

Ecological Forces Structuring a Soft-Sediment Community

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Thesis Abstract

In a world undergoing rapid climate change, a greater understanding of the ecological interactions which structure our ecosystems may enable humans to predict, or even repair, anthropogenic changes upon our ecosystems. The Bay of Fundy, Canada, is an ideal system to investigate ecological interactions. Its moderate complexity of ecological factors makes it relatively easy to study, while high population densities, and replicate mudflats provide considerable investigational power. In this thesis, I explored biotic and abiotic factors that may structure the infaunal community of the intertidal mudflats in upper Bay of Fundy. I observed that winter stressors (e.g., ice presence and scour, air temperature, sediment hypoxia), as well as top-down predation, the input of resources in a system (bottom-up control), the activity of mesopredators (middle-out control), and sediment conditions were not exerting strong controlling influences upon this community. It seems likely that the infaunal community is predominantly structured by the arrival of individuals (larvae, juveniles and adults) into a site, and secondary movement (dispersal) of individuals post-settlement. Lastly, I utilized molecular scatology and next-generation sequencing to investigate the diet of one of the main top-down predators of this system, Semipalmated Sandpipers (*Calidris pusilla*). I observed that sandpipers were acting as generalists, foraging upon intertidal, pelagic, terrestrial, and freshwater prey items. Such a broad diet may explain why sandpiper predation was not exerting a strong controlling on the infaunal community. This diet information may alter the way we conserve this species, since current conservation efforts are directed towards beach and intertidal habitat. However, in light of the breadth of diet items

observed here, conservation efforts may have to also include terrestrial and freshwater systems.

Preface

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Contributions of Authors:

TGG planned the sampling designs, collected the data, did the analysis, and did all the writing for each chapter.

MAB, DD and DJH assisted in and oversaw the designing of the sampling programs, provided input for the analysis, and assisted in writing by editing and providing comments for each chapter.

AMAG assisted with data collections, and in the writing of Chapter 2 by providing comments.

JAA contributed to the sampling design of Chapter 4 and provided guidance for the development of the molecular and bioinformatics protocols. He assisted in the writing of Chapter 4 by contributing to the text and providing comments.

JHK performed all the molecular protocols and bioinformatics to collect all the data for Chapter 4. He also assisted in the writing of Chapter 4 by contributing to the text and providing comments.

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Chapter 1: General introduction

Ecology, from the Greek οἶκος, is the study of the “home.” A slightly more practical interpretation, however, suggests that Ecology is the study of interactions (Nybakken and Bertness 2005). These interactions can be between the living components of a natural system like predation or competition (Ambrose Jr 1991, Peterson et al. 2013), between non-living aspects of ecosystems as in the transport of suspended sediments by the tides (Wu et al. 2011, Passarelli et al. 2012), or between living and non-living constituents such as the influence of salinity on marine animals (Kristensen 2000, Queirós et al. 2013, Quintana et al. 2013). The value of Ecology primarily resides in quantifying interactions, within and between living and non-living aspects of an ecosystem, which structure the environments around us. Far from being of only theoretical importance, these interactions are accumulating attention in a world undergoing rapid climate alteration (Houghton et al. 2001, Stachowicz et al. 2002, Barange et al. 2014, Galbraith et al. 2014). At the same time, natural systems are currently experiencing a decrease in biodiversity, predominantly induced by human-related activities (Loreau et al. 2001). As human-related climate change (Barange et al. 2014) and habitat degradation/fragmentation (Fahrig 2003) are predicted to have increasingly negative impacts on both ecosystems and the natural resources on which we rely upon, the need for informed ecological management and conservation will only increase. Successful management or conservation of natural systems relies upon a clear understanding of the ecological interactions which influence community structure and dynamics, as well as ecosystem function (Terborgh et al. 2001, Myers et al. 2007,

Rayner et al. 2007). For instance in a New Zealand island reserve, land use managers attempted to protect breeding populations of Cooks Petrels (*Pterodroma cookii*) by eradicating feral cats. Unfortunately, feline predation was keeping populations of Pacific rats (*Rattus exulans*) in check, and removal of feral cats resulted in decreased Petrel breeding success due to rat predation (Rayner et al. 2007). This example emphasizes how ecosystem modification, even well intentioned ones, made in ignorance of key ecological interactions may result in detrimental alterations.

1.1 Biotic and abiotic forces that structure benthic marine communities

Many studies have attempted to understand the role of ecological interactions in structuring biological communities (Tilman et al. 2006, Chambers et al. 2013, Vanschoenwinkel et al. 2013, Pilditch et al. 2015). These studies are often conducted on benthic communities in the intertidal zone due to ease of access, as well as the ease of biotic and abiotic variable manipulation (Ólafsson et al. 1994, Snelgrove and Butman 1994, Todd 1998). Current models developed to explain the structure and dynamics of benthic communities revolve around the influences of environmental conditions, resource availability, competition, predation, physical disturbance, and propagule supply (Underwood and Fairweather 1989, Menge et al. 1997, Ghasemi et al. 2014). More specifically, in a marine benthic environment, abiotic factors (particle size, water content, penetrability and dissolved oxygen content in sediment, and exposure time of a patch to air (Stillman 2002, Lu et al. 2008, Ghasemi et al. 2014)), when combined with differential faunal tolerances to these conditions, exert an obvious influence on biological communities, affecting species presence/absence as well as density (Kelaheer

et al. 2001, Ferguson et al. 2013, Ghasemi et al. 2014). Physical disturbances can take many forms, but in temperate intertidal benthic environments, winter, a multifaceted disturbance, may exert a strong controlling influence. Winter is multifaceted because subzero temperatures may influence invertebrates via both thermal stress (Beukema 1992, Strasser and Pieloth 2001, Büttger et al. 2011) and the action of ice (Strasser et al. 2001, Belt et al. 2009, Büttger et al. 2011), including the scouring of the sediment (Armonies et al. 2001, Strasser et al. 2001, Scrosati and Heaven 2006, Büttger et al. 2011).

Disturbances and environmental conditions are not the dominant structuring processes in all ecosystems; some communities are primarily structured by the availability of resources, a situation often referred to as bottom-up control (Davis et al. 2014, van den Hoff et al. 2014). Resource availability can influence population density by altering birth, death, growth and movement rates of organisms, and so modify competition intensity and community composition (Davis et al. 2014, Schuldt et al. 2014, van den Hoff et al. 2014). At the same time, predation can influence communities by affecting density and size structure of prey (and predator) populations through dispersal, mortality, foraging rates or methods, reproductive output, and growth rates of individuals (Kamermans and Huitema 1994, Ólafsson et al. 1994, De Goeij et al. 2001, Berke et al. 2009). Predation can occur via apex predators in a top down manner (Heck and Valentine 2007, Hughes et al. 2014, Johnson et al. 2014), which often acts to stabilize prey population dynamics (Baum and Worm 2009). Predation may also be a result of mid-trophic level predators, often referred to as mesopredators (Prugh et al. 2009). These animals, frequently omnivores (Commuto and Ambrose Jr 1985, Ambrose

Jr 1991), can exert a strong structuring pressure upon biological communities, referred to here as middle-out control. Middle-out control refers to situations where mid-trophic level mesopredators exert a structuring influence on a community. Middle-out predation can, in some situations, destabilize prey populations, at least in the short term, such as during periods of low prey densities, or following mesopredator release (Elmhagen and Rushton 2007, Quijón and Snelgrove 2008, Greenville et al. 2014). Finally, the input of propagules (e.g., larvae for many marine animals) to a site, commonly referred to as a pre-settlement process, can affect community composition by influencing species presence/absence and population density. Propagule supply is a product of oceanographic conditions, local hydrology, initial number of propagules, and propagule behaviour or mortality (Ólafsson et al. 1994, Todd 1998, Pilditch et al. 2015). Movement of older individuals (juveniles and adults) into a site, considered a post-settlement process, may be just as, if not more, important (Pilditch et al. 2015).

1.2 Study area: Intertidal mudflats of the Bay of Fundy, Canada

The intertidal mudflats of the Bay of Fundy offer a useful setting to examine the ecological interactions introduced above. Experimental and sampling replication at various scales is possible as multiple mudflats (study sites) are available in the Bay of Fundy, representing well-defined habitat patches (Drolet et al. 2012). At finer scales, the cohesive fine-grained sediment supports a highly abundant and relatively diverse assemblage of infaunal species (Drolet et al. 2009, Gerwing et al. 2015a). Moreover, this system maintains an assorted group of epibenthic predators such as benthic fish (Jones 1952, Risk and Craig 1976), *Nassarius obsoletus*, the Eastern Mud snail (Coffin et al.

2008, Drolet et al. 2013a), and shorebirds like the Semipalmated Sandpiper (*Calidris pusilla*). Some of these predators are present for short, but intense, periods of time, such as the shorebirds (Hicklin and Smith 1984, Hicklin 1987). Infaunal densities up to 200,000 individuals per m², from numerous taxa (Gerwing et al. 2015a), are possible due to highly productive benthic diatoms which form the base of this food web (Hargrave et al. 1983, Trites et al. 2005). The food web is also supplemented by high inputs of detrital carbon, mostly from local saltmarshes (Stuart et al. 1985, Gordon Jr et al. 1986, Gordon Jr et al. 1987).

