cytoplasm are often filled with many food vacuoles (Bowser and Travis, 2002). All other studies have examined calcareous species, such as *Ammonia beccarii* (Goldstein and Corliss, 1994). Diatom frustules and bacteria with clay particles have been found inside food vacuoles in terminal chambers. Bacteria species are digested rapidly, and not seen in other chambers (Goldstein and Corliss, 1994). If the food is too large to be engulfed by phagocytosis, the pseudopods can shear off smaller pieces, which travel into the shell via large vacuoles, where they will join with acidic lysosomes to start the digestion process inside the test (Anderson and Lee, 1991). This would mean that in our agglutinated species, larger phytodetrital particles could be broken apart before entering the foraminiferal test, but no digestion occurs until they reach the intrashell cytoplasm.

Many previous studies have concluded that bacteria are the main food for benthic species (Bernhard and Bowser, 1992; Langer and Gehring, 1993; Goldstein and Corliss, 1994; Mojtahid et al., 2011) though algal food has most commonly been fed to foraminiferal cultures for decades (e.g., Myers, 1943; Arnold, 1954; Muller, 1975, and reviewed in Anderson et al., 1991). In culture studies of three species of *Allogromia*, *Ammonia*, and *Spiroloculina*, less than five of 28 different species of algae were

consumed significantly, whereas large numbers of bacteria were consumed (Muller, 1975). Two living calcareous species, *Ammonia tepida, Haynesina germanica,* have an orange-brown cytoplasm colour, probably from ingested bacteria and detritus because they consume >25,000 bacterial cells per hour (Mojtahid et al., 2011 but turn green when fed *Chlorella*, a unicellular alga with green pigments (Moodley et al., 2000). *Elphidium williamsoni* is often epiphytic on algal strands and is a greenish colour due to ingested chlorophyll pigments (Figure 5.5G). Bacteria-fed specimens often have a "cloudy" appearance on the outside because of the concentration of bacteria and cytoplasm that is a visual confirmation of feeding (Mojtahid et al., 2011). This secreted material is also rich in glycosaminoglycans that provide a high-energy substrate for bacteria and fungi to be "farmed" by the calcareous foraminifera (Langer, 1992). For saprophagous and bacterivorous deposit feeders, bacterial "farming" provides the nutrition needed to support rapid reproduction and growth (Muller and Lee, 1969). This behaviour may account for the high numbers and small-scale patchiness of foraminifera due to winnowing of phytodetrital pieces seen in salt marsh sediments.

In our cultures, *T. inflata* oriented itself with downward-directed pseudopodia emerging from the large aperture and *M. fusca* oriented aperture-down, sub-vertical, with a small horseshoe-shaped aperture. This is in accord with the feeding observations of the textularid agglutinant *Textularia bocki* on seagrass leaves (Langer and Gehring, 1993). There are also reports of this orientation for *M. fusca* and *J. macrescens* on dead leaves of salt marsh plants (Alve and Murray, 1999).

The collection of detritus around the aperture during feeding is not exclusive to salt marsh foraminifera but conforms to earlier observations (Goldstein and Corliss,

1994) for deep-sea calcareous rotalid taxa — planktonic *Globobulimina pacifica* and benthic *Uvigerina peregrina* — and for the shallow-water benthic *Ammonia beccarii*. The observations of aperture-down re-orientation in *M. fusca* and its apparent lack of lateral mobility have not been previously reported and are possibly important with regard to its patchy habitat in salt marshes where it is concentrated around decaying plant stems and leaves of low and middle marsh zones. The cryptic motility of the salt marsh foraminifera may reflect the abundance of available phytodetritus and associated decomposition by bacteria such as *Erythrobacter*, *Agrobacterium* and *Roseobacter* (Buchan et al., 2003). High year-round detrital food availability avoids dependence on seasonal algal blooms in a temperate marsh with winter ice cover, and would diminish need for energy to be expended on motility. An additional consideration is that rapid changes in salinity can affect the microtubules in the pseudopodia, which can decrease their movements and ability to "hunt" for food (Pascal et al., 2008). Therefore, in Chezzetcook Inlet (and mesocosm), short-term tidal fluctuations that change sediment-water interface salinity many times per day may negatively impact the use of pseudopodia for actively gathering food. This would cause the foraminifera to be highly dependent on the patchiness of resources, and rapid growth of feeding "cysts" would be most energy-efficient in the sediments.

The large population sizes of essentially sessile detritus-feeding organisms suggest that they have crucial roles in the salt marsh food web (Chapter 3). This is because these agglutinated forms follow the high patchiness of phytodetritus from salt marsh plants and bacteria. This helps transfer energy up the food web by providing

energy-rich patches for the larger meiofauna and small macrofauna that consume foraminifera through deposit feeding in the salt marsh sediment.

Lopez et al. (1979) have shown that in some calcareous species on salt marsh mudflats, including *Elphidium williamsoni*, kleptoplasty plays an important role in their nutrition, and the photosynthetic activity from symbiotic chloroplasts can account for 40–100% of the respiration in *E.williamsoni*. This species may "farm" the symbionts by retaining the chloroplasts from microalgae after immediately digesting the other cellular components (Goldstein and Alve, 2011). The color of *Helenina* suggests that it employs a similar feeding strategy. Chloroplast retention has the advantage of supplying nutrients from photosynthesis during conditions of adequate light, but it would requires thin tests not available in agglutinant foraminifera. Kleptoplasty may also explain why the salt marsh calcareous species are often found epiphytically on algae at the marsh surface, and only in smaller numbers in the salt marsh sediment. For low – high marsh agglutinated taxa, living within the sediment surface would also diminish photosynthetic ability within their thick tests. Another consideration is that calcareous species such as *Ammonia tepida* are known to prefer microphytobenthos (diatoms) when at the surface or are epiphytic on algae, but will switch their diet to bacteria if found within the shallow sediments (Pascal et al., 2008).

All observations in this study, however, were constrained by the artificiality of the *in vitro* light conditions and the constant temperature of the experiments in microcosm settings. In order to examine individual, living foraminifera *in situ*, Arnold (1974) designed a field microscope but this has limited practical application for a tidal salt marsh. Other laboratory study methods have used sediment samples in plexiglass trays

(Arnold, ibid.), where it was seen that buried living foraminifera soon emerged at the sediment surface, implying that this is their preferred habitat. However, removal from salt marsh sediments that are a crucial part of their natural biological/ecological setting is a problem highlighted by Murray (2006). To precisely define the niches for benthic foraminifera, one needs to know the specific responses to exact abiotic and biotic conditions and this requires removal from salt marsh sediments.

Study of the feeding relationships in foraminifera also has implications regarding previous stable isotope interpretations from paleoenvironmental studies. The biochemical signature from the foraminiferal tests may reflect their diet more clearly than abiotic factors of their environment (Mojtahid et al., 2011). Commonly, the abiotic drivers are considered to be salinity and shoreline elevation (i.e., submergence/exposure time). Selective feeding on the particulate organic matter (POM) from phytodetritus by benthic foraminifera on the western Antarctic Peninsula shelf led to the conclusion that different food sources lead to different fatty-acid biomarkers in the foraminiferal tests (Suhr et al., 2003). Another example comes from benthic foraminifera in San Francisco Bay estuary that responded to bloom patches of POM much faster than other meiofauna, and the distributions and population assemblages of foraminifera here are probably more related to food inputs than they are to other environmental parameters (Lesen, 2005). Therefore, the stable isotope chemistry of foraminiferal tests may reflect different diets and roles within the ecosystem, more than environmental or taxonomic differences (Suhr et al., 2003).

In our stable isotope studies (Chapter 4), POM had isotopic signatures between -19 (mudflat) and -21‰ (high marsh) $\delta^{13}C$, algae were between -13 and -15‰ $^{\delta 13}C$,

Spartina values between -12 and -13‰ $\delta^{13}C$, and terrestrial C_3 plants between -25 and -27 ‰ $\delta^{13}C$. Values of foraminifera ranged between c. -15 and -25 ‰ $\delta^{13}C$, with more depleted values in the middle and high marsh zones than those in the low marsh and mudflat (Figures 4.6 – 4.7). Although we do not have isolated bacterial isotopic signatures, our POM measurements would include bacteria. Other studies have shown estuarine bacteria to have a large range of isotopic values, depending on their immediate environment. For example, in culturing experiments, bacteria grown around decaying *Spartina* had values close to the *Spartina* itself (-11‰ $\delta^{13}C$), and those close to C_3 terrestrial plants had values c. -27‰ $\delta^{13}C$ (Coffin et al., 1989). However, in natural isotope studies, it is difficult to quantify the specific signature of bacteria in sediments, because of the amount needed to affect the POM (Ember et al., 1987). Regardless, the sediment POM and foraminiferal signatures reflect the transition from marine (higher values) to the terrestrial sources (lower values), which has implications for interpreting paleo-sea levels and -salinities in areas where salt marsh cores are not ground-truthed to modern analogs.

The culturing work we have carried out on the under-studied and yet dominant species of foraminifera in salt marsh sediments begins to fill in some previous blanks in understanding the motility, diet, feeding behaviour, and resilience of these organisms from three widely differing taxonomic groups: trochamminids, miliolids and rotalids. Follow-up experiments with a waterproof fibre-optic system to allow observations in the marsh mesocosm setting would be useful to determine how in-situ behaviours differ.

Other future work could involve different feeding experiments with different food sources, and different species of agglutinants, especially for the TEM work. We used

only *T. inflata* because of its large size and relatively thin test and active life habits. Bacteria were present in vacuoles of field-fed and bacteria-fed cultures. Future studies could examine detritus with all bacteria removed by heat-treatment. Other trial food sources should include species of diatoms and filamentous green algae, to see if salt marsh agglutinants consume microphytobenthos as commonly found in calcareous mudflat forms. Additionally, looking at feeding vacuoles of both *J. macrescens* and *M. fusca* would determine if all dominant salt marsh agglutinants are bacterivorous detritivores, or if they preferentially consume other resources. Studies of *J. macrescens* show that has a complex wall structure, but vacuole contents were not studied (Allen et al., 2000). Food preference in these abundant agglutinants has significance for the remineralizing of nutrients in the salt marsh sediment (Lesen, 2005), because foraminifera as a whole have a wide variety of feeding modes. Past studies have not determined if different habits are species-specific, or characterise functional-groups such as salt marsh agglutinants.

5.4.4 Abundance and Biomass: Implications of Foraminiferal Interactions with Meiofauna

Although we never witnessed this, some species of foraminifera are thought to be carnivorous, which could have direct impacts on the meiofaunal ecology of the salt marsh. For example, *Ammonia tepida*, normally a deposit feeder (bacteria and algae) has been known to consume nematodes, copepods and gastropod larvae (Dupuy et al., 2010). Although our feeding studies showed no direct feeding interactions of *T. inflata* and *M. fusca* with meiofauna (Table 5.1), it is possible that foraminifera can ensnare and consume small meiofauna. Foraminifera cannot move fast enough to actively hunt down

prey, but in sediments where nematodes are almost equally abundant, it is considered highly likely that foraminifera could digest meiofaunal material (Dupuy et al., 2010). In salt marsh and mudflat sediments, foraminifera are often the dominant meiofaunal species in terms of biomass and abundance (Table 5.4), and they form small-scale patches due to their limited mobility (Chandler, 1989). Because of this, foraminifera can rapidly deplete microbial resources (bacteria and phytodetritus), causing severe competition with other meiofauna (nematodes, copepods) in the same trophic role as foraminifera. Abundances as low as 100 per cm^3 can remove half of the sediment's food resources (Chandler, 1989).

The rapid consumption of bacteria and phytodetritus by foraminifera and interaction with other meiofauna in the salt marsh sediments is probably key in foraminiferal distribution, both on a small-scale and throughout the zones. At Chezzetcook Inlet, plant detritus is much more abundant in the middle and high marsh zones than the lower and mudflat zones (pers. obs.) and here, phytodetrital bacterivores such as *Trochammina*, *Jadammina* and *Miliammina* form dense populations (>75% of abundance and biomass) that outcompete other meiofaunal organisms. In the lower salt marsh zones, calcareous species begin to dominate the foraminiferal assemblages but in lower numbers compared to other meiofauna (c. 50% abundance; Table 5.4).

5.4.5. Additional salt marsh paleoenvironmental implications

In paleoenvironmental interpretations for sea level studies, the high-resolution biological studies of the higher marsh agglutinants provide new insight into their use as accurate (±5 cm vertical range) markers of sea level datums (Scott and Medioli, 1980a) within a dynamic shoreline environment with diurnal tides. The near-sedentary habit, adhesive

cytoplasm and congregating behaviour of these organisms are all adaptive features that would tend to allow these RSL marker organisms to remain within a very narrow vertical marsh range where they exploit an ample food supply in the vegetation undercover, independent of light-requiring organisms that are the food of mudflat calcareous species. The abundant salt marsh agglutinants creating adhesive feeding "cysts" probably play a crucial role in binding salt marsh sediments, as cyanobacterial and algal biofilms were always thought to do exclusively (e.g., Amos et al., 1998). Adhesion and lack of widespread mobility will keep these agglutinants in place in the absence of major post-mortem disturbance by storms, bioturbation or freeze-thaw processes, keeping the proxies in place until new sediment buries them and permanently records the biology and ecology into the geology.

5.5 Conclusions

In vitro cultures and TEM studies of key agglutinated foraminifera and mudflat calcareous foraminifera from the temperate region Chezzetcook salt marsh provide new insights into the living assemblages, forming a basis for refined interpretation of the fossil record and paleo-environments. In this study, we have successfully monitored feeding and life-activities of three common agglutinated salt marsh foraminiferal species using qualitative culturing observations of *Miliammina fusca* and *Jadammina macrescens*, both displaying only cryptic mobility. *Trochammina inflata* has relatively high mobility and is a saprophagous bacterivore. Detritus-gathering at the aperture is the key method for validating live specimens in a culture setting. Although no reproduction was observed, we have significantly added to the biological information needed to determine the niches

of salt marsh foraminifera used in high-resolution paleoenvironmental studies. The small-scale patchiness of these species seems to be dictated by food resources and cryptic mobility more than it is by favourable abiotic conditions because the species can thrive in a wide range of temperature, salinity and oxygen levels.

The TEM studies for examination of feeding modes in *Trochammina inflata* show that the species is a sapropelic detritivore and bacterivore that draws food into the outer chamber for digestion but also has limited mobility to search for areas of optimal food resources. This mixed diet of plant debris and bacteria would be expected to shift the stable isotope C:N values towards terrestrial values (see Chapter 4), and away from the traditional concept of marine or high salinity markers. *In vitro* feeding experiments on interactions between salt marsh foraminifera and associated meiofauna show minor or no interspecies predation. Biomass measurements establish that at Chezzetcook Inlet, phytodetrital bacterivores such as *Trochammina*, *Jadammina* and *Miliammina* form dense populations (>75% of abundance and biomass) that outcompete other meiofaunal organisms while in more open lower salt marsh zones, kleptoplastic calcareous species dominate the foraminiferal assemblages.

CHAPTER 6: CONCLUSIONS

6.0 Overview

The thesis project is a comprehensive multi- and interdisciplinary examination of benthic salt marsh foraminiferal and meiofaunal ecology from two cool temperate salt marshes in Nova Scotia, Canada: the mesotidal, old, Atlantic Coast Chezzetcook marsh, and the macrotidal, young, Bay of Fundy Windsor Causeway marsh. The work was undertaken in light of the importance of saltmarsh habitats and the rapidity with which this environment is being lost. An additional driver for this thesis revolves around foraminifera. While it is well-known that foraminifera reach extremely high abundances in salt marshes, their ecological roles have been mostly overlooked and little is known about their biology and functional importance within the salt marsh sediments. Nevertheless, fossil assemblages are considered keystones for interpretation of sea level change for various geologic times throughout the Phanerozoic.

The project addresses three independent but linked knowledge gaps: (1) there are no detailed multi-year foraminiferal abundance and distribution data that consider the interaction with coexisting fauna in the salt marsh sediment, (2) there are no high-resolution studies of temperate salt marsh food webs that include these ubiquitous marsh foraminifera and their associated fauna, and (3) there have been no feeding studies for cool temperate arenaceous marsh foraminifera. Knowledge of all these factors is required to assess the robustness of this food web base to disturbances that are currently affecting salt marshes and to refine the use of marsh foraminifera as paleo-sea level proxies.

Primarily, the thesis focused on the need to incorporate foraminiferal assemblages into salt marsh benthic ecology. Their abundance and trophic role in the marsh detrital cycle indicates an importance far beyond serving simply as a tool for paleoenvironmental analysis based on their fossilization in vertical elevational zones suitable for interpreting past sea levels (e.g., Scott et al., 2001). Additionally, the project contributes to a fuller understanding of salt marsh meiofaunal sediment biotic structure and function, starting with the detrital biomass from primary production and moving up the food web to larger consumers. As previous research focused on abiotic factors as key drivers to foraminiferal distributions, I have addressed prominent ecological questions about biological interactions that control the assemblages and distributions in the salt marsh sediment. These biological interactions have recently been stressed as vital to the future direction of marsh ecosystem research (e.g., Cesbron et al., 2016; Kemp et al., 2017). This section summarizes the key findings, discusses the biological and geological implications of my research, and addresses caveats and future directions.

6.1 Thesis Summary

Chapter 2 shows, for the first time, that a laboratory mesocosm can effectively represent a well-studied cool temperate salt marsh in Nova Scotia where *Spartina* grass is near its northernmost growth limit (Mann, 2000). To my knowledge, this is the first salt marsh mesocosm maintained in a laboratory setting. For a system like this to be used for future experiments, it first needed to be validated. We examined foraminiferal assemblages and distributions through a gradient of tidal flooding for two years. Comparison of laboratory foraminiferal assemblages with field data from the 1970s revealed no

significant differences in the relative abundances of key taxa used in sea-level studies (Scott et al., 1980a, b), with the high and middle mesocosm marsh zones being most similar. The similarity of field and mesocosm data established the validity of the laboratory mesocosm despite several differences in light intensity, absence of freezing and reduced plankton supply that might be tested in future studies. In the mesocosm, absolute abundances of foraminifera were much higher than in the field for the high- through low-marsh zones, probably in large part due to consistently favourable environmental conditions such as increased decomposition rates. It appears that these foraminiferal assemblages were primarily constrained by abiotic factors, mainly vertical elevation and tidal inundation, but the extremely high abundances may also reflect biotic factors, such as the exclusion of predatory or deposit-feeding macroconsumers (Buzas, 1978). The mudflat assemblage in particular appears to be more impacted by biological factors because of competition among a higher diversity of foraminifera and surface-sediment meiofauna and small macrofauna.

The mesocosm experiment showed that seasonality is not the key driving factor of temperate salt marsh foraminiferal assemblages and their distributions, and use of filtered water that excluded plankton and particulate detritus >50 microns (UV-killed) shows that these are not limiting food sources. Though foraminiferal species distribution patterns follow a strong physical gradient in the tidal zone, the foraminiferal assemblages exhibit spatial heterogeneity that is highly constrained by biotic factors, which were explored in Chapter 5. This small-scale heterogeneity, or "patchiness" is well-recognized in salt marsh foraminiferal studies (Lee and Muller, 1973; Morvan et al., 2006; Murray, 2006), requiring the process of pseudoreplication for sampling

(Chapter 2, see also Hurlbert, 1984; Debenay et al., 2006) to overcome this variability and maintain statistical rigor without time-consuming replicate sampling. Overall, the mesocosm work provides a solid validation for an indoor cool-temperate salt marsh laboratory that replicates field conditions over an extended period. The mesocosm allows year-round access to experimental materials in a climatic region where marshes are frozen 25% of the year and weather for field work is inclement about 50% of the time.

Chapters 3 and 4 explored whether there are key ecological differences between the upper and lower regions of the salt marsh. The results showed strong zonal differences, with the important implication that the zones need to be resolved separately to interpret correctly the structure and function of a modern ecosystem. This is especially true for the surface sediment system, where over 90% of all primary productivity is converted to biomass (Figure 6.1) but the nutritional pathways are virtually unresolved in terms of species composition and function. My work allows greater resolution of the detrital compartment as summarised here.