1.3 Thesis structure

In my thesis, I examined the relative importance of biotic and abiotic factors in structuring biological communities by quantifying their influence on the infaunal community (species presence/absence and density) of eight Bay of Fundy intertidal mudflats. The mudflat sites were selected primarily as typical mudflats visited by the Semipalmated Sandpipers in the past (Hicklin and Smith 1984, Hicklin 1987, Boates and Smith 1989, Wilson Jr 1989), as well as secondarily based on their history of being studied (Yeo 1977, Barbeau and Grecian 2003, Barbeau et al. 2009, Drolet et al. 2013b) and their accessibility. Note that this thesis often refers to Gerwing et al. (Accepted), which describes the details of how the mudflat community, individual taxa, and abiotic environmental conditions varied among the selected eight mudflats over two years. This paper provides an annual context for the results of Chapter 2, and the actual data used for the overall analysis conducted in Chapter 3.

1.3.1 Chapter 2

In Chapter 2 of my thesis, I investigated how the infaunal community was influenced by winter, a common disturbance in northern temperate latitudes. Specifically, I identified and quantified the intensity of winter stressors, namely temperature, ice presence, ice scour, and wind (Büttger et al. 2011, Drolet et al. 2013b), and determined their association with changes in community structure. Winter stressors and their effects on soft-sediment coastal ecosystems are understudied in temperate latitudes (Strasser et al. 2001, Thieltges et al. 2004, Büttger et al. 2011), and this work is important not only to understand how winter stressors impact the intertidal mudflats in the Bay of Fundy, but also to further elucidate their impacts in temperate systems.

1.3.2 Chapter 3

In Chapter 3, I investigated the infaunal community year-round over two years. I studied how it was associated with abiotic factors such as particle size (Aller and Aller 1998, Kristensen 2000), water content, exposure time (Stillman 2002), and penetrability of mudflat sediments (Kennedy 2012). I also assessed the relative contribution of biological forces, namely:

(i) top-down effects like predation by benthic fish (Risk and Craig 1976, Gilmurray and Daborn 1981) and sandpipers (Hicklin and Smith 1984, Hamilton et al. 2006, Cheverie et al. 2014), and bioturbation and predation by the mud snail *N. obsoletus* (Cranford 1988, Coffin et al. 2012);

(ii) bottom-up effects like benthic diatom production (Levinton and Kelaher 2004, Fraser et al. 2006a, Fraser et al. 2006b) and organic matter content in sediments (Christensen et al. 2000, Kristensen 2000); and

(iii) middle-out effects, specifically predation/bioturbation by errant polychaetes (Ambrose Jr 1984b, a, 1991, Gillet et al. 2012, Queirós et al. 2013).

For the analysis, I examined the effect of these biotic and abiotic variables upon the entire infaunal community (resemblance matrix calculated from the densities of 10 taxa). Multivariate analyses (PERMANOVA) and the non-parametric statistical program PRIMER were used to determine the proportion of the infaunal community variation each biotic and abiotic variable accounted for; in other words, I quantified the relative importance of each variable. Statistical analyses that allow for partitioning of variation of structuring processes represent a useful advancement in investigating the relative importance of these processes. Using such a method, Menge (1991) was able to show that the relative importance of pre- and post-settlement processes varied geographic locations. My use of PERMANOVA allowed me to adequately model the spatial and temporal structure of our data set. Therefore, when I investigated the relative importance of biotic and abiotic factors in the system, the analysis took into account my sampling structure (sampling site, plot, round, year) (Clarke 1993, Anderson et al. 2008, Clarke et al. 2008).

Studies that investigate the controlling influence of biotic and abiotic factors often utilize a small number of species (usually only one) over a limited spatiotemporal scale (Menge 1991, Ólafsson et al. 1994, Todd 1998, Nozawa et al. 2013, Jones and Ricciardi 2014). Strengths of my study are that it included 10 infaunal taxa, and investigated the

influence of numerous biotic and abiotic variables upon the entire infaunal community, over the entire upper Bay of Fundy, spanning two years. The work in Chapter 3 contributes to our understanding of patterns that structure the mudflat community, complimenting and building upon earlier studies conducted on finer spatiotemporal scales. Furthermore, the methods utilized in Chapter 3, when applied to other systems, will not only expand the understanding of forces that structure biological communities, but also ease comparability between studies, providing deeper insight on how and why the relative importance of structuring variables may vary.

1.3.3 Chapter 4

In Chapter 4, I further investigated predation by sandpipers, one of the top-down predators examined in Chapter 3. I developed and evaluated the usefulness of a non-invasive method of sandpiper diet determination, identification of prey DNA in sandpiper feces (termed molecular scatology). Such a non-invasive method of diet determination is usefully for acquiring high quality data for this species. Diet information is key to understand the influence top-down predators are having on the infaunal community (Berke et al. 2009, van Gils et al. 2009, Cheverie et al. 2014), more specifically which prey items are being consumed. With regards to Semipalmated Sandpipers, historical studies using stomach content analysis suggested that while in the Bay of Fundy, sandpipers foraged preferentially upon a single, but abundant, prey species, the amphipod *Corophium volutator* (Hicklin and Smith 1979, 1984). Based on this, several studies investigated the influence sandpiper predation had upon populations of *C. volutator* (Matthews et al. 1992, Hamilton et al. 2006). However, recent work using stable isotope analysis and visual observations indicated that this shorebird

consumes a broader range of mudflat prey items than previously thought (MacDonald et al. 2012, Quinn and Hamilton 2012). Therefore, sandpiper predation may be directly influencing the entire infaunal community, not just *C. volutator*. Further, Semipalmated Sandpipers, like most North American shorebirds, are experiencing strong population declines, and facing increased extinction risks (Bart et al. 2007, Galbraith et al. 2014). As an animal's diet influences every aspect of its biology, understanding diet is essential in designing effective conservation/management plans (Fryxell et al. 2014). The diet information presented in Chapter 4 elucidates, not only the relationship between these top-down predators and the infaunal community, but also provides a more complete understanding of the breadth of sandpiper diet, offering insight into potential conservation challenges (exposure to contaminants and bioaccumulation of toxins) facing this species.

1.3.4 Chapter 5

In Chapter 5, I integrated the main finding of my thesis, and discussed how they influence our understanding of mudflat ecosystems, and more generally, our understanding of forces that structure biological communities.

1.4 Implications

As indicated above, the work presented in this thesis contributes to our understanding of ecological interactions that structure the intertidal mudflats in the Bay of Fundy. The relationships observed in this thesis, when contrasted with similar interactions from other systems (Tilman 1996, Gage and Cooper 2005, Bracken et al. 2014), could offer general insights into the types of processes, and their relative importance, that structure

biological communities. However, between-study variation in methods limits our ability to compare studies and synthesize general theories. The methods presented in Chapters 3 and 4 are easily applicable to studies conducted in any ecosystem, potentially allowing easier comparison between studies. A greater understanding of the relative importance of key interactions (top-down predation, bottom-up resources, etc.) in structuring not only individual ecosystems, but general processes spanning multiple systems, will enable us to predict how natural systems vary, as well as how our actions may alter these ecosystems. Such information may enable us to prevent or even remediate further human-induced impacts.

Chapter 2: Resilience of an intertidal infaunal community to winter stressors

2.1 Abstract

Disturbances can greatly affect densities and richness of biological communities. Given the relatively severe winters in Atlantic Canada, including on mudflats in the Bay of Fundy, winter may be an important structuring force for intertidal infaunal communities. Further, stressors may include effects of sub-zero temperatures, temperature variations, wind, different types of ice, scour, and low sediment oxygen content. We sampled eight major mudflats in the Bay of Fundy (a macrotidal, temperate system) before (December) and after (March) winter over two years, to quantify the biotic community as well as various environmental variables related to both sediment conditions and winter severity. Infaunal communities exhibited statistically significant, but small changes over winter. Furthermore, patterns were not consistent among years, sites or taxa: some taxa decreased in density, others did not change, and a few increased. Finally, the over-winter community change was only weakly correlated to winter stressors. Analysis of the multivariate correlation indicated that physical disturbance of sediments (i.e., scour density and depth, variance in drift ice cover) and sediment oxygen content may influence community structure. Overall, winter (strictly defined as the period with ice present in our study) did not greatly influence the infaunal community, and the mudflat infaunal community appears resilient to winter stressors.

2.2 Introduction

A disturbance is a discrete event in time or space that alters resources, substrate availability or the physical environment, potentially disrupting community or population structure (White and Pickett 1985, Petraitis et al. 1989). Ecologists have long been interested not only in what constitutes a disturbance (Bleakney 1972, Ayling 1981, White and Pickett 1985), but also how disturbances influence biological communities (Levin 1984, Whitlatch et al. 1998). A disturbance, depending on its severity and frequency, may lead to decreases or increases in population densities and taxa richness (Reise 1991, Hobbs and Huenneke 1992, Chambers et al. 2013). Increases in biodiversity occur, for example, when the density of highly competitive taxa is reduced, allowing colonizers with lower competitive ability to become established (Pacala and Rees 1998, Kondoh 2001, Fox 2013). Furthermore, if occurring heterogeneously across a landscape, a disturbance can result in a mosaic of different successional stages (Reise 1991, Hobbs and Huenneke 1992, Chambers et al. 2013). The timing of a disturbance may also be important, since its impacts may be amplified if occurring when populations are vulnerable (Petraitis et al. 1989, Hobbs and Huenneke 1992). However, a system (community or population) may be able to recover from or withstand a disturbance, and so be resilient (Walker 1995, Folke et al. 2010). Resilience to a specific disturbance is a result of characteristics such as tolerances (e.g., thermal or fire resistance; tolerance of a disturbance is often referred to as being resistant to that disturbance), method and frequency of reproduction, as well as mobility of taxa (Gunderson 2000, Walker et al. 2004, Folke et al. 2010).