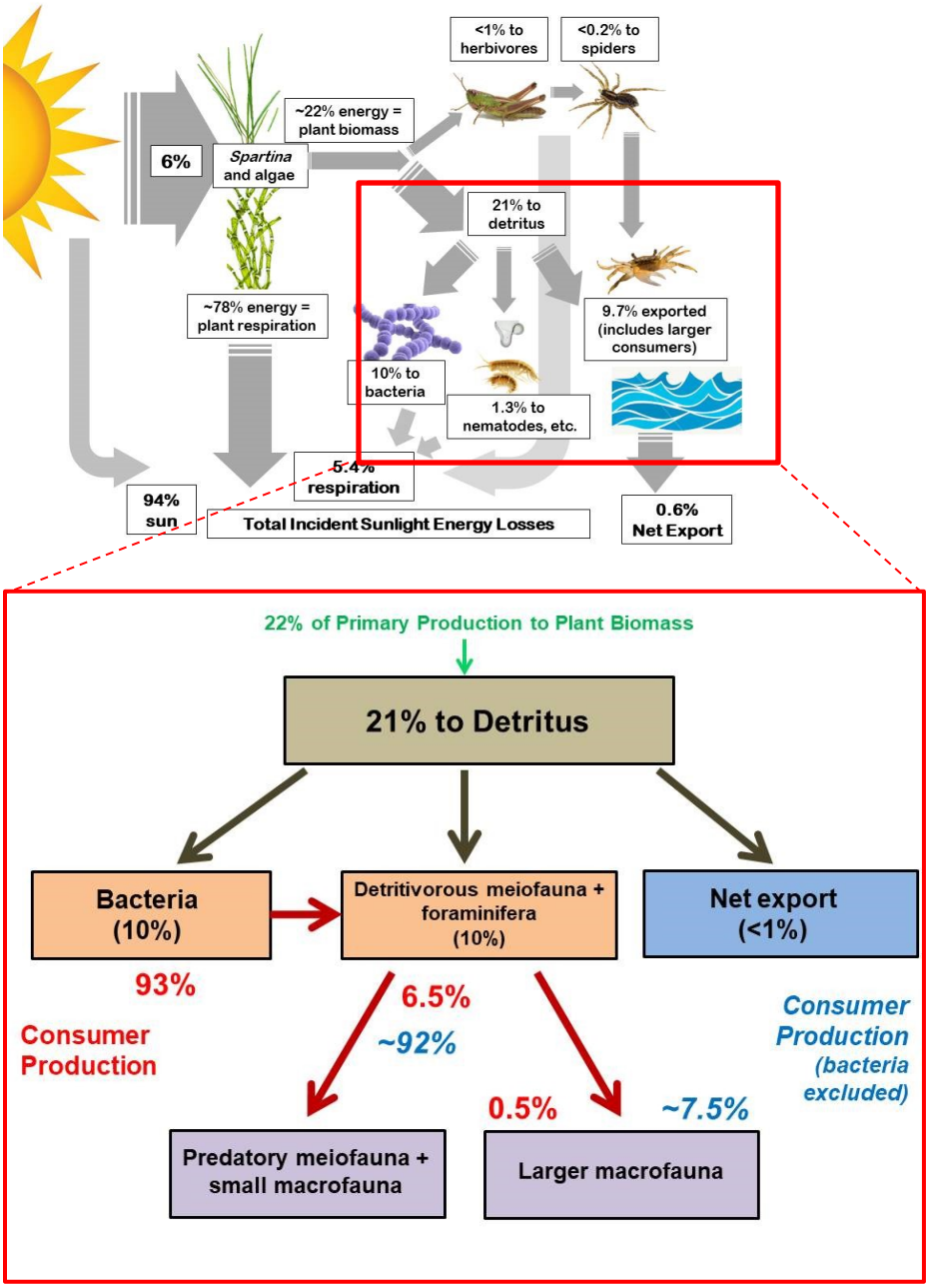

Figure 6.1: Expansion of Figure 1.1 (modified from Teal, 1962) to emphasize the detrital food web (red square) based on the surface-sediment meiofaunal and small macrofaunal feeding interactions estimated for Nova Scotian marshes in this thesis. Of the 21% to detritus, almost half (10%) goes to each of bacteria and meiofauna + foraminifera, and l% is exported. Within the production values of consumers, percentage values from NS marshes are shown in red. When bacteria are excluded, meiofauna, foraminifera and macrofauna estimates of production are given in italicized blue. Values are based on estimates given in Figure 6.4 and Table 6.1, using production:biomass ratios for a global dataset reviewed by Giere (2009) and Gerlach (1978).

Table 6.1. Biomass and production estimates used to calculate detrital "small food web" production percentage values for Figure 6.1. B = Biomass (either g m^{-2} or kcal m^{-2}); P = Production (either g m^{-2} yr^{-1} or kcal m^{-2} yr^{-1}, as ratios remain constant regardless of units). Arrows represent the multiplication of biomass by the calculated P/B ratio to give estimated production values.

Information reviewed by Giere* (2009) and Gerlach§ (1978) for conversions in Figure 6.4	Information used from biomass calculations (Chapter 5, Table 5.4, Figure 6.4)	Percentage of Production (with bacteria)	Percentage of Production (without bacteria)
P/B ratios			
Bacteria: 300* (0.5 B →150 P)	Bacteria: 30 B → 9000 P	93%	
Meiofauna: 10 – 13*§ (12 B →171 P)	Meiofauna: 17.5 B → 175 P	2%	26%
	Predatory: 5.8 B → <75 P	<0.8%	11%
Foraminifera : 2 – 5§ (0.5 B → 1 P)	Foraminifera: 72.5 B → 365 P	4%	55%
		0.5%	<7.5%
Macrofauna : 2*§ (14 B → 29 P)	Macrofauna (mostly small): 25 B → 50 P		
Note (Giere, 2009): Meiofauna estimated at 30% of biomass, 80% of production Macrofauna estimated at 70% of biomass, 20% of production			

This table is made of multiple estimates. Column 1 shows values from Giere (2009) and/or Gerlach (1978). Column 2 show values multiplied by one of the P/B values from Column 1. There were no published distinctions of Production for detritivorous vs predatory meiofauna, so I have estimated meiofauna using 10 P/B and predatory meiofauna using 12 P/B because Giere (2009) also showed higher respiration rates for predatory nematodes vs. detritivorous nematodes. The P/B of foraminifera in Column 1 is reported by Gerlach (1978) as 2 – 5 P/B. I use 5 because microfauna + meiofauna have higher values than just meiofauna alone.

In Chapter 3, food-web technology is used to explore the question of how much taxonomic resolution is enough to represent a salt marsh ecosystem, and this resulted in the most taxonomically-resolved food webs for two salt marshes anywhere in the world. The only other salt marsh ever examined in similar taxonomic detail was the Mediterranean-climate Carpinteria marsh in California (Lafferty et al., 2006), but that study focused on parasites and its webs contained fewer than half of the taxonomic nodes used in the Nova Scotian salt marsh food webs. Inclusion of greater taxonomic resolution of the "small food web" and invertebrates prevents a vertebrate-heavy bias in the food-web topology, and therefore scales-down vertebrate-dominance in the overall structure of the ecosystem. If anything, food webs should be invertebrate-biased.

However, in these highly-resolved webs, removing foraminifera did not significantly change the food-web topology, despite their dominance in the detrital system, as abundance and biomass data are not included in these binary food webs, so taxa numbers are less than those of the rest of the invertebrates.

My work also reveals that there are few significant differences between the two cool temperate Nova Scotian marshes despite their large differences in maturity, size, tidal range and nutrient regime. This implies that taxonomic resolution is the primary factor determining food web variability: despite their eight-fold difference in tidal height and five-fold difference in marsh maturity (Figure 6.2), the two marshes have similar systems of trophic functions, except for the Windsor mudflat. A further implication of geological importance is that biological proxies cannot be easily used to identify a macrotidal salt-marsh system in the fossil record unless the mudflat facies is clearly represented and differentiated from the low – high marsh zones. Windsor salt marsh shows resilience, and hence promises to conservation and restoration efforts elsewhere. Food web results revealed the promise of restoration success in a short period of time at Windsor, due to the similarities between young Windsor, and old Chezzetcook.

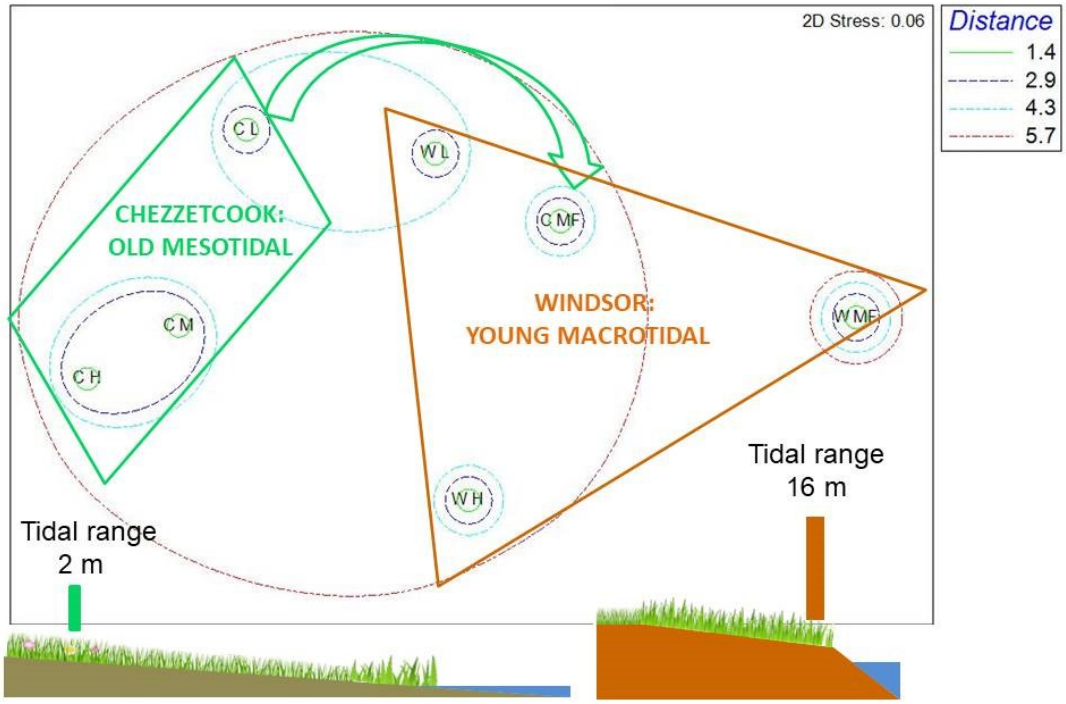

Figure 6.2. Multidimensional Scaling (MDS) plot of the food web topological characteristics of the zones of Chezzetcook (green) and Windsor (brown) salt marshes from Figure 3.8. The high and middle marshes of Chezzetcook are clustered closely; however the mudflat zone shows more similarities with the Windsor marsh. The Windsor mudflat food web is the most isolated of all the zonal food webs.

However, when comparing individual zones, the marshes had pronounced differences in food web topology (connectivity, number of species, links per species), especially between the high-middle versus low-mudflat zones. Use of static (binary) food webs (Chapter 3), however, comes with challenges that need to be examined. The static food webs used here are based on presence-absence information for species, feeding information from gut-content analyses, published literature, and direct feeding observations. They do not include relative abundance, biomass, or energy assimilation that could be used to quantify and validate the feeding links inferred from the dataset.

Chapter 4 follows the presence-absence food web analyses of Chapter 3 to quantify the "who eats whom" in the salt marsh sediments using $\delta^{13}C$ and $\delta^{15}N$ isotopes.

Although gut content analyses are useful tools in determining feeding interactions, they are nearly impossible for meiofaunal and small-macrofaunal-sized organisms that make up the detritus-feeding system (Figure 6.1), and they also represent one-time feeding relationships. Stable isotope analysis reflects long-term feeding patterns and emperically traces organic matter through the food web (Schmid-Araya et al., 2016). Stable carbon isotopes, $\delta^{13}C$, indicate the source of carbon in the system, from marine or terrestrial systems, pelagic or benthic systems (Haines, 1976; Lamb et al., 2006). Further, the ratio C:N is commonly used as measure of terrestrial versus marine carbon sources.

This is the first time, to my knowledge, that stable isotope analyses have been applied to develop foraminiferal, meiofaunal and small macrofaunal signatures in a salt marsh. This is also the first documentation for the faunas of the two temperate salt marshes of eastern Canada. Despite large differences in age, tidal regime, sedimentation rate, ice scour, and vascular plant diversity, the two marshes are not significantly different overall. C:N values of meso- and macrotidal marshes are not significantly different between or within localities. However, separating individual marsh zones results in significant clustering of isotopic signatures, especially in terms of $\delta^{13}C$. This is because of the higher diversity at Chezzetcook of C_3 plants compared with the *Spartina*-dominated Windsor marsh. For both marshes, sediment organic matter (SOM) had relatively consistent stable isotope signatures, regardless of zone or age. At Chezzetcook, there was a slight depletion of $\delta^{13}C$ in the SOM from the mudflat through high marsh, but this was not prominent. This has implications for using isotope values from bulk sediment for paleoenvironmental interpretation (section 6.3). There are also

no prominent signatures for the meiofaunal consumers, other than a slight increase in trophic position (higher $\delta^{15}N$) from meiofaunal detrital feeders to invertebrate predators. This was expected, as meiofaunal consumers are feeding on the mixed-source SOM that lacks key isotopic signatures.

In Chapter 5, I examined the biology of agglutinated salt marsh foraminifera in more detail to better understand feeding behaviour, thus biotic factors that might influence foraminiferal distribution in the marsh. We successfully monitored feeding and life activities of three common species, *Trochammina inflata*, *Jadammina macrescens*, and *Miliammina fusca* in Petri dish cultures and identified nine effective ways of non-terminally determining living specimens in culture, where cryptic mobility and opaque tests makes it difficult to monitor intrashell protoplasm. *In vivo* cultures and transmission electron microscopy (TEM) shows that these foraminifera are detritus-gathering, saprophagous bacterivores that quickly consume organic matter in the salt marsh sediment, competing with co-occurring meiofaunal invertebrates such as ostracods, nematodes, and harpacticoid copepods. The high numbers (upwards of 80% of all meiofaunal-sized species) and small-scale patchiness of foraminifera in the salt marsh sediments can also be explained by this opportunistic feeding mode, which further validates the predominant biotic interactions within the sediment system.

6.2. Salt Marsh Foraminifera and Meiofauna: Biological Implications and Contributions

The food web studies, designed to determine how much taxonomic detail is enough for salt marsh ecological interpretations, produced two key results. Firstly, for a salt marsh,

with strong spatial gradients, separate food webs need to be created for the zones, specifically for the high-middle marsh zones versus the low marsh-mudflat zones. The ecosystem structure and function cannot be correctly evaluated by considering the marsh as a whole. This has implications for other ecosystems with strong spatial gradients. For example, at Chezzetcook, the high- and middle-marsh zones are terrestrially-dominated (more diverse vascular plants, and more terrestrial invertebrates), whereas the younger, macrotidal marsh at Windsor is dominated by mudflat and *Spartina alterniflora* low-marsh zone. Interacting species are considerably different in the surface sediment of these zones. These spatial differences have also been noted for latitudinal gradients of river networks (Romanuk et al., 2006) and within estuaries with a salinity gradient (Wood et al., 2015), and also within channel environments (Kwak and Zedler, 1997).

Secondly, in detritally-dominated systems such as mudflats and salt marshes, there needs to be high taxonomic resolution of the "small players" within the surface sediment: foraminifera, copepods, nematodes, ostracods, and other meiofauna and small macrofauna. Such resolution, although previously identified as crucial, has rarely been attempted, probably due to the small size of the organisms and high time and energy requirements to sample, identify, separate, and quantify protists and small metazoans (see review by Giere, 2009). Researchers tend to focus on topics within their expertise: sedimentology, hydrology, macroflora, algae and microphytobenthos, standing-stock foraminifera, and specific groups of metazoans, including shrimp, crabs and fish. Rarely do studies look holistically at the system. Even in this thesis, I focused on foraminifera and small metazoans, although a wide range of players was included in food web and isotopic studies.

In terms of including the "small food web" (Kuipers et al., 1981), these taxonomic nodes represented over half of the trophic species in high-resolution food webs, for which connectivity (*C*) values are lower than in low-resolution webs because aggregated nodes have more realized links per species. Lower individual species connectivity implies ecosystem stability (Dunne et al., 2004). Thus, a correct interpretation of ecosystem structure and stability is strongly influenced by resolution, which has key implications when using binary food webs for salt-marsh conservation and restoration planning. In the Chezzetcook and Windsor high-resolution webs, invertebrates have higher connectance and vertebrates have lower connectance in our low-resolution webs. This leads to the erroneous interpretation that the vertebrates are stabilizing the ecosystem, whereas they represent less than 2% of the movement of energy from the detrital system (Schwinghamer et al., 1986).

Although it is "daunting" (Woodward et al., 2005) and time-consuming to determine diets and predators of the meiofauna and small macrofauna by zone in the surface sediments, the project has responded to the plea of many scientists: until now, no webs were both fully quantified and highly-resolved. We have documented quantitatively, for the first time, the vital link from detritus and microbiota up the food chain to the macrofauna.

The stable isotope analysis (SIA) of the cool temperate marshes (Chapter 4) confirms the results of the few pioneer studies of brackish marshes in southern California (Kwak and Zedler, 1997; Cloern et al., 2002) and Maine, USA (Tanner et al., 2010). Complex SIA changes are apparent through the food web, as well as a wide range of values for foraminifera and metazoan meiofauna (Figure 6.3). The most conservative

values are provided by macrofauna, such as birds. These biological findings have implications for the selection of materials by geologists for SIA signals of paleoenvironments and correlation of sections. The most important contribution of SIA for the two Nova Scotia salt marshes is the high degree of mixing and decompositional change of primary products entering the consumer system via sedimentary organic matter (SOM). The SOM values are slightly more depleted in the upper zones of the marsh where C_3 plants dominate, but they are not highly different from values lower in the marsh. We also have shown that foraminifera and associated meiofauna have mixtures of isotopic values, which matches their detritivorous, opportunistic feeding mode. These wide ranges of values do not support a narrow characterisation of the binary food webs of Chapter 3, but they confirm the importance of meiofauna in the detrital sediment system. Additionally, as noted in the food web studies, the isotopic distinction between the upper- and lower- marsh zones at Chezzetcook is sufficient to warrant individual examination of trophic structure by zone.

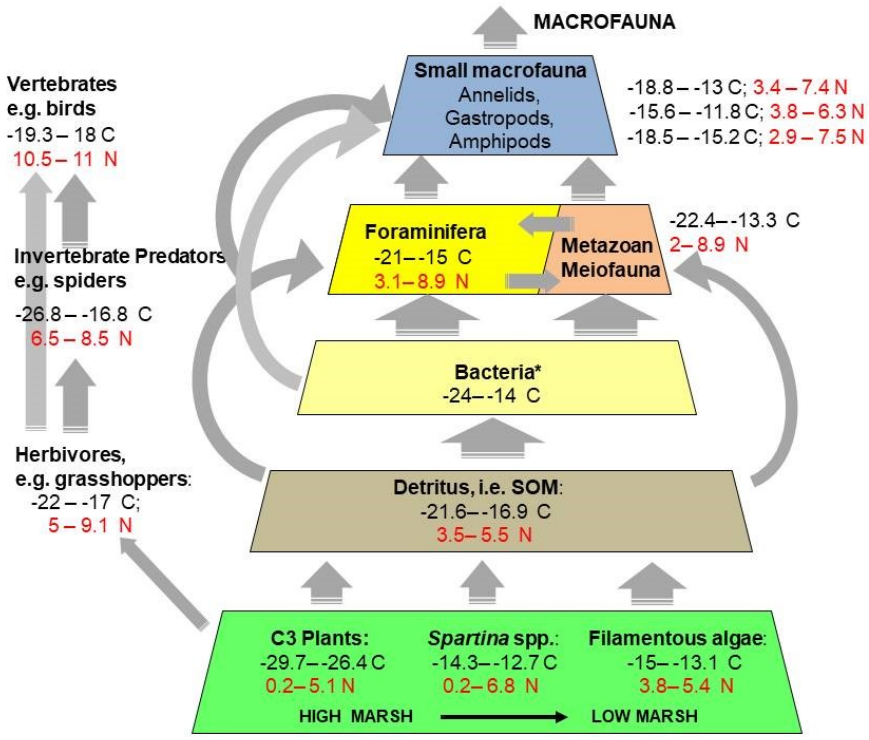

Figure 6.3: Simplified food pyramid of Chezzetcook Inlet with ranges of carbon and nitrogen stable isotope signatures (as ‰ $\delta^{13}C$ and $\delta^{15}N$). Large and overlapping ranges emphasize the food-source mixing dominant in the salt marsh detrivorous system. The dominant primary producers are arranged from high to low marsh areas. *Carbon values for bacteria are from Coffin et al. (1989), with more depleted values in C_3-plant areas, and more enriched values in *Spartina* marsh areas. No nitrogen values are given because bacteria are known to have high $\delta^{15}N$ values due to nitrogen-fixation, but these values are not incorporated into consumers.

Key implications from both Chapters 2 and 5 are related to the controls on foraminiferal assemblages and distributions. Although abiotic factors (principally elevation and salinity along a tidal gradient) govern major initial distributional controls on foraminifera and meiofauna, small-scale biotic interactions have recently been identified as important, overlooked controls and are highlighted for future studies by Cesbron et al. (2016) and Kemp et al. (2017). For example, competition between foraminifera and metazoans, and between different species of foraminifera, may represent a secondary control over the foraminifera in the mesocosm (Chapter 2) and could explain

the biomass and abundances calculated in Chapter 5. Without large predatory macroconsumers in the mesocosm, their own biotic interactions, such as competitive control, may also keep the foraminiferal numbers high, as seen in predator exclusion experiments by Buzas (1978). This competitive control of foraminifera also kept harpacticoid copepod numbers minimal in Chandler's 1989 seminal study of foraminifera in benthic communities.

Our biological studies of benthic foraminifera give insights into understanding the drivers of distribution and how these species can attain such high abundances in the sediments. Their ability to rapidly form mucous balls ("feeding cysts") allows them to take advantage of food pulses, including a pulsed food supply based on tidal shifts, or short-term food pulses in areas of high decomposition (e.g., carrion or macrophyte litter). Based on TEM work using *Trochammina inflata*, the mucous balls are probably bacterial-coated phytodetritus. This rapid feeding with cryptic mobility may explain the small-scale patchiness of foraminifera and meiofauna in salt marsh sediments. Foraminifera represent 50-80% of meiofaunal abundance and can account for 30% of the biomass, implying consumption of up to 50% of the incoming phytodetritus as found for deep sea fauna (Shirayama and Horikoshi, 1989). I showed that foraminifera dominate in abundance and biomass in comparison with the metazoan meiofauna in all marsh zones, although they have lower abundance in lower zones of the marsh (Figure 6.4).

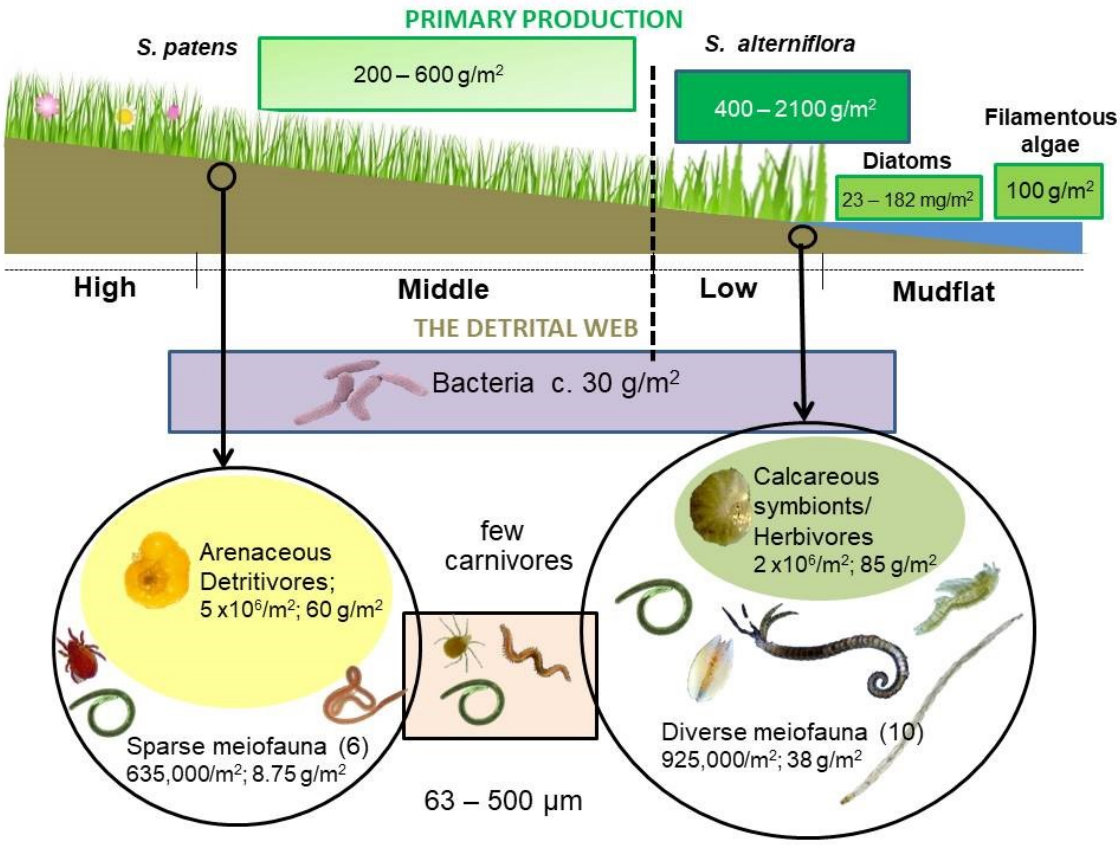

Figure 6.4: Dry weight bulk biomass estimates of the production and sediment consumer (detrital) system of Nova Scotia marshes. *Spartina* is above-ground production from Mackinnon and Lane (1993) for Petpeswick Inlet (near Chezzetcook) and Daborn et al. (2003) for Windsor. Diatoms values shown as Chlorophyll *a* concentrations for Windsor (Daborn et al., 2003), and algae are estimated using *Cladophora* mats from New England (Roman et al., 1990). Bacteria estimates from Coupland (1979). Meiofaunal (63 – 500 µm) abundances and biomass estimates are extrapolated from values per 2.5 ml from averages of high and middle marsh zones, and low and mudflat zones of Chezzetcook Inlet. Meiofauna in brackets are the number of major taxa (including nematodes and copepods).

6.3. Salt Marsh Foraminifera and Meiofauna: Geological Implications and Contributions

Because salt marshes and foraminifera have been used for decades for paleoenvironmental research, the ecological and biological insights discussed in this thesis also lead to interesting geological implications and contributions to research. The

mesocosm studies show that all classical RSL studies are missing a key facet: small-scale variability on a regional (different salt marshes within a similar area) and local scale (within one salt marsh system) that presents a significant challenge for creating meaningful training sets for transfer functions. These small-scale differences are probably commonly related to biotic constraints on foraminifera in the sediment, rather than to the physical drivers (elevation, salinity) that are the usual variables tested in the paleo-transfer function studies. Possibly patchiness and other measures of species variability need to be incorporated in the transfer functions to resolve problems pointed out by Kemp et al. (2017) and Anvaim-Kativ et al. (2017), and could be used to advise previous studies such as Gehrels et al. (2005) due to restricted motility and therefore greater accuracy of high marsh taxa. The mesocosm data show that spatial differences, not seasonal differences, dictate the vertical assemblages (high, middle, low marsh), even in cool temperate environments with winter freezing. Logically, this makes sense as the fossil records of these assemblages lose the signal of seasonal variability of absolute abundances of agglutinated individuals; modern assemblages expressed as relative abundances of calcareous and agglutinant taxa do show strong seasonal changes (Horton and Edwards, 2003; Lei et al., 2017; Saad and Wade, 2017). This is also because post-mortem depositional processes, such as dissolution of calcareous tests (Murray and Alve, 2000), bioturbation, wave and storm energy, and ice scouring, could remove any seasonal signatures down core. Using only middle-high marsh zones, instead of low-mudflat zones, for paleointerpretations also minimizes this seasonal and post-depositional variability. Biotic processes (biofilms, food pulses, burrows made by infaunal macrofauna such as crabs) can also cause favourable environments for patches of

foraminifera and meiofauna, deemphasizing the abiotic drivers of assemblages and distributions (Giere, 2009), at least when looking at modern surface distributions to interpret deeper assemblages (Duchemin et al., 2005).

In terms of SIA, the lack of definitive bulk SOM signatures in the surface sediments of Windsor and Chezzetcook zones could cloud the interpretation of SOM values in fossil sediments. Unless researchers are comparing exclusively C_3 plant high marsh areas to exclusively C_4 low marsh areas (as by Chmura and Aharon, 1995), salt marsh sediments have the potential for errors when using SIA for sea-level reconstruction (see also Kemp et al., 2017). The cool-temperate marsh zones of Nova Scotia are dominated by C_4 grasses in both the high and low marshes, giving wide isotopic ranges (between -22 and -16 ‰ $\delta^{13}C$), showing that the elevational zones cannot be separated by sediment isotopic values alone. Another complex aspect of detritus-based food webs that requires caution when using stable isotopes is interpretation of coastal paleoenvironments and small isotope excursions, where, in the geologic record, excursions as small as ± 2 ppt are correlated to events such as mass extinctions. The small food web of salt marshes shows considerable mixing of isotopic values of detritus, foraminifera and meiofauna (Figure 6.5). My high resolution data of the small food web confirm the difficulty in assigning precise marine and brackish values. The data also show that SOM values at Chezzetcook and Windsor are a mixture of wholly marine and wholly terrestrial values, regardless of the source of primary production leading to the detritus.

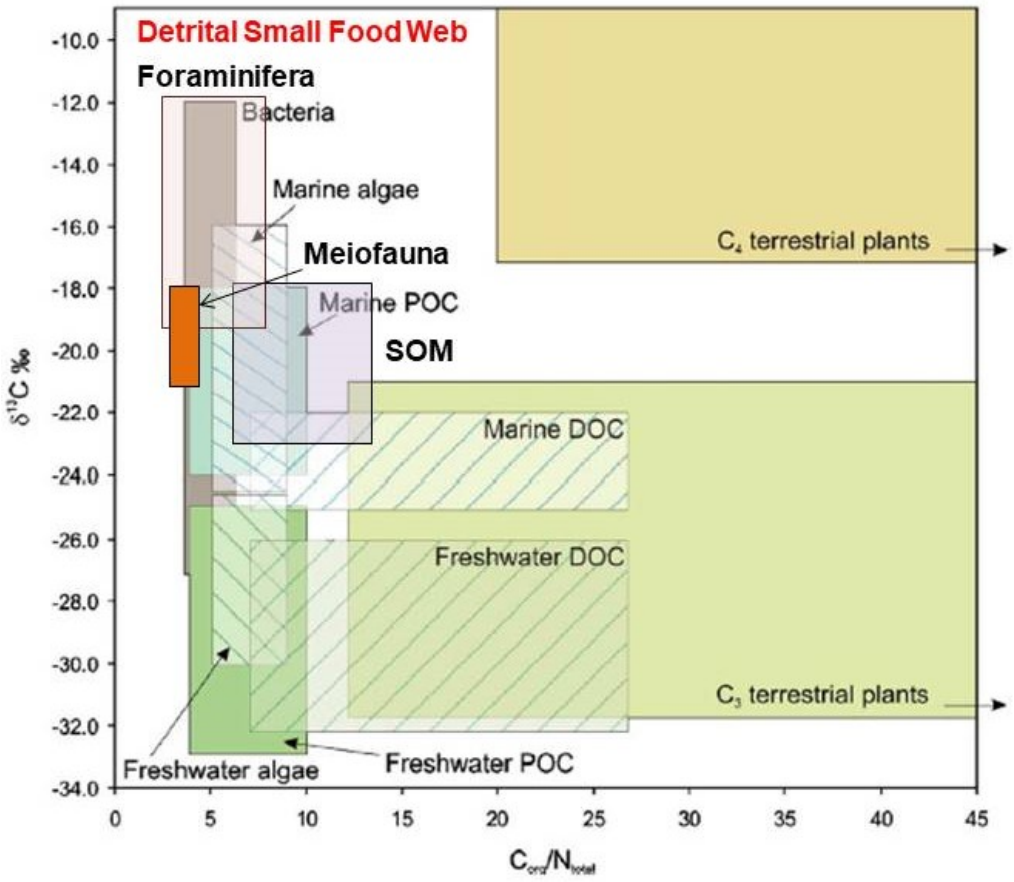

Figure 6.5: Isotopic signatures of C:N and ‰ $\delta^{13}C$ of coastal sources, with the detrital small food web signature ranges from this study added. SOM: Sediment Organic Matter; POC: Particulate Organic Carbon; DOC: Dissolved Organic Carbon. Modified from Lamb et al. (2006).

Several studies from other regions have suggested that the high-middle marsh complex of tidal zones, with an abundance of agglutinated foraminifera species, is key for paleoenvironmental interpretations of RSL (Duchemin et al., 2005, Horton and Murray, 2007; Kemp et al., 2017). New data on agglutinant feeding and limited or cryptic motility in laboratory cultures (Chapter 5) point to possible explanations for the conservative distributions of these taxa that confirm their value for high-resolution (mm-scale) RSL studies, as also determined by Horton and Edwards (2003) for a more temperate marsh in Ireland. Furthermore, biotic processes and post-mortem taphonomic

processes appear to dominate in the lower zones of the cool temperate marshes where meio- and macrofaunal bioturbation is higher, population numbers are lower, and the calcareous foraminifera may dissolve after death, especially in increasingly acidified global seas. As a result, low marsh sediment faunal assemblages should record the past ecosystem less effectively. However, it is important to note that organic remains of these calcareous faunas can be extracted using palynological methods, combined with numerical correlation of the organic remains and the living populations. Thus, they can be used as proxies (Frail-Gauthier and Mudie, 2014) for Holocene salt marsh studies, and potentially back to Paleozoic time (as scolecodonts, chitinozoa and various acritarchs are now known to be egg cases or resting eggs). These non-pollen palynomorphs (NPP) may be an effective way to look at traces of meiofauna and small invertebrate macrofauna (Mudie et al., 2011).

Regarding the place of food web data in geology, fossil records are inevitably a partial picture of an ecosystem, as not everything is preserved. Decomposition and diagenesis may modify assemblages to the point that interpretations are basically erroneous. Any inferred trophic structure of marshes and zones will lack the skeletal remains of many key players (Figure 6.1) in the older geological record (mostly meiofauna and small macrofauna without hard exoskeletons, such as nematodes, copepods, and annelids). The addition of NPP studies of organic-walled skeletal linings, resting eggs, and exo- or endoskeletal parts to classical work in micropaleontology and paleoecology may assist in resolving this major problem.

An additional question concerns changes in trophic structure through time. There is little evidence of salt marsh vegetation prior to the Cretaceous rise of angiosperms with

gametophytes protected within seeds that provide primitive saltwater protection (Greb et al., 2006). The Cenozoic spread of drought- or cold-tolerant C_4 plants with cellular adaptations to salt storage or secretion represents another milestone in salt marsh evolution. Mid-Cenozoic C_4 grasses were better adapted to osmotic stress and hence to low-middle salt marshes where salinity is consistently high (Strömberg, 2011). Halophytic adaptive events would change radically the organization and physical structure/zonation of marshes through time, and this limits the time-interval for direct relevance of the data in this thesis. Nevertheless, Chapters 3 and 4 show that marshes with major structural and taxonomic differences (young, macrotidal Windsor, versus old, mesotidal Chezzetcook) share the same ecological functions. Salt marshes in different latitudinal zones without the same key species (e.g., fiddler crabs in the eastern USA, absent from Canadian marshes) share basic ecological properties. This may be true for wetlands throughout the geologic record: ancient coastal wetlands may have been structurally and taxonomically different but Greb et al. (2006) consider that some were functionally and dynamically similar to modern tidal wetlands.

As regards the importance of salt marshes for carbon storage, the differences between Windsor and Chezzetcook raise some important points. The winter ice scouring of Windsor may limit its ability to store carbon, in terms of *Spartina* burial in the sediments, in comparison to Chezzetcook. Ice scouring and tidal transport removes this carbon elsewhere, although thin bands of dead *Spartina* in the high marsh suggest a locally good storage potential. Dead grass would tend to be transported down the Avon River into the Minas Basin, serving detrital sediment webs elsewhere. In terms of storage, Chezzetcook has greater potential than Windsor (Chezzetcook: 106 g C m^{-2} yr^{-1}, Chmura

et al., 2003; Bay of Fundy low marsh areas, such as the majority of Windsor marsh: ~68 g C m^{-2} yr^{-1}, Connor et al., 2001).

Surprisingly, the cool temperate Nova Scotia marshes, where *Spartina* grass is near its northern growth limit (Mann, 2000), are highly productive. Hatcher and Mann (1975) examined productivity of *Spartina alterniflora* at Petpeswick Inlet (adjoining Chezzetcook) in 1975 and found it to be the most productive northernmost marsh (710 g dry weight m^{-2} yr^{-1}). Storage values for Chezzetcook are 106 g m^{-2} yr^{-1} (Chmura et al., 2003), equalling or exceeding some Connecticut and North Carolina marshes, and generally contradicting the long-held theory that salt marshes lose productivity with increasing latitude, based on the decrease from 1000 – 3000 g m^{-2} yr^{-1} in Southeastern USA, to 250 – 450 g m^{-2} yr^{-1} in Northeastern USA marshes (Hatcher et al., 1981; Kirwan et al., 2009). Windsor Causeway has the greatest values for a high-latitude salt marsh, averaging 1107 g m^{-2} yr^{-1} (Daborn et al., 2003), but dyked marshes in the upper Bay of Fundy average less than half of the Windsor production (120 – 560 g m^{-2} yr^{-1}).

Windsor may have higher annual *Spartina* productivity, but *Spartina* detritus is better retained in the mesotidal Chezzetcook marsh with a partially silled entrance. There is also high variability in soil carbon accumulation within local areas (e.g., Bay of Fundy), mostly due to suspended sediments and tidal flushing, resulting in less sequestration in the *Spartina patens* zone than the *S. alterniflora* zone (Chmura et al., 2003). The more dynamic mudflat-neritic shelf zone has algal mats and wave-exposed sediments that are prone to storm erosion, and ice and current scour. These subsystems would be less effective carbon traps, allowing greater amounts of blue carbon export to the coastal waters.

In terms of outflow and detritus, Mann (1988, 2000) discussed contradictions to the importance of the detrital outwelling theories of, for example, Teal (1962). The present thesis shows that detritus reworking is how the salt marsh ecosystem functions and is vital to supporting secondary productivity. Little of this particulate detritus (particulate organic matter) may leave the salt marsh system and enter coastal waters. However, dissolved organic matter derived from breakdown of detrital particles is exported from the marsh and plays an important role in coastal carbon enrichment and/or sequestration. In the Bay of Fundy, however, much of the POM is exported due to ice scour. My work within the detrital system focuses on the carbon cycling within the salt marsh itself; the salt marsh "small food webs" are where the most important ecosystem workings are located (over 80% of detritus production), and where they remain (less than 2% is exported).

Chezzetcook tidal flushing is one of the most rapid along the Nova Scotian coast (14 hours) because of its relatively small area (14 km^2) and shallow channels $\leq$ 9 m (Canadian Council of Ministers of the Environment, 2007), suggesting C export may be higher than in adjoining Petpeswick with deeper basins, shallow sills and longer (32-hrs) flushing time that limits export of POC (Hatcher and Mann, 1974; Kranck, 1980). Erosion of marsh mud at Chezzetcook as a result of sea-level transgression and Atlantic storms is another mechanism of carbon export to the Scotian Shelf, making this mature, mesotidal marsh both a local sink and source for carbon.

Finally, foraminifera and meiofauna in the salt marsh surface sediments are important not only for carbon cycling of phytodetritus but for microstabilization of fine-grained sediment. The feeding modes of the benthic salt marsh foraminifera (sticky

pseudopodial nets) bind sediments and thus assist in stabilizing the surface sediment, a function commonly attributed exclusively to surface diatoms. In assessing the carbon-storage capability of a salt marsh, key taxa and controls on biomass transfer and loss in the food web, especially at lower trophic levels, need to be taken into account.

6.4. Future Directions

The thesis has addressed the concern that foraminifera and associated meiofauna need to be resolved and incorporated within any framework for the salt marsh ecosystem. Because of this wide-ranging issue, the results I have attained have led to as many questions as answers. Here I briefly discuss some of the caveats, and therefore future directions, needed to carry this important research forward.

An important future direction arises from the mesocosm (Chapter 2). The laboratory salt marsh mesocosm represents an ideal system, and our initial experiment was for validation, to examine foraminiferal assemblages with most environmental parameters controlled. There were no macroconsumers, an unrealistic food input (no phytoplankton or particulate organic carbon >50 microns), no cold interval, or day/light variations from seasons or weather conditions. Following a robust, quantitative analysis, the mesocosm effectively represents the field foraminiferal assemblages, and it can be used for specific studies and experiments (see Chapter 14 in Scott et al., 2014). Examining spatial and temporal dynamics with foraminifera and their associated meiofauna is a key next step, following initial exploratory studies which are not presented here.

From the food web studies of Chapter 3, the simple niche model of Williams and Martinez (2000) currently in use is not adequate for high-resolution studies because it only works well for S<50 whereas our webs had S>100. There is a need for new models, such as the combined niche-hierarchy model (Cattin et al., 2004), which may more effectively represent the natural system, but this model is not part of the FoodWeb3D program. High taxonomic resolution requires the development of new, more complex assessment models.