Winter on the intertidal mudflats of the Bay of Fundy, Canada, is a multifaceted disturbance potentially affecting benthic marine invertebrates. Winter stressors, as well as their impacts, have been observed in the Wadden Sea (Strasser et al. 2001, Thielges et al. 2004, Büttger et al. 2011), Antarctica (Everitt et al. 1980, Peck and Bullough 1993, Barnes 1995b, a), and the Arctic (Conlan et al. 1998). The effect of winter is of particular interest, including in the Bay of Fundy, because most benthic invertebrate populations are at the low point in their annual density cycle during winter, and may be more vulnerable than at other times (Petraitis et al. 1989, Hobbs and Huenneke 1992).

Winter is multifaceted because subzero temperatures may influence invertebrates via both thermal stress (Beukema 1992, Strasser and Pieloth 2001, Büttger et al. 2011) and the action of ice (Strasser et al. 2001, Belt et al. 2009, Büttger et al. 2011). Further, ice in the Bay of Fundy is classified into two broad categories: crust and drift ice. Crust ice occurs when the sediment and/or water above the sediment freezes (Knight and Dalrymple 1976, Gordon Jr and Desplanque 1983), and can extend from nearly 40 cm above the sediment to 15 cm below the surface (Kennedy 2012, Drolet et al. 2013b). Drift ice consists of blocks ranging in size from a few cm³ to several m³ (Knight and Dalrymple 1976, Gordon Jr and Desplanque 1983, Drolet et al. 2013b), that can be moved by water currents and/or wind. Crust ice's influence on infauna is likely related to freezing (Knight and Dalrymple 1976, Gordon Jr and Desplanque 1983, Strasser et al. 2001), while drift ice's influence is strongly tied to scour (Armonies et al. 2001, Strasser et al. 2001, Scrosati and Heaven 2006, Büttger et al. 2011).

Wind may also influence ice mobility, scour, or temperature; thus when examining winter-related variables, wind exposure must also be considered. Finally, ice may sever

the connection between the sediment and the overlying water, thus reducing dissolved oxygen availability in sediment pore water, intensifying anoxic/hypoxic conditions (Barnes 1999). Reduction in dissolved oxygen is known to induce mortality in benthic invertebrates (Günther 1992, Rosenberg et al. 2001, Diaz and Rosenberg 2008) and changes in community structure (Altieri and Witman 2006, Altieri 2008, Ferguson et al. 2013). In sum, winter is a complex disturbance, more complicated than just cold and ice.

Winter stressors and their effects on soft-sediment coastal ecosystems are understudied in temperate latitudes (Strasser et al. 2001, Thieltges et al. 2004, Büttger et al. 2011). The main objective of our study was to quantify over-winter change of the invertebrate community on intertidal mudflats in the Bay of Fundy. To that end, we sampled eight large mudflats spanning the extent of the upper Bay of Fundy, before and after winter, over two years. Specifically, we asked: (1) Does the intertidal invertebrate community vary over winter? (2) If so, which taxa drive this community change? (3) Which winter stressors are associated with the observed community and taxa-level change?

2.3 Methods

2.3.1 Study sites

Our study was conducted on intertidal mudflats in the upper Bay of Fundy, Canada (Figure 2.1). The Bay of Fundy is a macrotidal system, with tidal amplitudes ranging from 8-16 m in the upper regions (Desplanque and Mossman 2004b). Eight mudflats were sampled: Mary's Point (MP), Daniels Flats (DF), Grande Anse (GA), Pecks Cove (PC) and Minudie (MN) located in Chignecto Bay, and Moose Cove (MC), Avonport

(AV) and Starrs Point (SP) located in Minas Basin. While similar in many ways, these mudflats are representative of the subtle variation in habitat features present in this region (Table 2.1, Figure A1.1 and Table A1.1 in Appendix 1). During winter, depending on the orientation of a mudflat relative to the dominant westerly winds, and the interaction between tidal currents and weather systems (including wind direction and strength), the mudflat may be covered with drift ice, crust ice, both, or free of ice. Drift ice may remain on a mudflat ranging from hours to many days (Knight and Dalrymple 1976, Gordon Jr and Desplanque 1983, Macfarlane et al. 2013).

2.3.2 Quantification of ice conditions via aerial surveys

For our study, we defined winter as the period of time ice was present on intertidal mudflats (mid-January to end of February in 2010 and 2011). In 2010, we surveyed ice conditions by walking transects on mudflats. Since only one mudflat could be visited by a sampling team per day, and ice conditions on a mudflat can vary greatly from one day to the next, ice cover data for 2010 was not useful for spatial comparisons and are not presented. In 2011 we did same-day sampling of all mudflats by airplane. Ice conditions were quantified using aerial surveys at all 8 mudflats within 2 h of low tide on the same day, when daylight low tides coincided with mild weather and good visibility (three sampling dates: 29 January, 14 February and 24 February). From the air two observers independently quantified the proportion of each mudflat covered with drift ice and crust ice (Gordon Jr and Desplanque 1983). Photographs were also taken from various altitudes, and images were then analyzed using Image J (rsbweb.nih.gov/ij/) to determine the proportion of each mudflat covered in each type of ice. All visual observations taken onsite were within 5% of image analysis values; values derived from

the images were used in subsequent analyses. We calculated average percent cover as well as variance ($n = 3$ sampling dates).

2.3.3 Ground-based data collection

We sampled mudflat biota and sediment conditions pre-and post-winter, during the weeks of 8 December 2009 and 10 March 2010 for the first winter, and the weeks of 4 December 2010 and 16 March 2011 for the second winter. During a given week, we sampled all eight mudflats (termed sites), with two sites randomly visited per day, typically one in Chignecto Bay and one in Minas Basin. At each mudflat, two transects, running perpendicular to the low water line, were established 700-1000 m from each other, depending on along-shore length of the mudflat. Transects were 700-1800 m long (depending on the across-shore length of the mudflat), from the shoreward start of the mudflat to the highest low tide line, and were divided into four equal zones based upon distance from shore, for random stratified sampling.

For mudflat infauna, three sampling locations (termed plots) were randomly selected per zone, for a total of 12 plots per transect, 24 plots per site. At each plot, a 7 cm diameter corer was pushed into the sediment as deep as possible (5-10 cm until hard bottom or the end of the corer was reached). Within 12 h of collection, samples were passed through a 250- μ m sieve (Crewe et al. 2001) to retain all benthic life stages of macrofauna, as well as large meiofauna, and preserved in 95% ethanol. Preserved samples were later sorted and invertebrates identified and counted under a dissecting microscope. Densities of the amphipod *Corophium volutator*, bivalve *Macoma* spp., Copepoda, Ostracoda and polychaetes (to family) were quantified.

Mudflat sediment characteristics were quantified from cores collected along the transects mentioned above, both before and after winter. One sediment sample (corer: 3 cm diameter, 5 cm deep) was randomly collected from each zone (4 per transect, 8 per site, 64 per sampling round). The top 1 cm of each core was separated and weighed. This sediment was then dried in a drying oven (110 °C, for 12 h), weighed again, and placed in a desiccator. Percent water content was then calculated as: $(\text{mass wet sediment} - \text{mass dry sediment}) / (\text{mass wet sediment}) \times 100$. This dry sediment was then ashed in a muffle furnace at 550 °C for 4 h and weighed; percent organic matter content was calculated as $(\text{mass dry sediment} - \text{mass of ashed sediment}) / (\text{mass of dry sediment}) \times 100$. Volume-weighted mean sediment particle size was then determined for each sample using a Malvern Mastersizer 2000 (www.malvern.com). Particle size was measured in triplicate and an average value per sample was calculated (Rodriguez 2005).

In addition to data obtained from aerial surveys, information on winter stressor variables was collected as follows. To assess dissolved oxygen content in the sediment, we visually measured depth to the apparent redox potential discontinuity (aRPD; Gerwing et al., 2013) to the nearest 0.5 cm in each plot. Measurements were made in the void left in the sediment following removal of the 7-cm diameter core (for infauna sampling), as described in Gerwing et al. (2013). Depth of the aRPD in the sediment is a good relative indicator of sediment oxygen content (specifically, dissolved oxygen content in pore water) when comparing different locations (Gerwing et al. 2015b). Three measures of the aRPD were examined: average and variance in pre-winter aRPD depth per mudflat ($n = 24$ plots), and the change in aRPD depth over winter (average post-winter value

minus average pre-winter value per mudflat) to reflect the change in pore water oxygen content. We quantified ice scour once per winter, in early to mid-March 2010 and 2011, following the arrival of warmer air temperatures and ice break up, during the annual peak in scour occurrence (Drolet et al. 2013b). Along each established transect (described above), we randomly selected 20 locations (1-m² plots; 5 plots per zone per transect), and recorded in each plot density of scour (number of scour marks m⁻²) and depth of deepest scour (see Drolet et al. (2013b) for information and images on what constitutes scour). We then calculated average scour density and average depth of deepest scour per plot, as well as the variance (n = 40 plots), for each site. Variance in scour density and depth are a measure of spatial variation in scour conditions within a mudflat, and along with the average values reflects how impacted a site is by ice scour.

Since air temperature is related to mudflat sediment temperature (Kennedy 2012), we measured air temperature at mudflats by placing two iBcod temperature recorders (Alpha Mach) on the shoreline of each mudflat between 12 Jan and 26 Feb 2011. A reading was taken every 4 h, and we calculated the average and variance (n = 438 per recorder per site), and extracted the minimum and maximum. We also quantified wind exposure at each mudflat using cotton tatter flags in 2011. A linear relationship exists between flag weight loss and wind exposure (Miller et al. 1987, Quine and White 1994). Two groups of five flags were spaced ~1 km apart on the shore at each mudflat. We initially deployed flags (pre-weighed after 12 h in a drying oven at 110 °C) on 7 February 2011, but did not use these data because flags became buried in snow. Flags were deployed again on 1 April 2011 for 30 d; while this does not provide exact wind exposure over winter, it reflects the relative exposure of mudflats. Flags were collected,

dried for 12 h at 110°C, and then weighed again. Average flag weight loss per mudflat (n = 10 flags) was calculated.

2.3.4 Data analyses

2.3.4.1 Community and individual taxon change

We used PRIMER with the PERMANOVA (Permutational Multivariate Analysis of Variance) add-on (McArdle and Anderson 2001) to quantify how the mudflat invertebrate community changed over winter. The community was composed of 10 taxa: *C. volutator*, *Macoma* spp., Copepoda, Ostracoda, as well as the polychaetes Nereididae, Nephtyidae, Phyllodocidae, Cirratulidae, Spionidae, and Capitellidae. For the resemblance matrix, we added a dummy variable of 1 to deal with plots with zero densities, transformed the data using fourth root to improve assessment of effects of rare and common taxa on community structure, and used the Bray-Curtis coefficient. A dummy variable can be considered a “dummy species,” to correct calculations of resemblance based upon samples comprised of numerous taxa with densities of zero (Clarke and Gorley 2006). In the PERMANOVA, Site (8 levels), Season (2 levels: pre- and post-winter), and Year (2 levels) were fixed factors; Transect (2 levels) nested within Site, and Plot (error term) were random factors. Due to a significant three-way interaction between fixed factors (Site x Season x Year), we conducted a separate PERMANOVA for each year. For 2009-2010, there was a significant Site x Season interaction, so we conducted a PERMANOVA analysis for each site separately as a posthoc analysis. A sequential Bonferroni-type *p* value correction (Benjamini and Hochberg 1995) was applied for over-winter community change at each site.

Community composition, pre- and post-winter, were visualized using a non-metric multidimensional scaling (nMDS) plot. Overlaid vectors represent the correlations (Pearson correlation coefficients) between taxa and nMDS axes. The nMDS plots had a stress < 0.2 , and so was considered a good 2-dimensional representation of higher dimensional trends (Clarke 1993). SIMPER (Similarity Percentages; Clarke & Ainsworth 1993, Clarke 1993) was used to identify the contribution of each taxon to a significant over-winter community change. The ratio of each taxon's average dissimilarity to standard deviation of the dissimilarities (Diss/SD) represents how consistently each taxon contributed to the community variance. Values greater than 1 represents taxa which consistently contribute to the over-winter community change. Taxa with Diss/SD below 1 did not consistently contribute to the over-winter community change.

SIMPER, supported by ANOVAs (Table A1.3 in Appendix 1), was also used to qualify the over winter-change of each taxon. Taxa which consistently contributed to the overwinter community change (Diss/SD ratio above 1) and which increased or decreased over winter were interpreted to do so consistently, and denoted with a + or –, respectively. Taxa with a Diss/SD ratio below 1 were interpreted to not change consistently over winter, and denoted with no change (nc).

2.3.4.2 Which factors correlate with the community's change over winter?

We used RELATE (Spearman correlation, with 999 permutations; Clarke & Ainsworth 1993) in PRIMER to determine if a correlation existed between community and stressor resemblance matrices. We used an alpha value of 0.1 in these analyses because we were

looking for patterns to generate hypotheses about possible mechanisms underlying community change. We did not use more predictive methods, such as PRIMER's multivariate regression analysis, because our ice data were collected at a different scale than our biota and sediment data (aerially at the level of site versus at the level of plot, respectively). Such methods would have required substantial data pooling and all resolution would have been lost.

First, we tested if post-winter infaunal community was related to pre-winter infaunal community for each winter (2009-2010 and 2010-2011). This comparison provided insight on how much over-winter community variation could be related to winter variables (i.e., if pre- and post-winter communities are not significantly correlated, then winter variables may be associated with much of the change). The community resemblance matrices, pre- and post-winter, were constructed using the mean density ($n = 24$ cores) of each of 10 taxa for each site (Figure 2.3), and the Bray-Curtis coefficient; no other data transformation was used. The matrix had an 8×8 dimension based on our 8 mudflats. Second, we tested if post-winter sediment conditions were correlated to pre-winter sediment conditions for both winters, to provide insight on whether or not the infaunal community inhabited an environment that changed greatly over winter. The sediment resemblance matrices were constructed using mean values per site ($n = 8$ cores or 24 locations) for sediment variables (average volume-weighted mean particle size, % water content, % organic matter content, and aRPD depth) that were then normalized. Euclidean distances were used in this matrix. Third, we tested whether the over-winter change in infaunal community related to the over-winter change in sediment conditions for both winters. The resemblance matrices for the over-winter changes in infaunal

community and sediment conditions were constructed by calculating proportional changes $((\text{post-winter value} - \text{pre-winter value}) / \text{pre-winter value})$ from site averages, and using Euclidean distances. To avoid dividing by zero when pre-winter taxa densities were estimated at zero, we added a value of 1 to all site averages (both pre- and post-winter) prior to calculating proportional density changes; this value was below the detection threshold for taxa densities in our sampling program.

Finally, we tested if the proportional over-winter change (resemblance matrix constructed as stated above) in infaunal community structure correlated with winter variables in 2010-2011. The resemblance matrix of winter variables was constructed using normalized values and Euclidean distances for average pre-winter aRPD depth, pre-winter aRPD depth variance, over-winter change in aRPD depth, average percent cover of crust ice and of drift ice, variance in percent cover in crust ice and in drift ice, average scour density and depth, variance in scour density and depth, average air temperature, minimum air temperature, air temperature variance, and wind exposure. These winter variables were selected as good representative winter variables for this analysis, and did not correlate highly with each other (univariate Pearson correlation coefficient < 0.85 ; Anderson et al. 2008). If a significant multivariate (RELATE) correlation existed, then PRIMER's BEST routine (BIO-ENV, Spearman correlation; 999 permutations) was used to identify which winter variable(s) associated with the community change resemblance matrix (Clarke and Ainsworth 1993, Clarke and Gorley 2006).

2.3.4.3 Which winter variables associate with each taxon's over-winter change?

We constructed a resemblance matrix (Euclidean distance, 8 x 8 dimensions) for each individual taxon's proportional over-winter change in 2010-2011 ((post-winter density – pre-winter density)/pre-winter density for each site), and added 1 before the proportion calculation when pre-winter density was zero. We compared each taxon's resemblance matrix to the resemblance matrix for winter variables (described above) using RELATE (Spearman correlation; 999 permutations). If a significant correlation was detected, BEST (BIO-ENV, 999 permutations) was used to identify the winter variable(s) most associated with the taxon-specific over-winter change.

2.4 Results

2.4.1 General patterns

Taxa richness before and after winter for both years varied little (Figure 2.2; Table A1.3 in Appendix 1); however, substantial variation existed between sites and years.

Individual invertebrate taxa also had considerable variation in density between sites and years (Figure 2.3; Table A1.3 in Appendix 1). Over-winter change in density of taxa was variable, and not necessarily consistent between sites and years, with some taxa increasing over winter, others decreasing, and yet others exhibiting no change. A geographical relationship in community structure was apparent (Figure 2.4): sites from different bays (Chignecto Bay: MN, PC, GA, DF, MP; and Minas Basin: SP, AV, MC) clustered separately, and sites geographically closer within a bay clustered together, independent of year and season of sampling. Moreover, Chignecto Bay sites were

clustered more than Minas Basin sites, suggesting that there was higher inter-mudflat variation in community structure in the Minas Basin mudflats. Also, for each site, pre- and post-winter community composition clustered together. Table 2.1 summarizes ice, scour, wind, and air temperature conditions, while Appendix 1 provides greater detail in the spatiotemporal variation in winter conditions among sites.