Our SIA studies have shown a need to examine subcomponents of heterogeneous systems separately (zones of tidal salt marshes) and that the foraminiferal and meiofaunal components give wide ranges of carbon and nitrogen values, based on the mixed sources from the sediment. For such a system, mixing models are challenging to construct, but important advances could be made from their application (see Chapter 4).

Experiments on feeding of agglutinated foraminifera in mud substrates require specialised equipment to further assess the apparent link between form and feeding function in foraminifera. The validity of the link has considerable implications for fossil foraminiferal assemblages where form is preserved but function cannot be measured directly. Additional TEM work using other species of agglutinated salt marsh foraminifera, and with more rigorous and inclusive feeding experiments, could conclusively assess feeding preferences of all the key species used in paleoenvironmental interpretations.

With regard to future geological directions, a key analysis would construct highly-resolved salt marsh food webs through geologic time, throughout and possibly before the Cenozoic. Greb et al. (2006) stressed that the fossil record is our only tool for

understanding how key evolutionary and extinction events changed wetlands, including the evolution of salt-tolerant grasses that now dominate tidal salt marshes. Wetlands also co-evolved with their consumers, such as arthropods, which were key to nutrient cycling in the earliest wetlands and are vital to the detrital "small food web" of modern salt marshes. Using stable isotope analyses of fossils and creating detailed food webs using decay-resistant foraminifera, meiofauna, and their organic-walled NPP remains, one could assess the ecosystem through time and investigate whether structure and function are related to these key taxonomic groups. Additionally, this approach could be relevant to refining chronostratigraphic correlation using SIA data, as in the Ypresian Stage (Paleocene/Eocene boundary) Carbon Isotope Excursion event, where there is a shift in $\delta^{13}C$ by 2 – 4 ‰ (Aubry et al., 2007). SIA validation can also help discern differences in marine and terrestrial sources and develop good mixing models to discern sources in generalist detritivorous systems, such as salt marshes.

6.5 Final Remarks

This thesis project has addressed key data gaps in salt marsh surface sediment ecosystems, starting with the original question of "*what role do living salt marsh foraminifera play*?" To address this, we needed a laboratory salt marsh mesocosm for a year-round supply of cool, temperate region foraminifera and meiofauna for novel interaction studies. Validation of the mesocosm ecology against 1970s geological field data allowed these organisms to be used for feeding and species faunal interaction studies. Additional new field work over five years and extensive literature research allowed exploration of the question "*how many species are enough for marsh food-web*

studies?", providing the answer that there is "*no limit except for those imposed by existing food-web models*." The new field data reveal minimal differences between meso- and macrotidal marshes in Nova Scotia, except for macrotidal mudflat assemblages that may be discriminated in modern and geological records. SIA data show the complexity of detritus-based food chains and the wide range of possible values, and caution is required when interpreting paleoenvironments from $\delta^{13}C$ and $\delta^{15}N$ or when correlating coastal facies based on small isotopic excursions. Feeding experiments combined with TEM give new insight into the role of agglutinated foraminiferal form and function in modern salt marshes, potentially allowing the forms of fossil marsh foraminifera to be used as markers of motility and surface sediment cohesion.

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APPENDIX A-1 – SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Table A-1: Statistics table for Table 2.2 salinities. Salinity comparisons across seasons (top panel), zones (bottom panel), and between the field (4A – 7D) and mesocosm (T1 and T2; zones defined in Table 2.1) (bottom right). Statistically different differences ($p<0.05$ for Kruskal-Wallis or Mann-Whitney non-parametric tests) are bolded. F-W = Fall+winter; Sp = Spring; Su = Summer.

FIELD mean salinity values (psu) ± *standard deviation*				**K (observed, critical) values**	**Kruskal-Wallis p-values**	**Risk***
	F-W	**Sp**	**Su**			
4A	4.75 *±1.26*	6.25 *±3.69*	15.22 *±5.97*	11.67, 5.99	**p = 0.003**	<0.29
4B	2.5 *±1.73*	6.38 *±4.24*	14.0 *±6.6*	11.3, 5.99	**p = 0.004**	<0.35
20B	9.67 *±4.51*	16.72 *±5.77*	24.75 *±3.76*	7.77, 5.99	**p = 0.021**	<2.1
7C	23.0 *±2.1*	23.0 *±5.14*	25.7 *±5.43*	2.1, 5.99	p = 0.351	35.1
7D	26.3 *±3.51*	25.5 *±2.07*	28.2 *±2.4*	2.6, 5.99	p = 0.166	16.6

MESOCOSM mean salinity values (psu) ± *standard deviation*				**K (observed, critical) values**	**Kruskal-Wallis p-values**	**Risk**
	F-W	**Sp**	**Su**			
T1-H	3.85 *±3.76*	4.0 *±2.83*	6.25 *±3.5*	1.22, 5.99	p=0.544	54.4
T1-M	7 *±2.1*	4.5 *±3.54*	7 *±4.4*	1.01, 5.99	p=0.60	60.27
T2-M	26.85 *±2.48*	25.5 *±0.71*	26.25 *±1.89*	0.672, 5.99	p=0.715	71.46
T2-L	27.57 *±2.37*	27 *±1.41*	26.75 *±1.5*	0.26, 5.99	p=0.878	87.83
T2-MF	27.5 *±2.37*	27 *±1.41*	27.75 *±1.29*	0.46, 5.99	p=0.795	79.46

FIELD zonal salinity mean values (psu) ± *standard deviation*	**K (observed, critical) values**	**Kruskal-Wallis p-values**	**Risk**
4A: 9.8 ± *6.53* 4B: 8.9 ± *6.83* 20B: 17.5 ±*7.24* 7C: 23.9 ± *4.4* 7D: 26.7 ± *2.63*	52.5, 9.49	**p<0.0001**	<0.01

MESOCOSM zonal salinity mean values (psu) ± *standard deviation*	**K (observed, critical) values**	**Kruskal-Wallis significance**	**Risk**
T1-H : 4.6 ±*3.48* T1-M : 6.6 ±*2.99* T2-M : 26.5 ±*2.07* T2-L : 27.2 ±*1.92* T2-MF : 27.5 ±*1.85*	48.62, 9.49	**p<0.001**	<0.01

Mann-Whitney significance of FIELD vs MESOCOSM for each zone, based on mean values listed above:

4A vs T1-H: U=204; expected=136.5; p=0.017; Risk= <1.71
4B vs T1-M: U=161.5; expected=136.5; p=0.383; Risk=38.31
20B vs T2-M: U=14.5; expected=91.0; p=0.000; Risk=<0.02
7C vs T2-L; U=53.5; expected=117.0; p=0.01; Risk=<1.02
7D vs T2-MF; U=84.0; expected=97.5; p=0.544; Risk=54.4

*Risk = The risk to **reject** the null hypothesis (H0) while it is **true** is _____ (value as percentage).
H0 (null): The samples come from the same population; Ha (alternative): The samples do not come from the same population.

Table A-2: Statistics table for Table 2.3 seasonality counts. Seasonal comparisons of the average total abundances (top), and average relative abundances of main species of foraminifera (bottom) in field (4A through 7D) and mesocosm (T1 and T2; zones defined in Table 2.1). Statistically different results ($p<0.05$ for Kruskal-Wallis or Mann-Whitney non-parametric tests) are bolded. F-W = Fall-winter; Sp = Spring; Su = Summer. *high standard deviation around mean.

FIELD **Average total foraminiferal counts across seasons ± *standard deviations***				**K (observed, critical) values**	**Kruskal-Wallis significance**	**Risk**
	F-W	**Sp**	**Su**			
4A	1660 *±452*	1319 *±1337*	2735 *±1257*	7.24, 5.99	**p=0.027**	<2.68
4B	1128 *±605*	832 *±839*	2135 *±1293*	8.45, 5.99	**p=0.015**	<1.46
20B	1065 *±582*	1780 *±476*	1612 *±520*	2.57, 5.99	p=0.277	27.73
7C	2257 *±1048*	2260 *±1270*	2533 *±1224*	0.09, 5.99	p=0.956	95.57
7D	1030 *±258*	1340 *±704*	1996* *±1454*	0.57, 5.99	p=0.753	75.27
MESOCOSM **Average total foraminiferal counts across seasons ± *standard deviations***				**K (observed, critical) values**	**Kruskal-Wallis significance**	**Risk**
	F-W	**Sp**	**Su**			
T1-H	6392 *±1182*	6705 *±1183*	4425* *±1450*	3.5, 5.99	p=0.173	17.34
T1-M	3618 *±1725*	3615 *±2193*	3228* *±959*	0, 5.99	p=1.0	100
T2-M	8075* *±2302*	6516* *±2087*	5911 *±841*	2.44, 5.99	p=0.295	29.48
T2-L	4535* *±1169*	4275 *±356*	4266 *±660*	0.42, 5.99	p=0.810	81.0
T2-MF	921 *±257*	791 *±417*	780 *±272*	0.89, 5.99	p=0.64	63.99

FIELD **Average relative abundances (%) of main foraminifera across seasons ± standard deviations**						**MESOCOSM** **Average relative abundances (%) of main foraminifera across seasons ± standard deviations**					
Trochammina 281nflate + Jadammina macrescens											
	F-W	**Sp**	**Su**	K-value	Significance	Risk		**F-W**	**Sp**	**Su**	K-value	Significance	Risk
4A :	75.8 *±5.7*	68 *±11.5*	74.9 *±8.3*	2.02	p=0.365	36.5	T1-H :	63.3 *±6.3*	63.1 *±5.2*	60.5 *±13.6*	1.55	p=0.461	46.1
4B:	77 *±5.6*	72 *±5*	77 *±7.4*	3.75	p=0.153	15.3	T1-M:	67.3 *±7.7*	57.7* *±27.3*	66.8 *±15.9*	0.21	p=0.9	90.3
20B:	7 *±3.7*	4.8 *±2.4*	4.6 *±2.2*	1.37	p=0.503	50.3	T2-M:	52.1 *±4.6*	53.5 *±6.2*	46.8* *±8.3*	1.35	p=0.509	50.9
7C:	3.1 *±4.1*	0.8 *±1.3*	4.2 *±6.1*	2.15	p=0.342	34.2	T2-L:	4.0 *±1.8*	2.9 *±0.2*	2.9 *±1.6*	3.06	p=0.216	21.6

Tiphotrocha comprimata												
	F-W	**Sp**	**Su**	K-value	Significance	Risk		**F-W**	**Sp**	**Su**	K-value	Significance	Risk
4A :	16.7	17.2	13.9	1.54	p=0.463	46.3	T1-H :	14.5	18.0	15.8*	1.67	p=0.434	43.4
	±4.9	*±5.2*	*±4.6*					*±3.6*	*±1.1*	*±4.5*			
4B:	17.6	21.4	16.2	6.09	**p=0.048**	<4.8	T1-M:	7.6	12.6	11.8	6.83	**p=0.033**	<3.29
	±3.0	*±4.6*	*±4.1*					*±1.7*	*±4.2*	*±3.0*			
20B:	3.5	5.3	3.5	2.23	p=0.328	32.8	T2-M:	22.1	23.6	18.8	1.24	p=0.539	53.9
	±3.9	*±1.9*	*±2.3*					*±7.5*	*±8.5*	*±6.1*			
Miliammina fusca													
	F-W	**Sp**	**Su**	K-value	Significance	Risk		**F-W**	**Sp**	**Su**	K-value	Significance	Risk
20B :	87	87.8	88	0.15	p=0.926	92.6	T1-H :	13.3	10.5	13.5*	1.61	p=0.447	44.8
	±6.5	*±3.1*	*±7.5*					*±4.4*	*±2.7*	*±6.5*			
7C :	77.9	87	79.8	1.53	p=0.46	46.6	T1-M :	20.4	26.4*	16.9	0.1	p=0.95	95.0
	±16.8	*±9.3*	*±14.6*					*±8.6*	*±33.4*	*±13.1*			
7D :	69.3	79	74.5	1.39	p=0.499	49.9	T2-M :	22.9	27.5*	24.7	0.15	p=0.928	92.8
	±20.2	*±20.2*	*±9.4*					*±5.2*	*±11.1*	*±2.8*			
							T2-L :	86.4	88.0	93.7	5.75	p=0.056	5.64
								±3.8	*±11.1*	*±1.7*			
							T2-MF :	60.2	56.9	49.4	2.32	p=0.313	31.3
								±8.6	*±2.4*	*±10.3*			
Calcareous species (*Elphidium* spp., *Helenina anderseni*, and *Haynesina orbiculare*)													
	F-W	**Sp**	**Su**	K-value	Significance	Risk		**F-W**	**Sp**	**Su**	K-value	Significance	Risk
7C :	16.5	8.7	9.5	0.59	p=0.744	74.4	T2-L :	5.9	6.7*	1.7	0.66	p=0.721	72.1
	±18.1	*±8*	*±8.2*					*±6.5*	*±9.5*	*±1.1*			
7D :	12.6	15.4*	7.2	0.89	p=0.64	64.4	T2-MF :	8.9*	19.3	22.7*	4.29	p=0.117	11.7
	±10.3	*±25.8*	*±5.3*					*±7.1*	*±1.9*	*±16.1*			

Table A-3. Statistics table for Table 2.4 comparisons of the average relative abundances (%) of dominant foraminifera from the zones (elevation; 4A high marsh through 7D mudflat) and location (field or mesocosm). *Calcareous species include *Elphidium* spp., *Helenina anderseni*, and *Haynesina orbiculare.* Statistically significant differences ($p<0.05$) are shown in bold. Kruskal-Wallis non-parametric tests used for *k*-samples, Mann-Whitney non-parametric tests used for 2 samples.

Species	**FIELD Mean ±SD**	**K-values (observed, critical)**	**Elevation comparison & Risk**	**MESOCOSM Mean ±SD**	**K-values (observed, critical)**	**Elevation comparison & Risk**	**FIELD – MESOCOSM comparison Mann-Whitney U, expected values; significance**
Trochammina 283nflate + *Jadammina macrescens*	4A: 72.3 ± 9.7 4B: 75.1 ± 6.4 20B: 5.4 ±2.8 7C: 2.8 ± 4.4	58.55, 7.82	**p<0.0001** <0.01	4A : 62.4 ± 8.4 4B : 65.4 ± 12.7 20B : 50.8 ± 6.1 7C : 3.4 ± 1.7	38.84, 7.82	**p<0.0001** <0.01	4A: 251, 162.5; **p=0.007** 4B: 241, 162.5; **p=0.016** 20B: 0, 91; **p<0.0001** 7C: 72, 126; **p=0.041**
Tiphotrocha comprimata	4A: 15.8 ± 5.0 4B: 18.6 ± 4.6 20B: 4.19 ± 2.7	32.6, 5.99	**p<0.0001** <0.01	4A :15.5 ± 3.7 4B : 9.7 ± 3.3 20B : 21.3 ± 6.9	20.14, 5.99	**p<0.0001** <0.01	4A: 159, 162.5; p=0.926 4B: 307, 162.5; **p<0.0001** 20B: 0, 91; **p<0.0001**
Miliammina fusca	20B: 87.6 ± 5.3 7C: 81.1 ± 14.1 7D: 74.6 ± 15.8	5.34, 5.99	p=0.069 6.92	4A: 12.9 ± 4.7 4B: 20.2 ± 13.5 20B: 22.2 ± 5.2 7C: 88.7 ± 5.4 7D: 56.7 ± 9.4	54.98, 9.49	**p<0.0001** <0.01	20B: 182, 91; **p<0.0001** 7C: 89.5, 126; p=0.171 7D:175, 105; **p=0.002**
Calcareous species*	7C: 12.0 ± 12.8 7D: 11.1± 13.7	U: 141.5 expected: 135	p=0.828 82.8	7C: 4.8 ± 5.8 7D: 14.3 ± 11.4	U: 39 expected: 98	**p=0.007** <0.71	7C: 187, 126; **p=0.021** 7D: 75, 105; p=0.198

APPENDIX A-2: SUPPLEMENTARY DATA FOR CHAPTER 2

This material is permantantly archived as Electronic supplementary material at Dalhousie University.

Supplementary A includes: ordered lists of data used in calculations for Chapter 2, including: location (mesocosm or field), marsh zone, salinity, total foraminiferal abundance, and relative abundances of main foraminifera (per 10 ml).

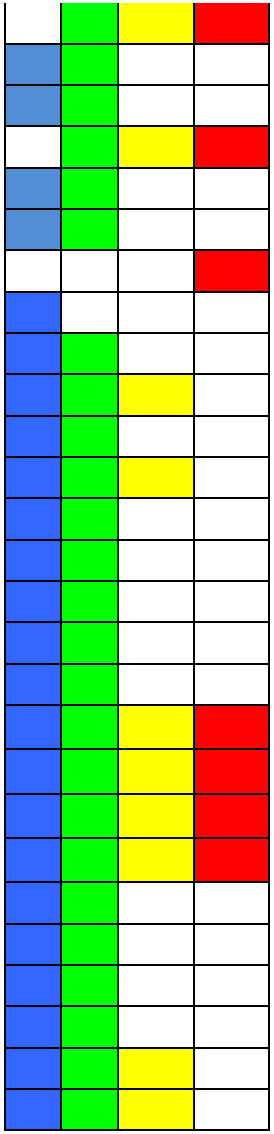
APPENDIX B: SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Appendix B-1: Species lists for Chezzetcook and Windsor food webs for Chapter 3. Species found at both marshes are labelled as "both." Node ID is what is used in binary matrices. Supplement B-1 contains additional information, including ecological (feeding) references. Also shown here are major taxonomic groups, systematic taxonomy references, common names, and the zones of the marsh where species are located (HM = high marsh, MM = middle marsh, LM = low marsh, MF = mudflat).

						Zone Location			
Location	**Taxonomic Classification**	**Node ID**	**Species**	**Systematic Taxonomy Reference**	**Common name**	MF	LM	MM	HM
Chezz	OTHER source (Algae, Bacteria)	1	*Ulva* spp.	Linnaeus, 1753 (Unaccepted: *Enteromorpha* spp. Link, 1820)	Algae mats				
Both	OTHER source (Algae, Bacteria)	2	*Chaetomorpha linum*	(O.F.Müller) Kützing, 1845	Filamentous green algae				
Both	OTHER source (Algae, Bacteria)	3	*Cladophora* sp.	Kützing, 1843	green algae (branched filaments)				
Both	OTHER source (Algae, Bacteria)	4	*Ulothrix* sp.	Kützing, 1833	Filamentous green algae				
Both	OTHER source (Algae, Bacteria)	5	*Rhizoclonium* sp.	Kützing, 1843	Filamentous green algae (mats around grass)				
Both	OTHER source (Algae, Bacteria)	6	*Vaucheria litorea*	C.Agardh, 1823	Mat-forming filamentous yellow-green				
Both	OTHER source (Algae, Bacteria)	7	Diatoms e.g., *Pinnularia* and *Navicula*		Phytoplankton/Pennate Diatoms				
Both	OTHER source (Photosynthetic Protist)	8	Dinoflagellates (e.g., *Peridinium*, *Protoperidinium*)		dinoflagellates				
Both	OTHER source (Algae, Bacteria)	9	Unspecified e.g., *Lyngbya, Microcoleus, Schizothrix*		Blue-green filamentous algae				
Both	OTHER source (Algae, Bacteria)	10	Bacteria		Unspecified Bacteria				
Chezz	OTHER source (Algae, Bacteria)	11	e.g., *Anabaena*	Bory de Saint-Vincent ex Bornet & Flahault, 1886	Bluegreen cyanobacteria - planktonic				
Chezz	OTHER source (Algae, Bacteria)	12	e.g., *Spirogyra*	Link, 1820	filamentous FW algae				
both	OTHER source (Algae, Bacteria)	13	Marine Detritus		Marine detritus				
both	OTHER source (Algae, Bacteria)	14	Terrestrial Detritus		Terrestrial detritus				
both	OTHER source (Algae, Bacteria)	15	Carrion		Carrion (dead animals)				
Chezz	OTHER source (Algae, Bacteria)	16*	*Xanthoria parietina*	(L.) Beltr., 1858	sunburst lichen (on rocks in LM/MM)				
Chezz	PLANTS	17	*Zostera marina*	Linnaeus, 1753	Eelgrass				
Chezz	PLANTS	18	*Ruppia maritima*	Linnaeus, 1753	Widgeon grass				
both	PLANTS	19	*Spartina alterniflora*	Loisel	Saltwater cordgrass				

both	PLANTS	20	*Spartina patens*	(Aiton) Muhl	Saltmeadow grass	
Chezz	PLANTS	21	*Spartina pectinata*	Bosc ex Link	freshwater cordgrass	
both	PLANTS	22	*Juncus gerardii*	Loisel	Rushes	
Chezz	PLANTS	23	*Juncus balticus*	Willd	Baltic rush	
Chezz	PLANTS	24	*Limonium carolinianum*	(Walter) Britton	Sea lavender	
both	PLANTS	25	*Salicornia maritima*	Wolff & Jefferies	Annual Glasswort	
Chezz	PLANTS	26	*Carex paleaceaBolboschoenus maritimus*	Schreb. ex Wahlenb.	chaffy Sedge /bulrush	
Chezz	PLANTS	27	*Glaux/Lysimachia maritima*	(L.) Galasso, Banfi & Soldano	Sea Milkwort	
Chezz	PLANTS	28	*Triglochin maritima*	L.	Arrow grass	
Chezz	PLANTS	29	*Solidago sempervirens*	L.	Seaside goldenrod	
Chezz	PLANTS	30	*Spergularia* spp. (*S. marina S. canadensis*)	(L.) Griseb / (Pers.) G. Don	sand spurrey	
Chezz	PLANTS	31	*Suaeda maritima*	(L.) Dumort	Herbaceous seepweed (sea blite)	
Chezz	PLANTS	32	*Puccinellia maritima*	(Huds.) Parl.	seaside alkali grass	
both	PLANTS	33	*Distichlis spicata*	(L.) Greene	saltgrass	
Chezz	PLANTS	34	*Atriplex* sp. (eg. *A. patula A. glabriuscula*)	L.	orache/spearscale	
Chezz	PLANTS	35	*Festuca rubra*	L.	red fescue grass	
Chezz	PLANTS	36	*Hierochloe odorata*	(L.) P. Beauv.	sweet grass	
Chezz	PLANTS	37	*Potentilla anserina*	L.	silverweed cinquefoil	
Chezz	PLANTS	38	*Caltha palustris*	L.	salt marsh buttercup	
Chezz	PLANTS	39	*Calamagrostis canadensis*	(Michx.) P.Beauv.	marsh reedgrass	
Both	PLANTS	40	*Plantago maritima*	L.	seaside plantain	
Chezz	FORAMINIFERA	41	*Haplophragmoides manilianensis*	Andersen, 1952		
Both	FORAMINIFERA	42	*Miliammina fusca*	Brady, 1870		
Chezz	FORAMINIFERA	43	*Polysaccammina ipohalina*	Scott, 1976		
Chezz	FORAMINIFERA	44	*Tiphotrocha comprimata*	Cushman & Brönnimann, 1948		
Both	FORAMINIFERA	45	*Trochammina inflata*	Montagu, 1808		
Chezz	FORAMINIFERA	46	*Ammobaculites dilatatus*	Cushman & Brönnimann, 1948		

Both	FORAMINIFERA	47	*Jadammina macrescens*	Brady, 1870		
Both	FORAMINIFERA	48	*Ammonia beccarii*	Linnaeus, 1758		
Both	FORAMINIFERA	49	*Helenina anderseni*	Warren, 1957		
Both	FORAMINIFERA	50	*Quinqueloculina seminula*	Linnaeus, 1758		
Both	FORAMINIFERA	51	*Haynesina orbiculare*	Brady, 1881		
Both	FORAMINIFERA	52	*Elphidium williamsoni*	Haynes, 1973		
Chezz	FORAMINIFERA	53	Thecamoebians			
Chezz	CNIDARIA	54	*Nematostella vectensis*	Stephenson, 1935	starlet sea anemone	
Both	CNIDARIA	55	*Protohydra leuckarti*	Greeff, 1870	hydrozoan	
Both	TURBELLARIAN	56	*Macrostomum* sp.	Schmidt, 1848	flatworm	
Windsor	TURBELLARIAN	57	*Pleioplana atomata*	Müller OF, 1776	flatworm	
Chezz	TURBELLARIAN	58	*Euplana gracilis*	Girard, 1853	flatworm	
Windsor	ACOELA	59	*Neochildia* sp.	Bush, 1975	acoelomorph	
Both	NEMERTEA	60	*Cerebratulus fuscus*	McIntosh, 1874	ribbon worm	
Windsor	NEMERTEA	61	*Oerstedia dorsalis*	Abildgaard, 1806	ribbon worm	
Both	NEMERTEA	62	*Micrura leidyi*	Verrill, 1892	ribbon worm	
Windsor	NEMERTEA	63	*Lineus viridis*	Müller, 1774	ribbon worm	
Both	NEMATODA	64	Nematode A e.g., *Diplolaimelloides* sp.		A -- Bacteria/organic matter	
Both	NEMATODA	65	Nematode B e.g., *Neochromadora* sp.		B -- Diatom/algae feeders	
Both	NEMATODA	66	Nematode C e.g., *Odontophora* sp.		C -- Scavengers	
Both	NEMATODA	67	Nematode D e.g., *Enoplus* and *Enoploides* sp.		D -- Predators	
Windsor	KINORHYNCHA	68	*Pycnophyes* sp.	Zelinka, 1907	kinorhynchan (mud dragon)	
Both	MOLLUSCA GASTROPODA	69	*Alderia modesta*	Lovén, 1844	Sarcasson sea slug	
Both	MOLLUSCA GASTROPODA	70	*Stiliger (Ercolania) fuscata*	Gould, 1870	Sarcasson sea slug	
Both	MOLLUSCA GASTROPODA	71	*Tritia (Ilyanassa) obsoleta*	Say, 1822	Eastern mud snail	
Both	MOLLUSCA GASTROPODA	72	*Ecrobia (Hydrobia) truncata*	Vanatta, 1924	tiny salt marsh snail	
Both	MOLLUSCA GASTROPODA	73	*Littorina littorea*	Linnaeus, 1758	common periwinkle	



Both	MOLLUSCA GASTROPODA	74	*Littorina saxatilis*	Olivi, 1792	rough periwinkle	
Chezz	MOLLUSCA GASTROPODA	75	*Melampus bidentatus*	Say, 1822	coffee bean snail	
Windsor	MOLLUSCA GASTROPODA	76	*Boonea bisuturalis*	Say, 1822	ectoparasitic snail	
Chezz	MOLLUSCA BIVALVIA	77	*Geukensia demissa*	Dillwyn, 1817	Ribbed mussel	
Both	MOLLUSCA BIVALVIA	78	*Mya arenaria*	Linnaeus, 1758	Soft-shelled clam	
Windsor	MOLLUSCA BIVALVIA	79	*Limecola (Macoma) balthica*	Linnaeus, 1758	Balthic clam	
Both	MOLLUSCA BIVALVIA	80	*Gemma gemma*	Totten, 1834	Amethyst gem clam	
Chezz	ANNELIDA OLIGOCHAETA	81	*Marionina* sp.	Michaelsen in Pfeffer, 1890	Enchytraeidae oligochaete	
Both	ANNELIDA OLIGOCHAETA	82	*Cernosvitoviella sp.*	Nielsen & Christensen, 1959	Enchytraeidae oligochaete	
Both	ANNELIDA OLIGOCHAETA	83	*Monopylephorus sp.*	Levinsen, 1884	Tubificidae species	
Both	ANNELIDA OLIGOCHAETA	84	*Tubificoides spp.*	Lastočkin, 1937	Tubificidae species	
Both	ANNELIDA OLIGOCHAETA	85	*Clitellio arenarius*	Müller, 1776	Tubificidae species	
Both	ANNELIDA OLIGOCHAETA	86	*Paranais litoralis*	Müller, 1780	Naididae species	
Both	ANNELIDA POLYCHAETA	87	*Polydora sp. (cornuta or ligni)*	Bosc, 1802	Spionidae species	
Both	ANNELIDA POLYCHAETA	88	*Pygospio elegans*	Claparède, 1863	Spionidae species	
Both	ANNELIDA POLYCHAETA	89	*Streblospio benedicti*	Webster, 1879	Spionidae species	
Windsor	ANNELIDA POLYCHAETA	90	*Spio filicornis*	Müller, 1776	Spionidae species	
Both	ANNELIDA POLYCHAETA	91	*Capitella capitata*	Fabricius, 1780	Capitellidae species	
Both	ANNELIDA POLYCHAETA	92	*Notomastus latericeus*	Sars, 1851	Capitellidae species	
Both	ANNELIDA POLYCHAETA	93	*Heteromastus filiformis*	Claparède, 1864	Capitellidae species	
Both	ANNELIDA POLYCHAETA	94	*Hobsonia florida*	Hartman, 1951	Ampharetidae species	
Both	ANNELIDA POLYCHAETA	95	*Fabricia stellaris*	Müller, 1774	Sabellidae species	
Windsor	ANNELIDA POLYCHAETA	96	*Manayunkia aestuarina*	Bourne, 1883	Sabellidae species	
Both	ANNELIDA POLYCHAETA	97	*Hediste diversicolor*	O.F. Müller, 1776	Nereidae species (e.g., clam worms, rag worms)	
Both	ANNELIDA POLYCHAETA	98	*Nereis pelagica*	Linnaeus, 1758	Nereidae species (e.g., clam worms, rag worms)	
Windsor	ANNELIDA POLYCHAETA	99	*Alitta virens*	M. Sars, 1835	Nereidae species (e.g., clam worms, rag worms)	
Chezz	ANNELIDA POLYCHAETA	100	*Tharyx* sp.	Webster & Benedict, 1887	Cirratulidae species	

Both	ANNELIDA POLYCHAETA	101	*Eteone* sp.	Savigny, 1818	Phyllodocidae species (blood worms)	
Windsor	ANNELIDA POLYCHAETA	102	*Glycera dibranchiata*	Ehlers, 1868	Phyllodocidae species (blood worms)	
Both	ANNELIDA POLYCHAETA	103	*Phyllodoce mucosa*	Örsted, 1843	Phyllodocidae species (blood worms)	
Both	ANNELIDA POLYCHAETA	104	*Nephtys* sp.	Cuvier, 1817	Nephtydiae species	
Both	ANNELIDA POLYCHAETA	105	*Terebella* sp.	Linnaeus, 1767	Terebellidae species	
Windsor	ANNELIDA POLYCHAETA	106	*Scoletoma fragilis*	O.F. Müller, 1776	Lumbrineridae species	
Chezz	ANNELIDA POLYCHAETA	107	*Leitoscoloplos fragilis*	Verrill, 1873	Orbiniidae species	
Both	CRUSTACEA COPEPODA	108	*Nannopus palustris*	Brady, 1880	Harpacticoid	
Both	CRUSTACEA COPEPODA	109	*Heterolaophonte* sp.	Lang, 1948	Harpacticoid	
Both	CRUSTACEA COPEPODA	110	*Coullana canadensis*	Willey, 1923	Harpacticoid	
Chezz	CRUSTACEA COPEPODA	111	*Tachidius brevicornis*	Lilljeborg, 1853	Harpacticoid	
Windsor	CRUSTACEA COPEPODA	112	*Pseudodiaptomus pelagicus*	Herrick, 1884	Calanoid	
Windsor	CRUSTACEA COPEPODA	113	*Eurytemora herdmani*	Thompson, Scott & Herdman, 1897	Calanoid	
Windsor	CRUSTACEA COPEPODA	114	*Acartia tonsa*	Dana, 1849	Calanoid	
Windsor	CRUSTACEA COPEPODA	115	*Pseudocalanus* sp.	Boeck, 1872	Calanoid	
Both	CRUSTACEA COPEPODA	116	*Temora longicornis*	Müller O.F., 1785	Calanoid	
both	CRUSTACEA COPEPODA	117	*Halicyclops magniceps*	Lilljeborg, 1853	Cyclopoid	
Chezz	CRUSTACEA COPEPODA	118	*Mesocyclops edax*	Forbes, 1891	Cyclopoid	
both	CRUSTACEA OSTRACODA	119	*Muellerina (Cythere) canadensis*	Brady, 1870	Cytheridae ostracods	
both	CRUSTACEA OSTRACODA	120	*Candona* sp.	Baird, 1845	Candonidae ostracods	
Chezz	CRUSTACEA OSTRACODA	121	*Leptocythere darbyi*	Keyser, 1975	ostracod	
Chezz	CRUSTACEA OSTRACODA	122	*Cyprideis salebrosa*	Bold, 1963	ostracod	
Chezz	CRUSTACEA OSTRACODA	123	*Cytherura gibba*	Mueller, 1785	ostracod	
Chezz	CRUSTACEA OSTRACODA	124	*Cytheromorpha curta*	Edwards, 1944	ostracod	
Both	CRUSTACEA AMPHIPODA	125	*Gammarus palustris*	Bousfield, 1969	Gammarid amphipod	
Both	CRUSTACEA AMPHIPODA	126	*Gammarus locusta*	Linnaeus, 1758	Gammarid amphipod	
Both	CRUSTACEA AMPHIPODA	127	*Gammarus oceanicus*	Segerstråle, 1947	Gammarid amphipod	

Both	CRUSTACEA AMPHIPODA	128	*Gammarus mucronatus*	Say, 1818	Gammarid amphipod	
Both	CRUSTACEA AMPHIPODA	129	*Americorchestia (Talorchestia) longicornis*	Say, 1818	Gammarid amphipod	
Both	CRUSTACEA AMPHIPODA	130	*Psammonyx nobilis*	Stimpson, 1853	lysianassid amphipod	
Windsor	CRUSTACEA AMPHIPODA	131	*Corophium volutator*	Pallas, 1766	Corophium amphipod	
Chezz	CRUSTACEA AMPHIPODA	132	*Orchestia grillus*	Bosc, 1802	Amphipod	
Chezz	CRUSTACEA AMPHIPODA	133	*Orchestia gammarellus*	Pallas, 1766	Amphipod	
Chezz	CRUSTACEA AMPHIPODA	134	*Uhlorchestia spartinophila*	Bousfield & Heard, 1986	Salt marsh amphipod	
Chezz	CRUSTACEA AMPHIPODA	135	*Melita nitida*	Smith, 1873	Amphipod	
Chezz	CRUSTACEA AMPHIPODA	136	*Leptochelia rapax*	Harger, 1879	Tanaid amphipod (look like tiny shrimp)	
Both	CRUSTACEA ISOPODA	137	*Jaera albifrons*	Leach, 1814	Isopod	
Both	CRUSTACEA ISOPODA	138	*Idotea phosphorea*	Harger, 1873	Isopod	
Chezz	CRUSTACEA ISOPODA	139	*Oniscus asellus*	Linnaeus, 1758	sow bug	
Chezz	CRUSTACEA ISOPODA	140	*Porcellio scaber*	Latreille, 1804	sow bug	
Windsor	CRUSTACEA MYSIDAE	141	*Neomysis americana*	Smith, 1873	mysid shrimp	
Both	CRUSTACEA DECAPODA	142	*Carcinus maenas*	Linnaeus, 1758	Green crab	
Both	CRUSTACEA DECAPODA	143	*Hyas* sp.	Leach, 1814	Toad crab	
Both	CRUSTACEA DECAPODA	144	*Palaemon (Palaemonetes) pugio*	Holthuis, 1949	Grass shrimp	
Both	CRUSTACEA DECAPODA	145	*Crangon septemspinosa*	Say, 1818	Sand shrimp	
Chezz	HEXAPODA ENTOGNATHA	146	*Anurida maritima*	Guérin-Méneville, 1836	Springtail	
Chezz	HEXAPODA ENTOGNATHA	147	Symphypleona species		Globular springtail	
Both	INSECTA DIPTERA	148	*Chironomus plumosus*	Linnaeus, 1758	non biting midge Chironomidae	
Both	INSECTA DIPTERA	149	*Culicoides sp.*	Latreille, 1809	Ceratopogonidae biting midge	
Chezz	INSECTA DIPTERA	150	*Dasyhelea* sp.		Ceratopogonidae (not)biting midge	
Both	INSECTA DIPTERA	151	*Tabanus nigrovittatus*	Macquart, 1847	Tabanidae salt marsh greenhead fly	
Both	INSECTA DIPTERA	152	*Hybomitra frontalis*	Walker, 1848	Tabanidae horsefly	
Both	INSECTA DIPTERA	153	*Chrysops carbonarius*	Walker, 1848	Tabanidae deerfly	
Both	INSECTA DIPTERA	154	Ephydridae *(e.g., Ephydra sp., Paracoenia fumosalis, Scatella sp.)*		Ephydridae shore fly	

Both	INSECTA DIPTERA	155	*Dolichopus sp.*		Dolichopodidae long-legged flies				
Chezz	INSECTA DIPTERA	156	Syrphidae (e.g., *Brachypalpus oarus, Eristalis dimidiata*)		Syrphidae hover fly				
Both	INSECTA DIPTERA	157	*Aedes (Ochlerotatus) sollicitans*	Walker, 1856	Culicidae Eastern salt marsh mosquito				
Both	INSECTA DIPTERA	158	*Aedes (Ochlerotatus) cantator*	Coquillett, 1903	Culicidae Brown salt marsh mosquito				
Chezz	INSECTA HEMIPTERA	159	*Trichocorixa verticalis*	Fieber, 1851	salt panne water boatman Coroxidae				
Both	INSECTA HEMIPTERA	160	Saldidae (e.g., *Micracanthia humilis, Pentacora sphacealata, Saldula pallipes*)	Amyot and Serville, 1843	shore bug Salidae				
Both	INSECTA HEMIPTERA	161	*Trigonotylus uhleri*	Reuter, 1876	plant bug Miridae				
Chezz	INSECTA HEMIPTERA	162	*Prokelisia marginata/dolus*	Van Duzee, 1897	Salt marsh plant hopper Delphacidae				
Chezz	INSECTA HEMIPTERA	163	*Draeculacephala sp.*		leafhopper Cicadellidae				
Both	INSECTA HEMIPTERA	164	*Philaenarcys spartina*	Hamilton, 1979	Salt marsh spittle bug Aphrophoridae				
Chezz	INSECTA HEMIPTERA	165	*Uroleucon pseudambrosiae*	Olive, 1963	Aphididae on Iva and Juncus				
Chezz	INSECTA HEMIPTERA	166	*Hyalopterus pruni*	Geoffroy	Mealy Plum Aphid Aphididae				
Chezz	INSECTA HEMIPTERA	167	*Staticobium staticis*	Theobald	Sea lavendar aphid Aphididae				
Chezz	INSECTA HEMIPTERA	168	*Mesovelia mulsanti*	White, 1879	Water treader Mesoveliidae				
Chezz	INSECTA HEMIPTERA	169	*Limnoporus sp.*	Stål, 1868	Water strider Gerridae				
Both	INSECTA ODONATA	170	*Erythrodiplax berenice*	Drury, 1773	seaside dragonlet Libellulidae				
Chezz	INSECTA ODONATA	171	*Sympetrum sp*	Newman, 1833	meadowhawk Libellulidae				
Chezz	INSECTA ODONATA	172	*Enallagma sp*	Charpentier, 1840	blue damselfly Coenagrionidae				
Both	INSECTA ORTHOPTERA	173	*Conocephalus spartinae*	Fox, 1912	Katydids salt masrsh Tettigoniidae				
Chezz	INSECTA ORTHOPTERA	174	*Scudderia furcata*	Brunner, 1878	fork-tailed bush katydid Tettigoniidae				
Chezz	INSECTA ORTHOPTERA	175	*Chorthippus curtipennis*	Harris, 1835	Marsh meadow grasshopper Acrididae				
Both	INSECTA ORTHOPTERA	176	*Paroxya sp.*	Scudder, 1877	swamp grasshopper Acrididae				
Chezz	INSECTA ORTHOPTERA	177	*Dichromorpha viridis*	Scudder, 1863	Short-winged green grasshopper Acrididae				
Both	INSECTA ORTHOPTERA	178	*Metaleptea brevicornis*	Johannson, 1763	clipped-winged grasshopper Acrididae				
Chezz	INSECTA NEUROPTERA	179	*Chrysopa sp.*	Leach in Brewster, 1815	Green lacewing Chrysopidae				
Chezz	INSECTA LEPIDOPTERA	180	*Cisseps fulvicollis*	Hübner, 1818	yellow collared moth Erebidae				
Chezz	INSECTA LEPIDOPTERA	181	*Celastrina sp.*	Tutt, 1906	Northern spring azure Lycaenidae				