2.4.2 Did the infaunal community change over winter?

The mudflat invertebrate community varied by year, site and season (Table 2.2; Figure 2.4). In 2009-2010, the over-winter change varied non-consistently among sites (Site x Season interaction). The infaunal community at AV, MN, PC and MP did not vary significantly over winter in 2009-2010 (Table 2.2), but the community at the other sites (SP, MC, GA and DF) did, with dissimilarity of 28-59% before and after winter (Table 2.3). For the sites which did vary significantly, the taxa which discriminated best ($\text{Diss}/\text{SD} > 1$) between and contributed most (% contribution) to the community change also differed among sites. Generally, *C. volutator*, Spionidae, ostracods, copepods, *Macoma* spp. and Phyllodocidae were good discriminating taxa, and contributed substantially (~10-20%) to the over-winter change at the majority of the sites. In the second year (2010-2011), the overwinter community change varied consistently among sites (non-significant 2-way interaction), though there was a site effect (Table 2.2). Overall average dissimilarity pre- versus post-winter was ~38% (pooled over sites; Table 2.4). *C. volutator* and Phyllodocidae were good discriminators and contributors (~11-15%) to the community change. For the remaining taxa, some accounted for a substantial proportion of the variation, but did not do so in a consistent manner (Table 2.4).

2.4.3 How does each taxon change over winter?

Many of the taxon-site-year combinations revealed no significant change over winter (between December and March; Table 2.5). Although there was no consistent overall pattern, some taxa exhibited a dominant pattern. For example, *C. volutator* predominately decreased over winter, while Spionidae, Phyllodocidae, Ostracoda and Copepoda declined in about half of the site-year combinations. Various polychaetes, the errant Nephtyidae and Nereididae, and the sessile Capitellidae and Cirratulidae, mostly did not significantly change in density between December and March. A few taxa showed an increase in density in some of site-year combinations. No site showed a consistent over-winter change for all taxa from one year to the next.

2.4.4 Which factors correlate with the community's change over winter?

For both 2009-2010 and 2010-2011, the pre-and post-winter infaunal communities were correlated (RELATE; 2009-2010: $\rho = 0.64$, $p = 0.002$; 2010-2011: $\rho = 0.63$, $p = 0.005$; Figure 2.4). Similarly, the pre- and post-winter sediment conditions were correlated (2009-2010: $\rho = 0.55$, $p = 0.02$; 2010-2011 $\rho = 0.76$, $p = 0.018$). However, the proportional over-winter change in taxa densities did not correlate with the proportional change in sediment conditions (2009-2010: $\rho = -0.22$, $p = 0.78$; 2010-2011 $\rho = -0.20$, $p = 0.70$). Nevertheless, the over-winter community change was weakly correlated with winter variables in 2010-2011, and the relationship was significant ($\rho = 0.284$, $p = 0.098$). The single winter variable that best grouped the sites in a manner consistent with over-winter community change was scour depth (both site variance and average, $p = 0.70$ and 0.69 , respectively; Table 2.6). The next best single winter variable was scour

density (both site variance and average). Variance in percent drift ice cover and average aRPD depth showed a moderate and weak correlation. The pairing of scour density variance and scour depth variance produced the best correlation with the over-winter community change and was significant (BEST; $\rho = 0.872$; $p = 0.001$).

2.4.5 Which winter variables associate with each taxon's over winter change?

Only the errant polychaete Nephtyidae showed a significant correlation between its proportional change over-winter and winter variables (Table 2.7). Winter variables associated with Nephtyidae over-winter change were similar to those observed with the community pattern, and included average scour depth ($\rho = 0.81$), scour depth variance ($\rho = 0.70$), average scour density ($\rho = 0.49$), variance in percent drift ice cover ($\rho = 0.30$), and average pre-winter aRPD depth ($\rho = 0.27$). The best combination of winter variables was the triplet of average scour depth and density, and scour depth variance (BEST, $\rho = 0.82$, $p = 0.02$).

2.5 Discussion

2.5.1 Resilience of the infaunal community to winter disturbance

Although we detected significant changes in the infaunal community structure of intertidal mudflats in the Bay of Fundy over winter, the changes were relatively small. Specifically, community structure for a given mudflat clustered together for pre- and post-winter samplings over two years (Figure 2.4). Indeed, post-winter community structure was strongly correlated with pre-winter community structure (for both study

years), suggesting that the influence of winter stressors (ice, wind, temperature, scour, hypoxia) on over-winter community change was limited. Further, post-winter sediment conditions (particle size, water content, organic matter content, and aRPD depth) also correlated strongly with pre-winter sediment conditions, further suggesting that winter stressors had little impact, as the sediment environment changed little. However, other studies have shown that sub-zero temperatures (Beukema 1992, Strasser and Pieloth 2001, Büttger et al. 2011), and ice and scour (Strasser et al. 2001, Belt et al. 2009, Büttger et al. 2011) can disturb infauna. Therefore, our observations suggest that during the winters of 2009-2011, the intertidal infaunal community in the Bay of Fundy was resilient to winter stressors.

The small, but significant, over-winter change in community structure in our study reflected responses by a wide variety of taxa. Some taxa showed strong decreases in density, others no change, and a few increases in density (Tables 2.3, 2.4, 2.5). In addition, taxon responses to winter varied between sites (suggesting a site by season interaction) and years. Such a variety of responses within a taxon has been observed before, although not in the Bay of Fundy, in the polychaetes Phyllodocidae (Armonies et al. 2001) and Capitellidae (Gordon Jr and Desplanque 1983, Wilson Jr 1991, Armonies et al. 2001). A more consistent response within a taxon has been observed, also not in the Bay of Fundy, for Spionidae, reported to decrease over winter (Armonies et al. 2001), and Cirratulidae to not change over winter (Wilson Jr 1991). *Corophium volutator*, was observed to smoothly decline over winter in the Bay of Fundy (Drolet et al. 2013b). As well, consistent with our study but observed in other systems, *Macoma balthica* has been observed to increase in density over winter (Beukema 1979, Gordon Jr

and Desplanque 1983), and ostracods to not change (Wilson Jr 1991). The variety of taxon-specific responses over winter supports our view that the community is relatively resilient to winter stressors (Grimm and Wissel 1997, Gunderson 2000, Walker et al. 2004, Folke et al. 2010).

Taxon-related features of our infauna that may impart resilience or resistance to winter stressors include being resistant to freezing. For example, *C. volutator* and some polychaetes can be encased in ice and survive after thawing (Macfarlane et al. 2013), therefore exhibiting resistance to freezing stress. Resilience may be a result of reproduction replacing winter-related mortality. Indeed, sessile polychaetes (Cirratulidae, Spionidae) have been reported to reproduce asexually in harsh conditions (Wilson Jr 1983, Petersen 1999). In addition, movement of individuals such as immigration into impacted sites by various dispersal vectors (Drolet et al. 2013a, Macfarlane et al. 2013), or emigration from local disturbances (e.g., scour) would contribute to resilience. Our study was not designed to determine which of these mechanisms may be operating in our system. However, some combination of these features was likely operating, and their relative importance may vary among taxa.

2.5.2 Possible effects of winter stressors

Given the small observed changes in community structure over winter, the weak association with winter stressors (ice, scour, wind, air temperature, and sediment oxygen content) should be expected. Nevertheless, in-depth analysis of the multivariate correlation was insightful to understand the multi-faceted aspect of winter and identify

variables which could be important in more severe winters (Armonies et al. 2001, Strasser et al. 2001, Büttger et al. 2011).

Variables related to scour (scour density and depth) may have a potential structuring influence (Table 2.6) in our system. Variance in drift ice cover also showed some correlation with community change, which given the identified correlation with scour is not surprising. Drift ice results in scour when it moves across the sediment. High temporal variance in drift ice cover signifies that drift ice was highly mobile, resulting in more scour. Scour has been observed to have negative impacts on coastal communities by inducing mortality or dislodging residents (Strasser et al. 2001, Belt et al. 2009, Büttger et al. 2011). Deeper scour implies a more severe scour event, likely leading to higher rates of mortality or movement. At the taxon-specific level, only the errant polychaete *Nephtyidae* was correlated with winter stressors. Interestingly, the same variables were correlated with *Nephtyidae*'s over-winter change as in the over-winter community analysis (scour, drift ice; Table 2.7). This initially was surprising, since *Nephtyidae* did not show a significant change in absolute densities before versus after winter (though densities were generally low, which would have made it difficult to detect differences; Figure 2.3 and Table 2.5). However, the proportional positive or negative change in density (averaged per site) over winter was associated with the amount of scour and variance in drift ice cover experienced at the sites. Thus, a mechanistic hypothesis derived from our study is that scour and drift ice may influence over-winter changes of some infaunal taxa, and community structure.

The other type of ice, crust ice, has previously been reported to negatively affect organisms because of thermal stress (Beukema 1991, 1992, Thieltges et al. 2004,

Büttger et al. 2011), or to help protect them. A layer of stationary ice limits low sediment temperatures and dampens temperature fluctuations (Gutt 2001, Partridge 2001, Scrosati and Eckersley 2007). In addition, crust ice has been hypothesized to shield the sediment, and its associated infauna, from ice scour (Knight and Dalrymple 1976, Barnes 1999, Gutt 2001). However in our study, crust ice cover (either average or temporal variance) did not show any correlation with over-winter change in the infaunal community or individual taxa density. This may be a result of experimental design, as we did not directly contrast infauna responses when covered and not covered by crust ice. Nevertheless, crust ice may have influenced our system indirectly through interactions with aRPD depth (a relative measure of oxygen content in sediment; Gerwing et al., 2015a). Specifically, crust ice can sever the connection between the sediment and the water column, and so exacerbate anoxic/hypoxic conditions (Barnes 1999) and cause the aRPD to move closer to the surface. Our study identified pre-winter aRPD as a variable correlated with over-winter change. However, as the correlation observed was with pre-winter aRPD depth, not over-winter aRPD depth change, we are unsure of the possible causal relationship, and are hesitant to speculate.