Chezz	INSECTA LEPIDOPTERA	182	*Lycaena sp.*	[Fabricius], 1807	Copper species Lycaenidae				
Chezz	INSECTA LEPIDOPTERA	183	*Vanessa sp.*	[Fabricius], 1807	Painted lady butterfly Nymphalidae				
Both	INSECTA LEPIDOPTERA	184	*Photedes enervata*	Guenée, 1852	Cordgrass moth Noctuidae				
Both	INSECTA LEPIDOPTERA	185	*Doryodes grandipennis*	Barnes and McDunnough, 1918	Long-winged moth Noctuidae				
Both	INSECTA HYMENOPTERA	186	*Bombus* sp.	Latreille, 1802	Bumblebee Apidae				
Both	INSECTA COLEOPTERA	187	*Propylea quatuordecimpunctata*	Linnaeus, 1758	14 Spotted Lady Beetle Coccinellidae				
Chezz	INSECTA COLEOPTERA	188	*Harmonia axyridis*	Pallas, 1773	Asian Lady Beetle Coccinellidae				
Both	INSECTA COLEOPTERA	189	*Naemia seriata*	Melsheimer, 1847	Seaside Lady Beetle Coccinellidae				
Chezz	INSECTA COLEOPTERA	190	*Coccinella septempunctata*	Linnaeus, 1758	Seven-spotted ladybird Coccinellidae				
Chezz	INSECTA COLEOPTERA	191	*Enochrus hamiltoni*	Horn, 1890	water scavenger beetle Hydrophilidae				
Chezz	INSECTA COLEOPTERA	192	*Tropisternus quadristriatus*	Horn, 1871	water scavenger beetle Hydrophilidae				
Both	INSECTA COLEOPTERA	193	*Aeletes politus*	J. L. LeConte, 1853	hister beetle Histeridae				
Chezz	INSECTA COLEOPTERA	194	*Bembidion* sp.	Latreille, 1802	ground beetle Carabidae				
Chezz	INSECTA COLEOPTERA	195	*Cicindela* sp.	Linnaeus, 1758	tiger beetle Carabidae				
Chezz	INSECTA COLEOPTERA	196	*Dyschiriodes sellatus*	Leconte, 1857	Carabid beetle				
Chezz	INSECTA COLEOPTERA	197	*Bledius basalis*	LeConte, 1863	salt marsh rove beetle Staphylinidae				
Chezz	INSECTA COLEOPTERA	198	*Brachygluta abdominalis*	Aubé, 1833	coastal rove beetle				
both	INSECTA COLEOPTERA	199	*Cimberis pallipennis*	Blatchley and Leng, 1916	weevil Nemonychidae				
Chezz	INSECTA COLEOPTERA	200	*Necrophila americana*	Linnaeus, 1758	carrion beetle Silphidae				
Both	INSECTA COLEOPTERA	201	*Ellychnia corrusca*	Linnaeus, 1767	firefly Lampyridae				
Windsor	INSECTA COLEOPTERA	202	*Pyropyga decipiens*	Harris, 1836	firefly Lampyridae				
Both	INSECTA COLEOPTERA	203	*Photuris fairchildi*	Barber, 1951	firefly Lampyridae				
Chezz	ARACHNIDA ARANEAE	204	*Araneus diadematus*	Clerck, 1757	Cross orbweaver				
Chezz	ARACHNIDA ARANEAE	205	*Argiope aurantia*	Lucas, 1833	Yellow and black garden spider				
both	ARACHNIDA ARANEAE	206	*Dolomedes triton*	Walckenaer, 1837	Six-spotted fishing spider				
both	ARACHNIDA ARANEAE	207	*Pardosa littoralis*	Banks, 1896	Thin legged wolf spider lycosidae				
Chezz	ARACHNIDA ARANEAE	208	*Dysdera crocata*	C. L. Koch, 1838	Pill bug eater				

Chezz	ARACHNIDA ARANEAE	209	*Grammonota trivittata*	Banks, 1895	Dwarf-weaver spider	
Both	ARACHNIDA ARANEAE	210	*Clubiona saltitans*	Emerton, 1919	leaf-curling sac spider	
Both	ARACHNIDA ARANEAE	211	*Glenognatha sp.*	Simon, 1887	long-jawed orb weaver spider	
Both	ARACHNIDA ARANEAE	212	*Enoplognatha sp.*	Pavesi, 1880	Salt marsh spider	
Chezz	ARACHNIDA ARANEAE	213	*Araniella displicata*	Hentz, 1847	6-spotted orbweaver	
both	ARACHNIDA ACARI	214	Anystidae e.g *Anystis sp.*		whirligig mites	
Chezz	ARACHNIDA ACARI	215	Euzetidae e.g *Euzetes sp.*		(smooth) Soil mite	
Both	ARACHNIDA ACARI	216	Liacaridae e.g., *Xenillus sp.*	Sellnick, 1928	Oribatida (ornamented) soil mite	
Both	ARACHNIDA ACARI	217	Trombiculidae e.g., *Ocypete sp*		red chigger (velvet) mite	
Both	ARACHNIDA ACARI	218	Arrenuridae e.g., Arrenurus sp.		salt marsh water mites	
Both	FISH CYPRINODONTIFORMES	219	*Fundulus heteroclitus*	Linnaeus, 1766	Mummichog/ killifish	
Both	FISH PERCIFORMES	220	*Marone saxatilis*	Walbaum, 1792	Striped bass	
Windsor	FISH PERCIFORMES	221	*Morone americana*	Gmelin, 1789	White perch	
Both	FISH CLUPEIFORMES	222	*Alosa pseudoharengus*	Wilson, 1811	Gaspereau/Alewife	
Windsor	FISH CLUPEIFORMES	223	*Alosa aestivalis*	Mitchill, 1814	Blue herring	
Both	FISH ANGUILLIFORMES	224	*Anguilla rostrata*	Lesueur, 1817	American eels	
Both	FISH ATHERINIFORMES	225	*Menidia menidia*	Linnaeus, 1766	Atlantic silverside	
Both	FISH GASTEROSTEIFORMES	226	*Pungitius pungitius*	Linnaeus, 1758	Ninespine stickleback	
Both	FISH GASTEROSTEIFORMES	227	*Gasterosteus aculeatus*	Linnaeus, 1758	Threespine stickleback	
Both	FISH SALMONIFORMES	228	*Salmo salar*	Linnaeus, 1758	Atlantic salmon	
Chezz	FISH SYNGNATHIFORMES	229	*Syngnathus fuscus*	Storer, 1839	northern pipefish	
Both	FISH PLEURONECTIFORMES	230	*(Pseudo)pleuronectes americanus*	Walbaum, 1792	Winter Flounder	
Windsor	FISH PLEURONECTIFORMES	231	*Pleuronectes putnami*	Gill, 1864	Smooth Flounder	
Windsor	FISH GADIFORMES	232	*Microgadus tomcod*	Walbaum, 1792	Tomcod	
Windsor	FISH OSMERIFORMES	233	*Osmerus mordax*	Mitchill, 1814	Rainbow smelt	
Both	BIRD CHARADRIIFORMES	234	*Charadrius semipalmatus*	Bonaparte, 1825	semipalmated plover	
Both	BIRD CHARADRIIFORMES	235	*Tringa semipalmata*	Gmelin, JF, 1789	willet	

Both	BIRD CHARADRIIFORMES	236	*Tringa melanoleuca*	Gmelin, JF, 1789	Greater yellowlegs	
Both	BIRD CHARADRIIFORMES	237	*Tringa flavipes*	Gmelin, JF, 1789	Lesser yellowlegs	
Both	BIRD CHARADRIIFORMES	238	*Calidris minutilla*	Vieillot, 1819	least sandpiper (stints)	
Both	BIRD CHARADRIIFORMES	239	*Calidris pusilla*	Linnaeus, 1766	semipalmated sandpiper	
Windsor	BIRD CHARADRIIFORMES	240	*Calidris alba*	Pallas, 1764	sanderling	
Windsor	BIRD CHARADRIIFORMES	241	*Calidris canutus*	Linnaeus, 1758	red knot	
Windsor	BIRD CHARADRIIFORMES	242	*Calidris fuscicollis*	Vieillot, 1819	white-rumped sandpiper	
Windsor	BIRD CHARADRIIFORMES	243	*Calidris alpina*	Linnaeus, 1758	dunlin	
Both	BIRD CHARADRIIFORMES	244	*Actitis macularius*	Linnaeus, 1766	spotted sandpiper	
Both	BIRD CHARADRIIFORMES	245	*Limnodromus griseus*	Gmelin, JF, 1789	short-billed dowitcher	
Windsor	BIRD CHARADRIIFORMES	246	*Pluvialis squatarola*	Linnaeus, 1758	Black-bellied plover	
Both	BIRD CHARADRIIFORMES	247	*Gallinago gallinago*	Linnaeus, 1758	Common snipe	
Both	BIRD CHARADRIIFORMES	248	*Larus smithsonianus*	Coues, 1862	American herring gull	
Both	BIRD CHARADRIIFORMES	249	*Larus marinus*	Linnaeus, 1758	Black-backed gulls	
Chezz	BIRD PASSERIFORMES	250	*Ammodramus nelsoni*	Allen, JA, 1875	Nelson's salt marsh sparrow	
Chezz	BIRD PASSERIFORMES	251	*Tachycineta bicolor*	Vieillot, 1808	Tree swallow	
Both	BIRD PASSERIFORMES	252	*Agelaius phoeniceus*	Linnaeus, 1766	red-winged black bird	
Both	BIRD PASSERIFORMES	253	*Cyanocitta cristata*	Linnaeus, 1758	Bluejay	
Both	BIRD PASSERIFORMES	254	*Corvus brachyrhynchos*	Brehm, CL, 1822	American crow	
Both	BIRD PASSERIFORMES	255	*Eremophila alpestris*	Linnaeus, 1758	Horned lark	
Chezz	BIRD GRUIFORMES	256	*Porzana carolina*	Linnaeus, 1758	Sora (Rail)	
Both	BIRD ANSERIFORMES	257	*Somateria mollissima*	Linnaeus, 1758	Common eider	
Both	BIRD ANSERIFORMES	258	*Anas rubripes*	Brewster, 1902	Black duck	
Both	BIRD ANSERIFORMES	259	*Anas/Spatula discors*	Linnaeus, 1766	Blue-winged teal	
Windsor	BIRD ANSERIFORMES	260	*Anas platyrhynchos*	Linnaeus, 1758	mallard	
Windsor	BIRD ANSERIFORMES	261	*Anas acuta*	Linnaeus, 1758	Northern pintail	
Windsor	BIRD ANSERIFORMES	262	*Anas crecca*	Linnaeus, 1758	green-winged teal	

Windsor	BIRD ANSERIFORMES	263	*Aix sponsa*	Linnaeus, 1758	Wood duck	
Windsor	BIRD ANSERIFORMES	264	*Aythya collaris*	Donovan, 1809	Ring-necked duck	
Both	BIRD ANSERIFORMES	265	*Branta canadensis*	Linnaeus, 1758	Canada goose	
Windsor	BIRD PELECANIFORMES	266	*Botaurus lentiginosus*	Rackett, 1813	American Bittern	
Both	BIRD CICONIIFORMES	267	*Ardea herodias*	Linnaeus, 1758	Great blue heron	
Both	BIRD CORACIIFORMES	268	*Megaceryle alcyon*	Linnaeus, 1758	Belted kingfisher	
Windsor	BIRD ACCIPITRIFORMES	269	*Circus cyaneus hudsonius*	Linnaeus, 1766	Marsh Hark (hen harrier)	
Both	BIRD ACCIPITRIFORMES	270	*Pandion haliaetus*	Linnaeus, 1758	Osprey	
Both	BIRD ACCIPITRIFORMES	271	*Haliaeetus leucocephalus*	Linnaeus, 1766	Bald Eagle	
Both	BIRD FALCONIFORMES	272	*Falco sparverius*	Linnaeus, 1758	American kestrel	
Both	BIRD FALCONIFORMES	273	*Falco columbarius*	Linnaeus, 1758	Merlin	
Both	BIRD STRIGIFORMES	274	*Strix varia*	Barton, 1799	Barred owl	
Both	MAMMALS CARNIVORA	275	*Procyon lotor*	Linnaeus, 1758	Raccoon	
Both	MAMMALS CARNIVORA	276	*Lutra canadensis*	Schreber, 1777	otter	
Windsor	MAMMALS CARNIVORA	277	*Vulpes vulpes*	Linnaeus, 1758	Red fox	
Chezz	MAMMALS CARNIVORA	278	*Mustela (Neovison) vison*	Schreber, 1777	American mink	
Both	MAMMALS RODENTIA	279	*Microtus pennsylvanicus*	Ord, 1815	Meadow vole	
Chezz	MAMMALS RODENTIA	280	*Ondatra zibethicus*	Linnaeus, 1766	Muskrat	
Both	MAMMALS EULIPOTYPHLA	281	*Sorex cinereus*	Kerr, 1792	Masked shrew	
Both	MAMMALS ARTIODACTYLA	282	*Odocoileus virginianus*	Zimmermann, 1780	White-tailed deer	

Appendix B-2: Amalgamation of nodes for creating low-resolution food webs, using IDs from Appendix B-1.

Location	Classification	Low Resolution ID	High Resolution Node IDs	Low Resolution Common name
Both	Basal	300	1, 2, 3, 4, 5, 6	Epipelic Algae
Both	Basal	301	7, 8, 9	Phytoplankton
Both	Basal	302	10, 11, 12	Bacteria
Both	Basal	303	13, 14	Detritus
Both	Basal	304	15	Carrion
Chezz	Basal	305	17, 18	Submergent vascular plants
Both	Basal	306	19, 20, 21, 22, 23	Spartina and Rushes
Both	Basal	307	25, 27, 31	Succulents
Both	Basal	308	26, 28, 32, 33, 35, 36, 39	Other grasses/sedges
Both	Basal	309	24, 29, 30, 34, 37, 38, 40	Flowering plants/shrubs
Both	Cnidarians	310	54, 55	Cnidarians
Both	Flatworms	311	56, 57, 58, 59, 60, 61, 62, 63	Turbellarians, Acoela, Nemertea
Both	Nematodes	312	64, 65, 66, 67	Nematodes
Both	Gastropods	313	69, 70	nudibranch
Both	Gastropods	314	71	mud snail
Both	Gastropods	315	73, 74	periwinkles
Chezz	Gastropods	316	75	coffee bean snail
Chezz	Bivalve	317	77	ribbed mussel
Both	Bivalve	318	78, 79, 80	clams
Both	Annelids	319	81, 82, 83, 84, 85, 86	oligochaetes
Both	Annelids	320	87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 107	polychaetes
Both	Copepods	321	108, 109, 110, 111, 112, 113, 114, 115, 116, 117, 118	copepods
Both	ostracods	322	119, 120, 121, 122, 123, 124	ostracods

Both	Amphipods	323	125, 126, 127, 128, 129, 130, 131, 132, 133, 134, 135, 136	amphipods
Both	isopods	324	137, 138	marine isopods
Chezz	isopods	325	139, 140	sowbugs
Both	Shrimp	326	141, 144, 145	shrimp
Both	Crabs	327	142, 143	crabs
Both	Diptera	328	148, 149, 150	midges
Both	Diptera	329	151, 152, 153	other biting flies
Both	Diptera	330	157, 158	mosquitoes
Both	Diptera	331	154, 155, 156	other flies
Chezz	Hemiptera	332	159	water boatmen Trichocorixa verticalis
Both	Hemiptera	333	160	shore bug Salidae
Both	Hemiptera	334	161, 162, 163, 164	plant bugs
Chezz	Hemiptera	335	165, 166, 167	Aphids
Chezz	Hemiptera	336	168, 169	water treaders/striders
Both	Odonata	337	170	Erythrodiplax berenice
Chezz	Odonata	338	171	Sympetrum sp
Chezz	Odonata	339	172	Enallagma sp
Both	Orthoptera	340	173, 174	Katydids
Both	Orthoptera	341	175, 176, 177, 178	Grasshoppers
Chezz	Neuroptera	342	179	Lacewing Chrysopa sp.
Both	Lepidoptera	343	180, 184, 185	moths
Chezz	Lepidoptera	344	181	Azure butterfly
Chezz	Lepidoptera	345	182	Copper butterfly
Chezz	Lepidoptera	346	183	painted lady butterfly
Both	Hymenoptera	347	186	Bumblebee
Both	Coleoptera	348	187, 188, 189, 190	Lady beetles
Chezz	Coleoptera	349	191, 192	water beetles
Chezz	Coleoptera	350	194, 195, 196	carabid beetles
Chezz	Coleoptera	351	197, 198	rove beetles
Both	Coleoptera	352	199	weevil
Chezz	Coleoptera	353	200	carrion beetle
Both	Coleoptera	354	201, 202, 203	fireflies
Both	Aranae	355	204, 205, 208, 209, 210, 211, 212, 213	weaver spiders
Both	Aranae	356	206, 207	fishing/wolf spiders

Both	Acari	357	214, 218	water mites
Both	Acari	358	215, 216, 217	soil/ground mites
Both	Fish	359	219	Mummichog/ killifish
Both	Fish	360	220	Striped bass
Windsor	Fish	361	221	White perch
Both	Fish	362	222	Gaspereau/Alewife
Windsor	Fish	363	223	Blue herring
Both	Fish	364	224	American eels
Both	Fish	365	225	Atlantic silverside
Both	Fish	366	226	Ninespine stickleback
Both	Fish	367	227	Threespine stickleback
Both	Fish	368	228	Atlantic salmon
Chezz	Fish	369	229	northern pipefish
Both	Fish	370	230	Winter Flounder
Windsor	Fish	371	231	Smooth Flounder
Windsor	Fish	372	232	Tomcod
Windsor	Fish	373	233	Rainbow smelt
Both	Birds	374	234	semipalmated plover
Both	Birds	375	235	willet
Both	Birds	376	236	Greater yellowlegs
Both	Birds	377	237	Lesser yellowlegs
Both	Birds	378	238	least sandpiper (stints)
Both	Birds	379	239	semipalmated sandpiper
Windsor	Birds	380	240	sanderling
Windsor	Birds	381	241	red knot
Windsor	Birds	382	242	white-rumped sandpiper
Windsor	Birds	383	243	dunlin
Both	Birds	384	244	spotted sandpiper
Both	Birds	385	245	short-billed dowitcher
Windsor	Birds	386	246	Black-bellied plover
Both	Birds	387	247	Common snipe
Both	Birds	388	248	American herring gull
Both	Birds	389	249	Black-backed gulls
Chezz	Birds	390	250	Nelson's salt marsh sparrow
Chezz	Birds	391	251	Tree swallow
Both	Birds	392	252	red-winged black bird
Both	Birds	393	253	Bluejay
Both	Birds	394	254	American crow
Both	Birds	395	255	Horned lark
Chezz	Birds	396	256	Sora (Rail)
Both	Birds	397	257	Common eider
Both	Birds	398	258	Black duck
Both	Birds	399	259	Blue-winged teal

Windsor	Birds	400	260	mallard
Windsor	Birds	401	261	Northern pintail
Windsor	Birds	402	262	green-winged teal
Windsor	Birds	403	263	Wood duck
Windsor	Birds	404	264	Ring-necked duck
Both	Birds	405	265	Canada goose
Windsor	Birds	406	266	American Bittern
Both	Birds	407	267	Great blue heron
Both	Birds	408	268	Belted kingfisher
Windsor	Birds	409	269	Marsh Hark (hen harrier)
Both	Birds	410	270	Osprey
Both	Birds	411	271	Bald Eagle
Both	Birds	412	272	American kestrel
Both	Birds	413	273	Merlin
Both	Birds	414	274	Barred owl
Both	Mammals	415	275	Raccoon
Both	Mammals	416	276	otter
Windsor	Mammals	417	277	Red fox
Chezz	Mammals	418	278	American mink
Both	Mammals	419	279	Meadow vole
Chezz	Mammals	420	280	Muskrat
Both	Mammals	421	281	Masked shrew
Both	Mammals	422	282	White-tailed deer

Appendix B-3: Statistical tables of mean (± standard deviations) trophic levels and connectivity values for resolutions, marshes, zones, and trophic groups (Tables 1 – 14) from food webs in Chapter 3. Coefficient of Variation (CV) statistics are in Table 15. Statistically significant differences ($p<0.05$) are shown in bold. Kruskal-Wallis non-parametric tests used for *k*-samples (K), Mann-Whitney non-parametric tests used for 2 samples (U). All data organized for these statistical tests can be found in Supplement B-4.

1. Comparison of Taxonomic Resolutions for Nova Scotia webs (Chezzetcook + Windsor).

Resolution	All species connecti vity	All species trophic level	Basal species connectivity	Invertebrate connectivity	Invertebrate trophic level	Vertebrate connectivity	Vertebrate trophic level
High	1 ±0.61	2.39 ±0.78	0.62 ±0.39	0.98 ±0.54	2.48 ±0.55	1.39 ±0.68	3.09 ±0.40
Medium	1 ±0.59	2.38 ±0.78	0.60 ±0.35	0.95 ±0.52	2.45 ±0.55	1.38 ±0.67	3.06 ±0.40
Low	1 ±0.50	2.78 ±0.80	0.75 ±0.21	1.16 ±0.62	2.63 ±0.71	0.92 ±0.39	3.16 ±0.43
K (observed, critical)	1.42, 5.99	25.92, 5.99	5.54, 5.99	7.31, 5.99	4.03, 5.99	20.41, 5.99	1.88, 5.99
p-value	0.491	**<0.0001**	0.063	**0.026**	0.134	**<0.0001**	0.391

2. Comparison of connectivity and trophic level of taxonomic groups in Nova Scotia webs (Chezzetcook + Windsor) for each resolution.

Taxonomic Groups	High Res connectivity	High Res trophic level	Medium Res connectivity	Medium Res trophic level	Low Res connectivity	Low Res trophic level
Invertebrates	0.98 ±0.54	2.48 ±0.55	0.95 ±0.52	2.45 ±0.55	1.16 ±0.62	2.63 ±0.71
Vertebrates	1.39 ±0.68	3.09 ±0.40	1.38 ±0.67	3.06 ±0.40	0.92 ±0.39	3.16 ±0.43
U , expected	3407, 5280	2143, 5280	3272, 5280	2117, 5280	1941, 1568	872, 1568
p-value	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.031**	**<0.0001**

3. Comparison of Taxonomic Resolutions for Windsor webs.

Resolution	All species connecti vity	All species trophic level	Basal species connectivity	Invertebrate connectivity	Invertebrate trophic level	Vertebrate connectivity	Vertebrate trophic level
High	1 ±0.51	2.56 ±0.78	0.67 ±0.44	0.98 ±0.47	2.51 ±0.57	1.19 ±0.54	3.22 ±0.42
Medium	1 ±0.49	2.52 ±0.76	0.63 ±0.40	0.96 ±0.45	2.46 ±0.58	1.19 ±0.52	3.10 ±0.36
Low	1 ±0.49	2.85 ±0.84	0.64 ±0.20	1.26 ±0.64	2.63 ±0.73	0.91 ±0.34	3.27 ±0.43
K (observed, critical)	0.14, 5.99	16.1, 5.99	0.99, 5.99	8.62, 5.99	2.23, 5.99	12.33, 5.99	7.46, 5.99
p-value	0.934	**0.000**	0.610	**0.013**	0.328	**0.002**	**0.024**

4. Comparison of connectivity and trophic level of taxonomic groups in Windsor webs for each resolution.

Taxonomic Groups	High Res connectivity	High Res trophic level	Medium Res connectivity	Medium Res trophic level	Low Res connectivity	Low Res trophic level
Invertebrates	0.98 ±0.47	2.54 ±0.57	0.96 ±0.45	2.46 ±0.58	1.26 ±0.64	2.63 ±0.73
Vertebrates	1.19 ±0.54	3.22 ±0.42	1.19 ±0.52	3.10 ±0.36	0.91 ±0.34	3.27 ±0.43
U , expected	2353, 3103	1072, 3103	2254, 3103	1161, 3103	1315, 957	485, 957
p-value	**0.011**	**<0.0001**	**0.004**	**<0.0001**	**0.003**	**<0.0001**

5. Comparison of Taxonomic Resolutions for Chezzetcook webs.

Resolution	All species connectivity	All species trophic level	Basal species connectivity	Invertebrate connectivity	Invertebrate trophic level	Vertebrate connectivity	Vertebrate trophic level
High	1 ±0.63	2.33 ±0.79	0.63 ±0.36	0.98 ±0.54	2.48 ±0.56	1.54 ±0.76	3.07 ±0.42
Medium	1 ±0.62	2.32 ±0.80	0.60 ±0.30	0.95 ±0.53	2.44 ±0.56	1.51 ±0.75	3.04 ±0.41
Low	1 ±0.46	2.77 ±0.85	0.69 ±0.17	1.07 ±0.53	2.63 ±0.67	0.99 ±0.39	3.28 ±0.45
K (observed, critical)	2.7, 5.99	27.9, 5.99	4.25, 5.99	4.42, 5.99	4.87, 5.99	15.21, 5.99	10.14, 5.99
p-value	0.259	**<0.0001**	0.119	0.110	0.088	**0.000**	**0.006**

6. Comparison of connectivity and trophic level of taxonomic groups in Chezzetcook webs for each resolution.

Taxonomic Groups	High Res connectivity	High Res trophic level	Medium Res connectivity	Medium Res trophic level	Low Res connectivity	Low Res trophic level
Invertebrates	0.98 ±0.54	2.48 ±0.56	0.95 ±0.53	2.44 ±0.56	1.07 ±0.53	2.63 ±0.67
Vertebrates	1.52 ±0.76	3.07 ±0.42	1.51 ±0.75	3.04 ±0.41	0.99 ±0.39	3.28 ±0.45
U , expected	1974, 3358	1418, 3358	1881, 3358	1427, 3358	1178.5, 1127	554, 1127
p-value	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.704	**<0.0001**

7. Comparison of Windsor and Chezzetcook high-resolution node values for different taxonomic groups.

Marsh	All species connectivity	All species trophic level	Basal species connectivity	All invertebrate connectivity	All invertebrate trophic level	All vertebrate connectivity	All vertebrate trophic level
Windsor	1 ±0.51	2.56 ±0.78	0.67 ±0.44	0.98 ±0.47	2.52 ±0.57	1.19 ±0.54	3.22 ±0.42
Chezzetcook	1 ±0.63	2.33 ±0.79	0.63 ±0.36	0.98 ±0.54	2.48 ±0.56	1.52 ±0.76	3.07 ±0.42
U, expected	24740, 23302	27259, 23302	317, 351	8097, 7811	8173, 7811	980, 1334	1651, 1334
p-value	0.269	**0.002**	0.565	0.620	0.514	**0.021**	**0.038**

	Foram connectivity	Annelid connectivity	Annelid trophic level	Crustacean connectivity	Crustacean trophic level	Insect/Arachnid connectivity	Insect/Arachnid trophic level
Windsor	0.6±0.15	1.2 ±0.28	2.36 ±0.31	1.0 ±0.53	2.20 ±0.24	0.97 ±0.57	2.93 ±0.69
Chezzetcook	0.49 ±0.18	0.93 ±0.25	2.27 ±0.21	0.76 ±0.49	2.16 ±0.27	1.18 ±0.61	2.72 ±0.63
U, expected	71, 52	418, 264	309.5, 264	540, 400	465, 400	935, 1260	1505.5, 1260
p-value	0.180	**0.001**	0.315	**0.025**	0.253	**0.031**	0.098

	Other inverts connectivity	Other inverts trophic level	Fish connectivity	Fish trophic level	Bird connectivity	Bird trophic level	Mammal connectivity	Mammal trophic level
Windsor	0.75 ±0.25	2.39 ±0.49	1.68 ±0.55	3.04 ±0.33	1.08 ±0.46	3.26 ±0.39	1.03 ±0.57	3.26 ±0.68
Chezzetcook	0.67±0.31	2.34 ±0.48	1.70 ±0.79	3.02 ±0.31	1.49 ±0.76	3.1 ±0.39	1.44 ±0.81	3.01 ±0.67
U, expected	286, 230	251, 230	52, 55	74, 55	418, 594.5	747.5, 594.5	15, 21	27.5, 21
p-value	0.176	0.583	0.86	0.193	**0.036**	0.069	0.431	0.391

8. Comparison of high-resolution Windsor marsh zones (HM = high marsh, LM = low marsh, MF = mudflat) node connectivity values for different taxonomic groups.

Marsh zone	All species	All invertebrates	All vertebrates	Basal resources	Foraminifera	Other invertebrates	Annelids
HM	1 ±0.56	1.08 ±0.60	1.16 ±0.47	0.55 ±0.22	0.33 ±0.02	0.66 ±0.15	0.93 ±0.14
LM	1 ±0.51	0.99 ±0.51	1.21 ±0.47	0.73 ±0.44	0.53 ±0.08	0.73 ±0.24	1.38 ±0.28
MF	1 ±0.44	1.01 ±0.43	1.07 ±0.48	0.83 ±0.43	0.71 ±0.10	0.71 ±0.21	1.25 ±0.30
K (observed, critical)	0.33, 5.99	0.69, 5.99	1.97, 5.99	2.52, 5.99	12.0, 5.99	1.31, 5.99	5.72, 5.99
p-value	0.848	0.707	0.374	0.283	**0.002**	0.519	0.057
	Crustaceans	Insects/ Arachnids	Fish	Birds	Mammals		
HM	0.43 ±0.22	1.3 ±0.6	1.98	1.09 ±0.42	1.32 ±0.62		
LM	1.11 ±0.53	0.98 ±0.65	1.54 ±0.52	1.06 ±0.40	1.25 ±0.38		
MF	1.09 ±0.52	0.92 ±0.49	1.54 ±0.44	0.90 ±0.37	0.70		
K (observed, critical)	9.55, 5.99	3.40, 5.99	1.96, 5.99	3.75, 5.99	1.67, 5.99		
p-value	**0.008**	0.136	0.374	0.153	0.434		

9. Comparison of high-resolution Windsor marsh zones (HM = high marsh, LM = low marsh, MF = mudflat) node trophic level values for different taxonomic groups.

Marsh zone	All species	All invertebrates	All vertebrates	Foraminifera	Other invertebrates	Annelids
HM	2.63 ±0.94	2.73 ±0.72	3.28 ±0.51	2.0 ±0.0	2.21 ±0.42	2.24 ±0.23
LM	2.53 ±0.79	2.5 ±0.58	3.19 ±0.42	2.0 ±0.06	2.38 ±0.50	2.38 ±0.35
MF	2.52 ±0.70	2.36 ±0.41	3.23 ±0.29	2.03 ±0.08	2.38 ±0.49	2.35 ±0.32
K (observed, critical)	1.48, 5.99	4.74, 5.99	0.95, 5.99	0.813, 5.99	1.00, 5.99	0.53, 5.99
p-value	0.477	0.094	0.622	0.666	0.606	0.767
	Crustaceans	Insects/ Arachnids	Fish	Birds	Mammals	
HM	2.10 ±0.14	2.99 ±0.72	2.82	3.31 ±0.48	3.22 ±0.75	
LM	2.16 ±0.22	2.87 ±0.69	3.06 ±0.37	1.85 ±0.76	1.89 ±0.65	
MF	2.23 ±0.26	2.81 ±0.59	3.00 ±0.32	3.30 ±0.21	3.73	
K (observed, critical)	1.57, 5.99	1.03, 5.99	0.67, 5.99	46.57, 5.99	3.80, 5.99	
p-value	0.455	**0.05**	0.716	**<0.0001**	0.149	

10. Comparison of connectivity and trophic level values between zones at Windsor marsh.

Taxonomic Groups	High marsh Connectivity	Low marsh Connectivity	Mudflat Connectivity	High marsh trophic level	Low marsh trophic level	Mudflat trophic level
Invertebrates	1.08 ±0.60	0.99 ±0.51	1.01 ±0.43	2.73 ±0.72	2.5 ±0.58	2.36 ±0.41
Vertebrates	1.16 ±0.47	1.21 ±0.47	1.07 ±0.48	3.28 ±0.51	3.19 ±0.42	3.23 ±0.29
Basal Resources	0.55 ±0.22	0.73 ±0.44	0.83 ±0.43	Mann-Whitney (U, expected)		
K (observed, critical)	16.09, 5.99	11.68, 5.99	2.99, 5.99	452, 759.5	458.5, 1340	157, 1455.5
p-value	**0.000**	**0.003**	0.225	**0.002**	**<0.0001**	**<0.0001**

11. Comparison of trophic levels of insects/arachnids versus crustaceans, across zones, at Windsor marsh.

Taxonomic Groups	High marsh Trophic level	Low marsh Trophic level	Mudflat Trophic level
Insects/Arachnids	2.99 ±0.72	2.87 ±0.69	2.81 ±0.59
Crustaceans	2.10 ±0.14	2.16 ±0.22	2.23 ±0.26
Mann-Whitney 2-sample test			
U, expected	130, 82.5	200.5, 716.2	83.5, 52.5
p-value	**0.038**	**0.011**	**0.041**

12. Comparison of high-resolution Chezzetcook marsh zones (HM = high marsh, MM= middle marsh, LM = low marsh, MF = mudflat) node connectivity values for different taxonomic groups.

Marsh zone	All invertebrates	All vertebrates	Basal resources	Foraminifera	Other invertebrates	Annelids
HM	1.08 ±0.57	1.42 ±0.77	0.57 ±0.21	0.28 ±0.05	0.54 ±0.25	0.89 ±0.00
MM	1.04 ±0.57	1.45 ±0.75	0.57 ±0.24	0.31 ±0.03	0.57 ±0.19	0.97 ±0.14
LM	0.96 ±0.51	1.33 ±0.61	0.72 ±0.45	0.56 ±0.09	0.73 ±0.23	1.25 ±0.32
MF	0.97 ±0.46	1.17 ±0.60	0.87 ±0.43	0.77 ±0.08	0.70 ±0.24	1.09 ±0.29
K (observed, critical)	3.02, 7.82	2.30, 7.82	4.43, 7.82	24.56, 7.82	6.27, 7.82	4.79, 7.82
p-value	0.382	0.392	0.219	**<0.0001**	0.099	0.188
	Crustaceans	Insects/ Arachnids	Fish	Birds	Mammals	
HM	0.29 ±0.24	1.25 ±0.5		1.43 ±0.79	1.39 ±0.77	
MM	0.36 ±0.23	1.25 ±0.53	2.23	1.44 ±0.76	1.36 ±0.81	
LM	0.91 ±0.51	1.02 ±0.61	1.67 ±0.71	1.21 ±0.55	1.18 ±0.50	
MF	1.18 ±0.58	0.78 ±0.57	1.64 ±0.63	0.94 ±0.42	0.74 ± 0.10	
K (observed, critical)	29.6, 7.82	8.83, 7.82	1.75, 5.99	5.58, 7.82	1.21, 7.82	
p-value	**<0.0001**	**0.032**	0.417	0.134	0.750	

13. Comparison of high-resolution Chezzetcook marsh zones (HM = high marsh, MM= middle marsh, LM = low marsh, MF = mudflat) node trophic level values for different taxonomic groups.

Marsh zone	All invertebrates	All vertebrates	Foraminifera	Other invertebrates	Annelids
HM	2.62 ±0.64	2.95 ±0.50	2.0 ±0.0	2.22 ±0.50	2.47 ±0.00
MM	2.63 ±0.64	3.07 ±0.50	2.0 ±0.0	2.21 ±0.38	2.31 ±0.22
LM	2.45 ±0.56	3.16 ±0.40	2.02 ±0.05	2.30 ±0.46	2.28 ±0.22
MF	2.31 ±0.40	3.15 ±0.32	2.02 ±0.06	2.36 ±0.50	2.24 ±0.22
K (observed, critical)	8.01, 7.82	2.37, 7.82	2.10, 7.82	1.20, 7.82	2.71, 7.82
p-value	**0.044**	0.392	0.551	0.753	0.438
	Crustaceans	Insects/ Arachnids	Fish	Birds	Mammals
HM	2.17 ±0.42	2.72 ±0.65		2.95 ±0.41	2.96 ±0.76
MM	2.14 ±0.34	2.82 ±0.65	2.76	3.10 ±0.40	3.04 ±0.80
LM	2.11 ±0.19	2.74 ±0.65	3.07 ±0.35	3.15 ±0.40	3.36 ±0.50
MF	2.20 ±0.24	2.71 ±0.66	3.01 ±0.32	3.21 ±0.28	3.41 ± 0.45
K (observed, critical)	4.03, 7.82	0.95, 7.82	1.38, 5.99	4.78, 7.82	1.25, 7.82
p-value	0.258	0.814	0.512	0.189	0.742

14. Comparison of trophic levels of insects/arachnids versus crustaceans, across zones, at Chezzetcook marsh.

Taxonomic Groups	High marsh Trophic level	Middle marsh Trophic level	Low marsh Trophic level	Mudflat Trophic level
Insects/Arachnids	2.72 ±0.65	2.82 ±0.65	2.74 ±0.65	2.71 ±0.66
Crustaceans	2.17 ±0.42	2.14 ±0.34	2.11 ±0.19	2.20 ±0.24
Mann-Whitney 2-sample test				
U, expected	411.5, 274.5	572, 366	407.5, 264	76, 54
p-value	**0.013**	**0.002**	**0.001**	0.137

15. Coefficient of Variation (CV) comparisons of taxonomic resolution variability (from high, medium and low) and salt marsh zones variability (HM, MM, LM, MF) for Chezzetcook and Windsor.

Variability	Chezzetcook	Windsor
CV Zones	15.24 ±25.21	16.06 ±33.39
CV Resolution	19.18 ±25.35	19.82 ±16.87
Mann-Whitney U, expected	126, 144.5	77.5, 144.5
p-value	0.534	**0.022**

APPENDIX B-4: SUPPLEMENTARY DATA FOR CHAPTER 3

This material is permantantly archived as Electronic supplementary material at Dalhousie University.

Supplementary B-1 includes: Species lists for Chezzetcook and Windsor food webs for Chapter 3. Species found at both marshes are labelled as "both." Node ID is what is used in binary matrices. Includes major taxonomic groups, systematic taxonomy references, common names, and the zones of the marsh where species are located (HM = high marsh, MM = middle marsh, LM = low marsh, MF = mudflat), and the most common references used in determining diets and feeding ecology which created the binary matrices.

Supplementary B-2 includes: Binary matrices (predator-prey links) used to create food webs with FoodWeb3D in Chapter 3.

Supplementary B-3 includes: Data nodes of the cumulative high resolution meta-food webs for Nova Scotia marshes in Chapter 3, including basic food web topology (Trophic Level, Connectivity, Generality of Predator, Vulnerability of Prey) for each node.

Supplementary B-4 includes: Organized data used for statistical comparisons of Appendix B-3 for Chapter 3 food webs.

APPENDIX C- SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Appendix C-1: Taxonomic names and common names for the sources and consumers of Chezzetcook and Windsor salt marshes from Tables 4.1 and 4.2.

Taxonomic name	Common name
Vascular plants	
Solidago sempervirens	Seaside goldenrod
Cyperaceae (*Carex palaeceae*)	Sedge
Limonium carolinianum	Sea lavender
Calamagrostis canadensis	Marsh reedgrass
Juncus sp.	Rushes
Distichlis spicata	Saltgrass
Spartina pectinata	Freshwater cordgrass
Spartina patens	Salt marsh hay
Spartina alterniflora	Salt marsh cordgrass
Salicornia sp.	Glasswort
Lichen	
Xanthoria parietina	Sunburst lichen
Algae	
Chaetomorpha	Filamentous green
Lyngbya (?)	Filamentous cyanobacteria
Cladophora (?)	Filamentous green
Macrofauna (> 2 cm)	
Arachnids and Insects	
Grammonata trivitata	Dwarf-weaver spider
Araneus diadematus (?)	Cross orb-weaver spider
Pardosa littoralis	Thin legged wolf spider
Doryodes grandipennis	Long-winged moth
Grasshopper (*Dichromorpha viridis*?)	Short-winged green grasshopper
Grasshopper (*Paroxya*?)	Swamp grasshopper
Grasshopper (*Chorthippus curtipennis*?)	Marsh meadow grasshopper
Coleoptera (Hydrophilidae)	Water beetle
Carabidae Coleoptera	Carabid beetle
Coccinellidae Coleoptera	Lady beetle
Diptera	Large fly larvae
Ephydridae	Shorefly (adult)
Tabanidae Diptera	Biting fly
Crustaceans	
Carcinus maenas	European green crab

Taxonomic name	Common name
Macrofauna (>2 cm)	
Molluscs	
Melampus bidentatus	Coffee bean snail
Gastropod (*Alderia modesta*?)	Sacoglossan sea slug
Littorina littorea	Common periwinkle
Littorina saxatilis	Rough periwinkle
Tritia obsoleta	Eastern mud snail
Mya arenaria	Soft-shelled clam
Geukensia demissa	Ribbed mussel
Annelids	
Hediste diversicolor	Ragworm
Small macrofauna (500 µm – 2 cm)	
Arachnids and Insects	
Trombiculidae mites	Red mites
Histeridae Coleoptera	Hister beetle
Ephydridae larvae	Shorefly larvae
Chrysops carbonarius larvae	Deerfly larvae
Ceratopogonidae (*Culicoides*)	Biting midges
Chironomidae (*Chironomus*)	Non-biting midges
Crustaceans	
Orchestia sp.	Amphipod
Talorchestia sp.	Amphipod
Leptochelia rapax	Tanaid Amphipod
Corophium volutator	Amphipod
Porcellio scaber	Sowbug isopod
Worms	
Enchytraeidae	Oligochaetes
Tubificidae	Oligochaetes
Turbellarians	Flatworms
Molluscs	
Ecrobia truncata	Salt marsh snail
Meiofauna (63 – 500 µm)	
Arachnids and Insects	
Euzetidae	Soil mites
Arrenuridae	Water mites

Appendix C-2: Statistical output from non-parametric ANOSIM (Analysis of Similarities) of untransformed Euclidean distances of isotope values for Windsor and Chezzetcook (marshes), Zones (high-HM, middle-MM, low-LM, mudflat-MF), major functional groups (vascular plants, algae/other, bulk sieved sediment (SOM), foraminifera, meiofauna, small macrofauna, macrofauna), and major taxonomic groups (from C_3 plants through birds). Only results discussed in text (Chapter 4) are shown here.