The taxa which contributed most to the over-winter community change (*C. volutator*, Phyllodocidae, Copepoda and Spionidae; Table 2.4) did not correlate with the measured winter stressor. A complementary study focused on *C. volutator*, and conducted during the same two winters as our study and at two of our sites, observed a similar pattern and provided further insights (Drolet et al. 2013b). Drolet et al. (2013b) observed that *C. volutator* density decreased linearly throughout winter, independent of temperature and ice events, eliminating the possibility of acute effects of winter stressors on survival. As

well, the possibility of emigration events to subtidal areas (where the winter environment is more benign; (Günther 1992, Beukema et al. 1998, Beukema and Dekker 2003)) was unlikely, because there were no sudden decreases in *C. volutator* density before or immediately upon the onset of winter (Drolet et al. 2013b). The constant decrease in density (which implies an increase in proportional mortality) as winter progressed suggests that the amount of stored energy in *C. volutator* individuals (which would decrease as the winter proceeded) is important for over-wintering survival (Drolet et al. 2013b). Similar mechanisms may be operating for our other taxa; however, as our study used spatially, rather than temporally, intensive sampling, we do not know the density trajectory during winter for our other taxa. Depletion of stored energy levels, emigration events (e.g., errant polychaetes as in Günther 1992) or other processes that are not immediately tied to winter stressors may have been important for other infauna during winter. Focal studies with multiple sampling times (not only pre- and post-winter samples) are needed to quantify detailed population trajectories during winter.

2.5.3 Winter in an annual context

From a human perspective, winter on the Bay of Fundy intertidal mudflats appears to be a severe disturbance. Air temperatures often approach -20° C, accumulations of ice encompassing entire sites are common, and scour is abundant and can penetrate deep into the sediment. However, our results suggest that winter, strictly defined as the period when ice was present, did not have a substantial effect on the infaunal community inhabiting intertidal mudflats. In fact, the infauna community appeared to be resilient to the winter-induced stressors of temperature, ice and hypoxia. This result is further

supported when patterns of infaunal densities and taxa richness were examined over the entire year (Gerwing et al. 2015a). Percent dissimilarity, a measure of the community change between temporal sampling units, revealed that over-winter change is likely a continuation of a seasonal trend. Percent dissimilarity tended to be low (~25-35%) during the peak in mudflat density and richness (July-August) and then increase (30-60%) as density/richness decreased during fall and winter (August-March; Gerwing et al., Accepted). The over-winter change appears to be simply a continuation of this pattern, a larger pattern likely not fully or directly related to winter stressors during our strictly-defined winter.

2.5.4 Conclusion

Although we detected a significant over-winter change in infaunal community structure on intertidal mudflats of the Bay of Fundy, it was small and not consistent (increases and decreases) over two winters. Moreover, correlations between community structure or taxa densities and winter stressors were generally weak. This suggests that the infaunal community was resilient to winter stresses. Further examination of the significant (though weak) multivariate correlation between over-winter community change and winter stressors provided insights on component stressors of a disturbance (*sensu* Hobbs and Huenneke 1992). We hypothesize that variables related to the physical disturbance of sediments (drift ice cover and variance, scour density and depth), as well as sediment dissolved oxygen content may have structuring influence in more severe winters. A next step will be to directly test these hypotheses at finer spatiotemporal scales using predictive methods of analysis as well as manipulative experiments.

2.6 Chapter 2 acknowledgements

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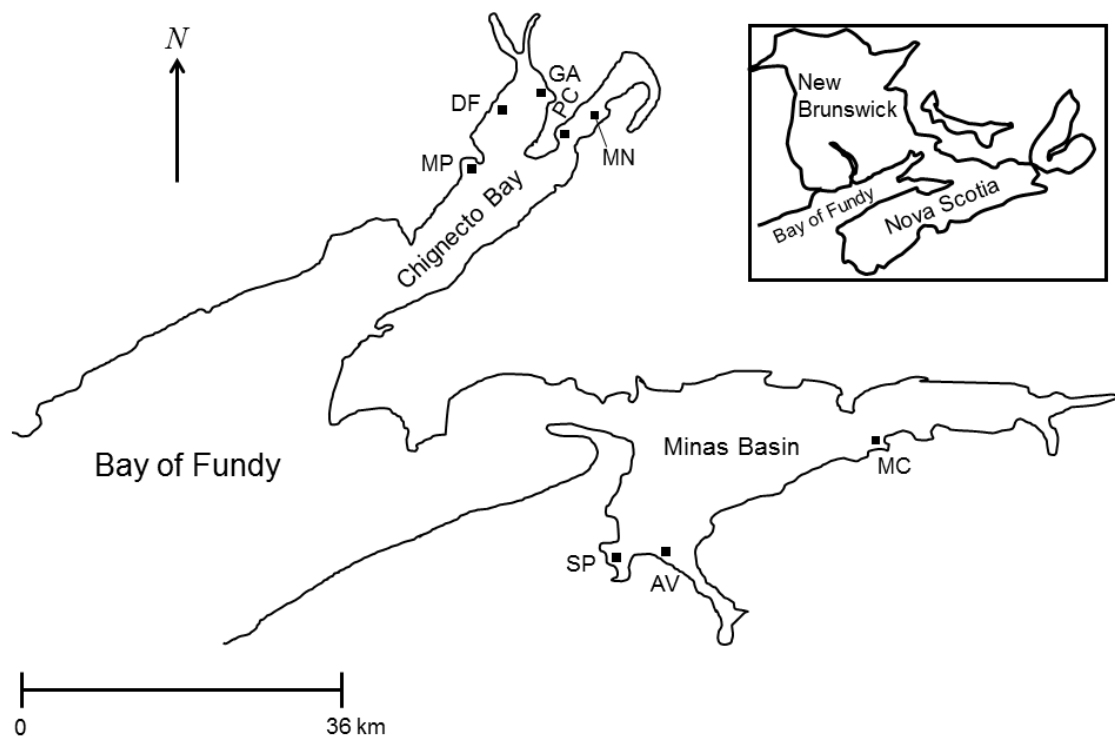


Figure 2.1: Study sites (intertidal mudflats) in the upper Bay of Fundy, Canada. Site names are Starrs Point (SP), Avonport (AV), Moose Cove (MC), Minudie (MN), Pecks Cove (PC), Grande Anse (GA), Daniels Flats (DF), and Mary's Point (MP). The insert indicates the location of the Bay of Fundy in Maritime Canada.

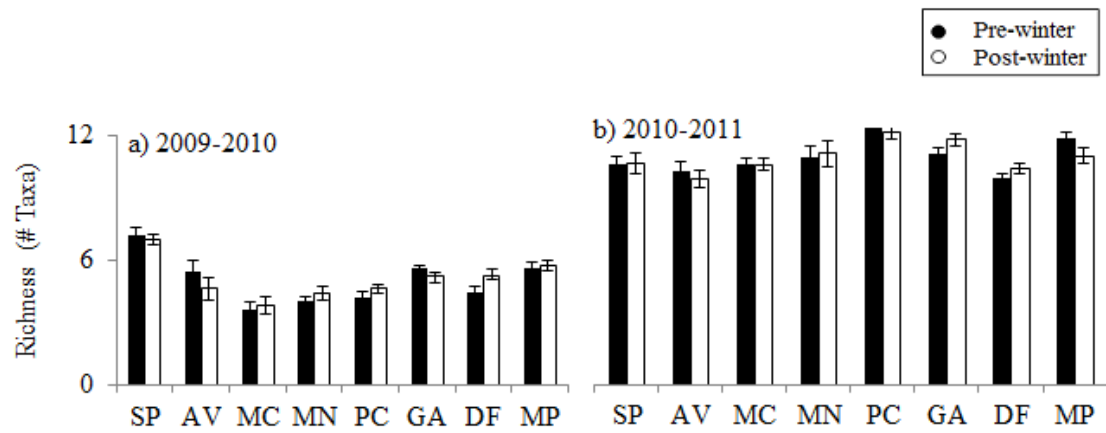


Figure 2.2: Taxa richness (mean $\pm$ SE, $n = 24$ cores) of infauna before (December) and after (March) winter for two years and at each mudflat site in the upper Bay of Fundy. See Table 2.1 for full site names.

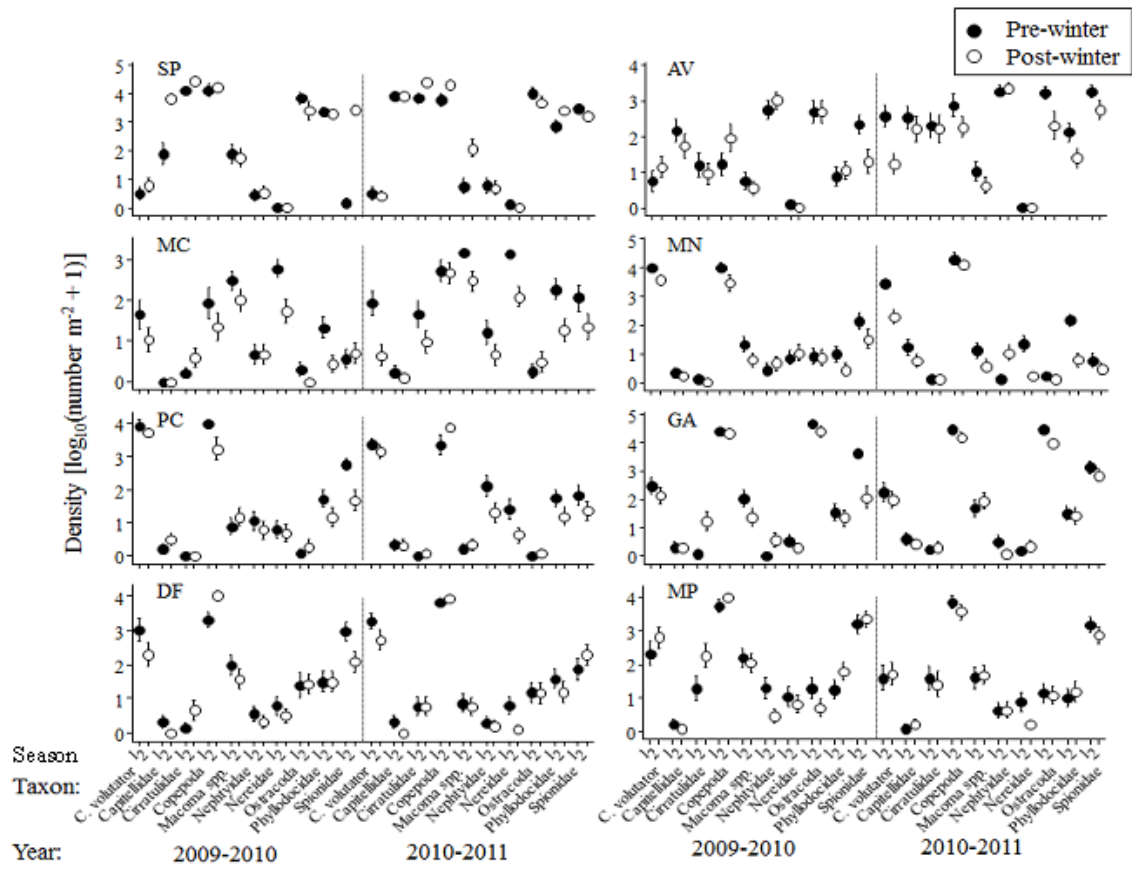


Figure 2.3: Pre-winter (December) and post-winter (March) density (mean $\pm$ SE, $n=24$ cores) of infaunal taxa at each mudflat site in the upper Bay of Fundy and for two years. See Table 2.1 for full site names.

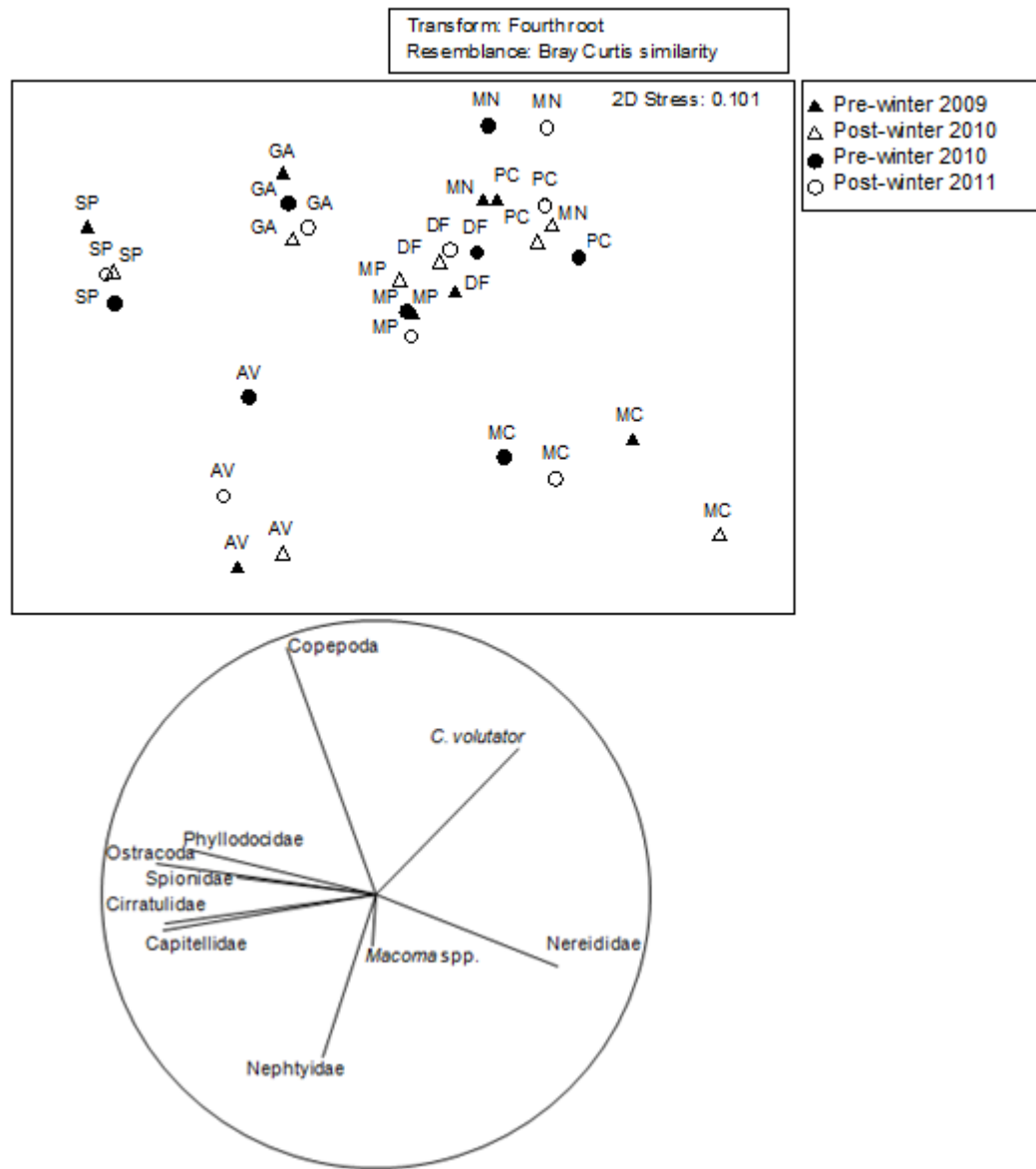


Figure 2.4: Non-metric multidimensional scaling (nMDS) plot of the intertidal mudflats in the Bay of Fundy (see Table 2.1 for full site names) based on pre- and post-winter infaunal community. Each symbol represents a site-time combination; the distance between symbols represents the difference in community composition between site-time combinations. The vector overlay beneath the nMDS plot represents correlations between taxa and nMDS axes. The vector of each taxon shows the direction of increased density across the nMDS plot. See Figure 2.3 for actual taxa densities.

Table 2.1: Summary (value or mean $\pm$ SE) of sediment and winter-related features from each intertidal mudflat site in the Bay of Fundy for the second winter (2010-2011). Since differences in pre- and post-winter sediment properties (particle size, and % water and organic matter content) were small, the pre- and post-winter values were pooled (n = 16 cores per site). Sediment particle size is the volume-weighted mean. n = 24 locations for apparent redox potential discontinuity (aRPD); n = 438 readings for air temperature; n = 10 tatter flags for wind exposure; n = 3 sampling dates for ice cover; n = 40 quadrats for scour data.