One-Way Global Test of Marshes (Chezzetcook vs Windsor, all zones and groups)
Sample statistic **(Global R): 0.048**
Significance level of sample statistic: **14.9% (p= 0.149, not significant)**
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 148

Two-Way Global Test of zones, across all marshes and taxonomic groups
Sample statistic **(Global R): 0.091**
Significance level of sample statistic: **0.5% (p = 0.005; significant)**
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 4

Pairwise Tests; significant comparisons are in BOLD

Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >= Observed
HM, MM	-0.025	79.6	Very large	999	795
HM, LM	0.112	**0.1**	Very large	999	0
HM, MF	0.038	20.5	Very large	999	204
HM, HM-MM	-0.115	91	115775100	999	909
HM, MM-LM	-0.071	46.7	45	45	21
HM, LM-MF	0.14	8	752538150	999	79
HM, HM-LM	-0.071	66.5	16215	999	664
MM, LM	0.076	6.2	Very large	999	61
MM, MF	0.022	21.1	Very large	999	210
MM, HM-MM	0.017	37.7	5379616	999	376
MM, MM-LM	0.108	32.1	28	28	9
MM, LM-MF	0.114	17.2	23535820	999	171
MM, HM-LM	-0.035	52.9	4060	999	528
LM, MF	0.076	9.7	Very large	999	96
LM, HM-MM	0.254	**1.8**	778789440	999	17

LM, MM-LM	0.439	10	60	60	6
LM, LM-MF	0.205	5.1	Very large	999	50
LM, HM-LM	0.095	25.4	37820	999	253
MF, HM-MM	0.165	5.6	1184040	999	55
MF, MM-LM	0.266	18.2	22	22	4
MF, LM-MF	0.062	27.4	4292145	999	273
MF, HM-LM	0.058	30.7	2024	999	306
HM-MM, MM-LM	0.537	12.5	8	8	1
HM-MM, LM-MF	0.506	**0.1**	6435	999	0
HM-MM, HM-LM	0.659	**0.8**	120	120	1
MM-LM, LM-MF	0.196	33.3	9	9	3
MM-LM, HM-LM	-0.111	75	4	4	3
LM-MF, HM-LM	-0.124	73.3	165	165	121

Two-Way Global Test of Major Taxonomic Groups across all zones and marshes

Sample statistic **(Global R): 0.096**
Significance level of sample statistic: **0.1% (p = 0.001; significant)**
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 0

Pairwise Tests; Significant pairwise comparisons in BOLD

Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >= Observed
vascular plant, Algae/Other	-0.169	98.8	962598	999	987
vascular plant, Bulk Sieved Sediment	0.145	**1.3**	Very large	999	12
vascular plant, Macrofauna	0.122	**0.1**	Very large	999	0
vascular plant, Macrofauna Small	0.11	**0.3**	Very large	999	2
vascular plant, Foraminifera	0.072	**3.5**	Very large	999	34
vascular plant, Meiofauna	-0.018	57.5	Very large	999	574
Algae/Other, Bulk Sieved Sediment	0.947	**0.1**	33649	999	0
Algae/Other, Macrofauna	-0.17	94.9	1370754	999	948
Algae/Other, Macrofauna Small	-0.106	76.4	324632	999	763
Algae/Other, Foraminifera	0.004	43.4	98280	999	433
Algae/Other, Meiofauna	-0.103	79.9	15504	999	798
Bulk Sieved Sediment, Macrofauna	0.215	**0.2**	Very large	999	1
Bulk Sieved Sediment, Macrofauna Small	0.212	**0.4**	Very large	999	3

Bulk Sieved Sediment, Foraminifera	0.06	7.5	Very large	999	74
Bulk Sieved Sediment, Meiofauna	0.306	**0.1**	1037158320	999	0
Macrofauna, Macrofauna Small	-0.002	46	Very large	999	459
Macrofauna, Foraminifera	0.11	**2**	Very large	999	19
Macrofauna, Meiofauna	0.052	20.4	Very large	999	203
Macrofauna Small, Foraminifera	0.049	7.3	Very large	999	72
Macrofauna Small, Meiofauna	0.054	18.5	Very large	999	184
Foraminifera, Meiofauna	-0.016	55.7	Very large	999	556

Appendix C-3: Statistical output of isotopic signatures of sources (vascular plants, algae, sediment organic matter, SOM) and consumers (macrofauna, small macrofauna, meiofauna and foraminifera) across zones for Windsor and Chezzetcook (Chapter 4). Individual values are in Supplement C-3. High marsh (HM), middle marsh (MM), low marsh (LM), mudflat (MF). Mann-Whitney two-sampled tests are shown as "U", and Kruskal-Wallis *n* tests shown as "K".

Windsor				Chezzetcook			
	C:N	**^{13}C**	**^{15}N**		**C:N**	**^{13}C**	**^{15}N**
Zones (all samples)				**Zones (all samples)**			
HM	8.34 ±6.34	-15.34 ±2.88	8.03 ±2.99	HM	11.31 ±10.31	-20.26 ±5.17	4.41 ±2.29
LM	8.40 ±7.34	-14.08 ±3.77	7.83 ±2.72	MM	11.18 ±9.38	-18.81±4.76	4.79 ±2.37
MF	6.64 ±3.47	-12.92 ±4.32	7.91 ±3.13	LM	9.31 ±9.84	-15.42 ±4.06	4.94 ±2.30
				MF	11.69 ±11.8	-13.94 ±5.57	5.14 ±2.41
K (observed, critical)	0.11, 5.99	2.03, 5.99	0.09, 5.99	K (observed, critical)	4.38, 7.82	23.88, 7.82	1.74, 7.82
p-value	0.946	0.362	0.957	p-value	0.223	**<0.0001**	0.628
Functional groups				**Functional groups**			
Sources				**Sources**			
Plants:				Plants:			
HM	13.84 ±11.33	-14.04 ± 0.24	6.34±1.76	HM	24.05 ±15.07	-19.54 ±7.2	3.31 ±2.2
LM	16.56 ±11.57	-13.74±0.36	5.38±1.33	MM	24.83 ±11.66	-20.96 ±7.16	3.89 ±1.95
				LM	23.04 ±8.32	-13.35 ±0.29	3.17 ±2.8
U / expected	135.5 / 152	91.5 / 152	210.5 / 152	K (observed, critical)	0.111, 5.99	9.60, 5.99	2.26, 5.99
p-value	0.596	**0.047**	0.055	p-value	0.946	**0.008**	0.324
SOM:				Algae:			
HM	9.38 ±0.05	-20.69±0.05	5.31±0.21	LM	12.93 ±4.1	-14.04 ±1.03	3.78 ±0.04
LM	8.91 ±0.14	-21.57±0.08	5.39±0.25	MF	10.23 ±0.61	-13.64 ±0.13	4.89 ±0.6
MF	9.0 ±0.06	-21.57±0.02	5.69±0.3				
K (observed, critical)	5.96, 5.99	5.42, 5.99	2.76, 5.99	U / expected	18 / 18	18 / 18	0 / 18
p-value	0.051	0.066	0.252	p-value	1.0	1.00	**0.002**

Windsor			
	C:N	**^{13}C**	**^{15}N**
Consumers			
All:			
HM	5.97 ±0.98	-15.76 ± 2.70	8.47 ±2.69
LM	6.27 ±3.39	-14.34 ±3.70	8.4 ±2.64
MF	5.77 ±3.11	-12.23 ±2.61	7.28 ±2.68
K (observed, critical)	3.36, 5.99	9.26, 5.99	2.94, 5.99
p-value	0.187	**0.01**	0.23
Macrofauna:			
HM	6.38 ±1.01	-15.7 ±2.93	8.16 ±0.67
LM	5.83 ±1.17	-15.38 ±3.1	8.49 ±1.38
MF	5.79 ± 2.48	-11.7 ±2.22	6.6 ±1.36
K (observed, critical)	2.08, 5.99	6.97, 5.99	8.39, 5.99
p-value	0.353	**0.031**	**0.015**
Small macrofauna:			
HM	5.21 ±0.26	-16.6 ±1.56	8.02 ±4.07
LM	5.26 ±0.95	-14.85 ±3.0	8.81 ±3.28
MF	3.85 ±0.04	-14.83 ±0.12	5.37 ±0.18
K (observed, critical)	7.51, 5.99	3.58, 5.99	1.76, 5.99
p-value	**0.023**	0.167	0.416

Chezzetcook			
	C:N	**^{13}C**	**^{15}N**
SOM:			
HM	13.94 ±2.57	-20.73 ±1.13	3.78 ±0.19
MM	9.0 ±1.66	-18.47 ±1.23	4.48 ±0.44
LM	7.92 ±0.33	-19.38 ±0.34	3.89 ±0.35
MF	7.13 ±0.25	-19.98 ±0.99	5.14 ±0.35
K (observed, critical)	23.13, 7.82	10.14, 7.82	22.06, 7.82
p-value	**<0.0001**	**0.017**	**<0.0001**
Consumers			
All:			
HM	5.23 ±2.07	-20.22 ±3.07	6.05 ±1.80
MM	4.59 ± 0.88	-17.08 ±3.25	6.04 ±2.94
LM	6.19 ± 4.86	-15.0 ±4.36	5.36 ±2.37
MF	7.17 ±5.61	-13.07 ±5.61	5.72 ±3.28
K (observed, critical)	2.79, 7.82	53.06, 7.82	4.09, 7.82
p-value	0.425	**<0.0001**	0.252
Macrofauna:			
HM	5.02 ±2.24	-21.44 ±3.58	6.83± 1.17
MM	4.42 ±0.92	-15.70 ±2.89	6.69 ±3.33
LM	4.98 ±1.66	-15.09 ±2.61	6.16 ±2.65
MF	5.40 ±1.70	-14.47 ±4.04	7.06 ±2.66
K (observed, critical)	6.64, 7.82	32.0, 7.82	5.72, 7.82
p-value	0.084	**<0.0001**	0.126

Chezzetcook			
	C:N	**^{13}C**	**^{15}N**
Small macrofauna:			
HM	5.35 ±1.0	-18.12 ±1.12	5.86 ± 1.78
MM	4.48	-18.77	3.39
LM	7.56 ± 6.50	-13.87 ±5.77	5.60 ±1.81
MF	12.10 ±8.07	-8.21 ±6.38	7.21 ±1.42
K (observed, critical)	8.11, 7.82	16.78, 7.82	7.02, 7.82
p-value	**0.044**	**0.001**	0.071
Meiofauna:			
MM	4.33 ± 0.08	-21.4 ±2.02	4.0 ±1.5
LM	5.67 ± 3.45	-16.32 ±3.92	3.79 ± 1.65
MF	4.34 ±0.51	-15.94 ±3.64	3.44 ±1.13
K (observed, critical)	0.71, 5.99	4.52, 5.99	0.299, 5.99
p-value	0.701	0.104	0.861
Foraminifera			
HM	6.32 ±3.13	-19.12 ±2.18	5.66 ±2.12
MM	5.03 ±0.99	-18.63 ±2.56	5.04 ±2.17
LM	6.68 ±6.77	-16.79 ±4.18	4.12 ±1.97
MF	8.50 ±7.95	-12.54 ±6.95	2.53 ±4.41
K (observed, critical)	1.69, 7.82	4.86, 7.82	7.61, 7.82
p-value	0.639	0.182	0.055

Mann-Whitney non-parametric tests for comparison of Windsor and Chezzetcook isotopic signatures, with all zones combined.

All Samples:	**C:N**	**^{13}C**	**^{15}N**
Windsor	8.21±6.79	-14.31±3.56	7.49 ±2.35
Chezzetcook	10.59±10.21	-17.37±5.35	4.72±2.26
	U=2251	U=3331	U=3980
	Expected=2430	Expected=2430	Expected=2430
	p-value =0.499	**p-value=0.001**	**p-value<0.0001**
All Plants:	**C:N**	**^{13}C**	**^{15}N**
Windsor	16.0±11.75	-13.89±0.36	5.99±1.7
Chezzetcook	24.14±13.29	-19.12±7.06	3.47±2.22
	U=992	U=1589	U=2474
	Expected=1554	Expected=1554	Expected=1554
	p-value=0.003	p-value=0.856	**p-value<0.0001**
All Sediments:	**C:N**	**^{13}C**	**^{15}N**
Windsor	9.08±0.20	-21.28±0.44	5.47±0.28
Chezzetcook	9.09±2.76	-19.54±1.23	4.37±0.65
	U=206	U=32	U=273
	Expected=148.5	Expected=148.5	Expected=148.5
	p-value=0.081	**p-value=0.00**	**p-value=0.00**
All consumers:	**C:N**	**^{13}C**	**^{15}N**
Windsor	6.06±3.20	-13.63±3.36	8.07±2.37
Chezzetcook	5.86±4.43	-16.26±4.70	5.30±2.24
	U=1320	U=1561	U=1780
	Expected=1092	Expected=1092	Expected=1092
	p-value=0.109	**p-value=0.001**	**p-value<0.0001**

Macrofauna:	**C:N**	**^{13}C**	**^{15}N**
Windsor	5.92±1.48	-14.39±3.06	8.00±1.42
Chezzetcook	4.98±1.79	-16.56±4.36	6.43±2.53
	U=1845	U=1679	U=1784
	Expected=1264	Expected=1264	Expected=1264
	p-value=0.00	**p-value=0.007**	**p-value=0.001**
Small macrofauna + Meiofauna:	**C:N**	**^{13}C**	**^{15}N**
Windsor	4.84±1.07	-14.75±2.53	8.02±3.15
Chezzetcook	6.64±5.36	-15.18±5.13	5.14±1.89
	U=503	U=749	U=915
	Expected=594	Expected=594	Expected=594
	p-value=0.324	p-value=0.092	**p-value=0.000**
Foraminifera:	**C:N**	**^{13}C**	**^{15}N**
Windsor	9.53±6.88	-11.02±4.65	7.94±3.59
Chezzetcook	6.65±5.60	-16.70±4.87	4.27±2.85
	U=146	U=180	U=175
	Expected=108.5	Expected=108.5	Expected=108.5
	p-value=0.164	**p-value=0.008**	**p-value=0.013**

Appendix C-4: Statistical output of coefficient of variations (CV) used in stable isotope analysis (Chapter 4). Individual values are in Supplement C-4. High marsh (HM), middle marsh (MM), low marsh (LM), mudflat (MF). SOM = bulk sieved sediment, or sediment organic matter.

Windsor				Chezzetcook			
	C:N	^{13}C	^{15}N		C:N	^{13}C	^{15}N
Zones				**Zones**			
HM	0.23	-0.007	0.048	HM	0.23	-0.013	0.058
HM-MM	0.30	-0.006	0.024	HM-MM	0.23	-0.018	0.057
LM	0.17	-0.011	0.065	MM	0.13	-0.016	0.071
MF	0.20	-0.028	0.026	LM	0.20	-0.021	0.085
				LM-MF	0.02	-0.042	0.053
				MF	0.22	-0.008	0.155
Functional groups				**Functional groups**			
Plants	0.22	-0.007	0.076	Plants	0.22	-0.007	0.095
SOM	0.11	-0.002	0.046	Algae	0.16	-0.009	0.021
Foraminifera	0.16	-0.012	0.137	SOM	0.18	-0.002	0.014
Small macrofauna	0.19	-0.006	0.015	Foraminifera	0.16	-0.021	0.206
Macrofauna	0.27	-0.028	0.025	Meiofauna	0.33	-0.029	0.057
				Small macrofauna	0.15	-0.041	0.094
				Macrofauna	0.16	-0.013	0.028
Total average CV	0.19	-0.01	0.05	Total average CV	0.19	-0.02	0.08

Mann-Whitney non-parametric tests for comparison of Windsor and Chezzetcook CVs. Expected value = 12 (zones), 17.5 (groups).

Zones:	**C:N**	**^{13}C**	**^{15}N**
Windsor	0.23±0.05	-0.013±0.01	0.041±0.02
Chezzetcook	0.17±0.08	-0.019±0.01	0.08±0.04
	U=16; p=0.46	U=18; p=0.24	U=3; p=0.07
Functional groups:			
Windsor	0.19±0.06	-0.011±0.01	0.06±0.05
Chezzetcook	0.20±0.06	-0.017±0.01	0.07±0.07
	U=20; p=0.75	U=23; p=0.42	U=16; p=0.87

Appendix C-5: Statistical table of mean trophic position comparisons between and within Chezzetcook and Windsor (Chapter 4). Full data is in Supplement C-5. High marsh (HM), middle marsh (MM), low marsh (LM), mudflat (MF). Mann-Whitney two-sampled tests are shown as "U", and Kruskal-Wallis *n* tests shown as "K".

All Consumers:	**Trophic Position**
Windsor	2.80±0.70
Chezzetcook	2.84±0.67
	U=1058
	Expected=1092
	p-value=0.814
Windsor HM	2.81±0.71
Chezzetcook HM + MM	2.88±0.55
	U=62
	Expected=66
	p-value=0.845
Windsor LM	2.78±0.57
Chezzetcook LM	2.71±0.54
	U=231
	Expected=217
	p-value=0.741
Windsor MF	2.43±0.46
Chezzetcook MF	2.48±0.47
	U=23
	Expected=22.5
	p-value=1.00

Macrofauna:	**Trophic Position**
Windsor	2.73±0.48
Chezzetcook	3.11±0.73
	U=104
	Expected=144
	p-value=0.213

Small macrofauna +meiofauna:	
Windsor	2.77±0.72
Chezzetcook	2.75±0.51
	U=203
	Expected=198
	p-value=0.908

Foraminifera:	**Trophic Position**:
Windsor	2.97±1.06
Chezzetcook	2.53±0.63
	U=57
	Expected=47.5
	p-value=0.522

Chezzetcook	**Trophic Position:**	**Windsor**	**Trophic Position:**
HM	3.13±0.45	HM	2.81±0.71
MM	2.82±0.78	LM	2.77±0.59
LM	2.71±0.54	MF	2.52±0.47
MF	2.80±0.84		K(observed)=0.89
	K (observed)=6.96		K(critical)=5.99
	K (critical)=7.82		p-value=0.642
	p-value=0.073		

Chezzetcook Macrofauna		**Windsor Macrofauna**	
HM	3.39±0.27	HM	2.84±0.26
MM	3.05±0.96	LM	2.95±0.51
LM	2.86±0.58	MF	2.37±0.40
MF	3.35±0.82		K(observed)=2.96
	K(observed)=4.27		K(critical)=5.99
	K(critical)=7.82		p-value=0.228
	p-value=0.234		

Chezzetcook Small macrofauna		**Windsor Small macrofauna +meiofauna**	
HM	2.94±0.49	HM	2.79±0.89
LM	2.85±0.50	LM	2.85±0.72
MF	3.23±0.50	MF	2.51±0.72
	K(observed)=1.97		K(observed)=0.29
	K(critical)=5.99		K(critical)=5.99
	p-value=0.374		p-value=0.866

Chezzetcook Meiofauna	
MM	2.62±0.57
LM	2.49±0.35
MF	2.33±0.42
	K(observed)=0.86
	K(critical)=5.99
	p-value=0.651

Chezzetcook Foraminifera	**Trophic Position:**	**Windsor Foraminifera**	**Trophic Position:**
HM	2.52±0.67	LM	2.36±0.23
MM	2.95±0.47	MF	3.88±1.26
LM	2.41±0.63		U=0
MF	1.89±0.43		Expected=3
	K(observed)=5.95		p=0.200
	K(critical)=7.82		
	p-value=0.114		

APPENDIX C-6: SUPPLEMENTARY DATA FOR CHAPTER 4

This material is permantantly archived as Electronic supplementary material at Dalhousie University.

Supplement C-1: 2014 Chezzetcook and Windsor stable isotope signatures from University of California, Davis.

Supplement C-2: 2015 Additional Chezzetcook stable isotope signatures from University of California, Davis.

Supplement C-3: Isotopic signature values, organized for statistics shown in Appendix C-3, for Chezzetcook, Windsor, Zones, and various taxonomic groups.

Supplement C-4: Combined Coefficient of Variation (CV) values of isotopic signatures used for Appendix C-4.

Supplement C-5: All calculated trophic positions of consumers of Chezzetcook and Windsor, used in Appendix C-5.

APPENDIX D: SUPPLEMENTARY MATERIAL FOR CHAPTER 5

This material is permantantly archived as Electronic supplementary material at Dalhousie University.

Supplement D-1: Raw count data of living versus Rose Bengal stained foraminifera individuals for Table 5.2 (Chapter 5).

Supplement D-2: Raw counts for all 2.5 ml surface sediment samples (1 through 23) of Chezzetcook meiofauna (63 - 500 um), used for Table 5.4. Includes pre- and post-weights of wet and dry specimens (mg).