Feature	Variable Type	SP Starrs Point	AV Avonport	MC Moose Cove	MN Minudie	PC Pecks Cove	GA Grande Anse	DF Daniels Flats	MP Mary's Point
Orientation of Mudflat Opening		Northeast	Northeast	West	West	East	West	East	South
Area of Mudflat (km ²)		4.0	1.5	1.1	8.0	2.0	10.0	8.0	5.0
Sediment Particle Size (μm)	Sediment	40.6 $\pm$ 12.2	42.9 $\pm$ 4.9	56.0 $\pm$ 10.9	21.0 $\pm$ 1.0	38.8 $\pm$ 1.5	16.6 $\pm$ 70.9	33.2 $\pm$ 2.7	43.0 $\pm$ 2.3
Sediment Organic Content (%)	Sediment	3.1 $\pm$ 0.2	3.3 $\pm$ 0.2	3.3 $\pm$ 0.2	3.7 $\pm$ 0.1	2.4 $\pm$ 0.1	4.6 $\pm$ 0.1	2.7 $\pm$ 0.1	2.5 $\pm$ 0.1
Sediment Water Content (%)	Sediment	30.9 $\pm$ 1.3	32.7 $\pm$ 1.1	31.6 $\pm$ 0.6	39.9 $\pm$ 1.7	28.8 $\pm$ 0.7	43.2 $\pm$ 0.8	35.3 $\pm$ 0.5	27.8 $\pm$ 1.1
Pre-winter aRPD Depth (cm)	Sediment/Winter	2.7 $\pm$ 0.3	4.2 $\pm$ 0.3	4.5 $\pm$ 0.4	6.3 $\pm$ 0.3	4.8 $\pm$ 0.3	6.2 $\pm$ 0.4	2.7 $\pm$ 0.2	1.8 $\pm$ 0.2
Post-winter aRPD Depth (cm)	Sediment/Winter	1.1 $\pm$ 0.4	1.1 $\pm$ 0.2	0.6 $\pm$ 0.2	6.9 $\pm$ 0.3	4.7 $\pm$ 0.2	8.8 $\pm$ 0.2	4.5 $\pm$ 0.1	4.8 $\pm$ 0.2
Air Temperature ($^{\circ}\text{C}$)	Winter	-1.8 $\pm$ 0.3	-2.8 $\pm$ 0.3	-3.2 $\pm$ 0.3	-4.2 $\pm$ 0.3	-3.8 $\pm$ 0.3	-4.3 $\pm$ 0.3	-4.1 $\pm$ 0.3	-4.1 $\pm$ 0.3
Min Air Temperature ($^{\circ}\text{C}$)	Winter	-17	-17.5	-18.0	-20.8	-21.3	-21.3	-22.8	-23.3
Max Air Temperature ($^{\circ}\text{C}$)	Winter	16.8	14.2	12.0	12.5	13.5	9.8	13.8	15.0
Wind Flag Weight Loss (g)	Winter	1.3 $\pm$ 0.1	1.0 $\pm$ 0.1	1.7 $\pm$ 0.2	0.9 $\pm$ 0.1	0.8 $\pm$ 0.2	1.3 $\pm$ 0.2	0.7 $\pm$ 0.1	0.6 $\pm$ 0.1
Cover Crust Ice (%)	Winter	35.5 $\pm$ 32.3	36.7 $\pm$ 31.8	60.0 $\pm$ 30.6	62.5 $\pm$ 31.3	45.0 $\pm$ 27.5	90.0 $\pm$ 5.8	61.8 $\pm$ 21.8	41.9 $\pm$ 29.0
Cover Drift Ice (%)	Winter	2.0 $\pm$ 1.0	0.0 $\pm$ 0.0	50.0 $\pm$ 15.3	50.0 $\pm$ 26.5	47.0 $\pm$ 24.6	32.2 $\pm$ 24.0	2.7 $\pm$ 1.5	4.3 $\pm$ 2.9
Scour Density (number m ⁻²)	Winter	0.11 $\pm$ 0.03	0.01 $\pm$ 0.01	0.08 $\pm$ 0.03	0.21 $\pm$ 0.04	0.16 $\pm$ 0.04	0.05 $\pm$ 0.02	0.04 $\pm$ 0.03	0.00 $\pm$ 0.00
Scour Depth (cm)	Winter	0.26 $\pm$ 0.07	0.03 $\pm$ 0.03	0.30 $\pm$ 0.15	1.43 $\pm$ 0.34	0.53 $\pm$ 0.16	0.63 $\pm$ 0.24	0.06 $\pm$ 0.05	0.00 $\pm$ 0.00

Table 2.2: PERMANOVA results investigating whether the mudflat infaunal community varied over winter in the Bay of Fundy. Significant and interpretable p values of fixed effects are in bold. Non-significant p values of fixed effects which approach significance are in italics. Due to a significant three-way interaction (Site x Season x Year, Pseudo- $F_{7,8} = 2.17, p = 0.03$), the analysis was conducted by year. Multiple comparisons for winter 2009-2010 (Site x Season interaction) were interpreted with p values corrected using a sequential Bonferroni-type adjustment. See full site names in Table 2.1.

Source of variation	df	MS	Pseudo-F	Unique Permutations	p
2009-2010					
Site	7	40366	15.22	998	0.001
Season	1	3847	4.61	999	0.015
Site x Season	7	3073	3.69	997	0.001
SP	1	3153	7.43	998	0.002
AV	1	2959	1.79	998	0.105
MC	1	6211	3.74	998	0.014
MN	1	1699	2.32	998	<i>0.071</i>
PC	1	1503	2.26	998	<i>0.070</i>
GA	1	1721	4.23	998	0.006
DF	1	4045	4.23	998	0.021
MP	1	1503	1.57	998	0.203
Transect(Site)	8	2652	2.98	998	0.001
Season x Transect(Site)	8	834	0.94	999	0.599
Residual	350	891			
2010-2011					
Site	7	35487	30.64	997	0.001
Season	1	8548	7.77	999	0.002
Site x Season	7	1786	1.62	999	0.117
Transect(Site)	8	1158	1.60	998	0.024
Season x Transect(Site)	8	1100	1.52	999	0.035
Residual	352	725			

Table 2.3: Results of SIMPER for the sites (SP, MC, GA, DF) that had a significant change in infaunal community over winter (between December and March) in 2009-2010 (see Table 2). Average dissimilarity of each taxon, and its percent contribution to overall dissimilarity between pre-winter and post-winter communities are presented. Diss/SD is the ratio of the average dissimilarity to standard deviation of the dissimilarities for each taxon; values greater or equal to 1 are in bold, and represent taxa which consistently contributed to the observed community change. See full site names in Table 2.1.

SP Overall average dissimilarity = 34.10					GA Overall average dissimilarity = 28.68				
Taxon	Average Dissimilarity (%)	Diss/SD	Contribution (%)	Cumulative contribution (%)	Taxon	Average Dissimilarity (%)	Diss/SD	Contribution (%)	Cumulative contribution (%)
Spionidae	6.6	2.8	19.3	19.3	Spionidae	5.3	1.2	18.3	18.3
Capitellidae	5.5	1.4	16.1	35.4	Ostracoda	4.9	1.2	17.0	35.3
Copepoda	5.1	1.2	14.9	50.3	C. volutator	3.8	1.3	13.4	48.7
Ostracoda	4.8	1.1	14.0	64.2	Macoma spp.	3.5	1.2	12.1	60.8
Cirratulidae	4.5	1.4	13.1	77.4	Cirratulidae	2.8	0.8	9.6	70.4
Macoma spp.	3.5	1.1	10.4	87.7	Phyllodocidae	2.7	1.1	9.6	80.0
<i>C. volutator</i>	1.6	0.8	4.6	92.4	Copepoda	2.4	1.4	8.5	88.5
Phyllodocidae	1.5	1.3	4.3	96.6	Nereididae	1.3	0.6	4.7	93.1
Nephtyidae	1.2	0.7	3.4	100	Nephtyidae	1.1	0.5	3.7	96.8
Nereididae	0	NA	0	100	Capitellidae	0.9	0.5	3.2	100
MC Overall average dissimilarity = 59.17					DF Overall average dissimilarity = 44.47				
Taxon	Average Dissimilarity (%)	Diss/SD	Contribution (%)	Cumulative contribution (%)	Taxon	Average Dissimilarity (%)	Diss/SD	Contribution (%)	Cumulative contribution (%)
Copepoda	11.6	1.1	19.6	19.6	C. volutator	8.2	1.2	18.4	18.4
Nereididae	10.2	0.9	17.2	36.8	Spionidae	7.6	1.1	17.2	35.6
C. volutator	9.8	1.0	16.5	53.3	Ostracoda	5.6	1.1	12.6	48.1
<i>Macoma spp.</i>	8.8	0.8	14.9	68.2	Copepoda	5.4	1.1	12.2	60.4
Phyllodocidae	6.5	1.0	11.0	79.2	Macoma spp.	5.3	1.2	11.8	72.2
Nephtyidae	4.4	0.8	7.5	86.7	Phyllodocidae	4.3	1.1	9.7	81.9
Spionidae	4.1	0.7	6.9	93.5	Nereididae	2.7	0.8	6.1	88.0
Cirratulidae	2.5	0.6	4.3	97.8	Nephtyidae	2.4	0.6	5.4	93.4
Ostracoda	1.3	0.4	2.2	100	Cirratulidae	2.2	0.5	4.9	98.3
Capitellidae	0	NA	0	100	Capitellidae	0.8	0.4	1.7	100

Table 2.4: Results of SIMPER for the change in mudflat invertebrate community over winter (between December and March) in 2010-2011, pooled over sites (see Table 2.2). Average dissimilarity of each taxon, and its percent contribution to overall dissimilarity between pre-winter and post-winter communities are presented. Diss/SD is the ratio of the average dissimilarity/standard deviation of the dissimilarity for each taxon; values greater or equal to 1 are in bold, and represent taxa which consistently contributed to the observed community change.

Overall average dissimilarity = 37.59%				
Taxon	Average Dissimilarity (%)	Diss/SD	Individual Contribution (%)	Cumulative Contribution (%)
<i>C. volutator</i>	5.5	1.0	14.6	14.6
Copepoda	5.3	0.9	14.1	28.6
Spionidae	4.4	0.9	11.8	40.4
Phyllodocidae	4.1	1.0	10.9	51.3
Ostracoda	3.6	0.8	9.4	60.8
Cirratulidae	3.5	0.7	9.3	70.1
<i>Macoma</i> spp.	3.4	0.9	9.0	79.1
Nephtyidae	3.2	0.7	8.4	87.5
Nereididae	2.6	0.6	7.0	94.5
Capitellidae	2.1	0.6	5.5	100

Table 2.5: Overview of the change over winter for each taxon (SIMPER; Tables 2.3 and 2.4). “+” represents taxa with a Diss/SD ratio = 1 or higher and which increased over winter. “-“ represents taxa with a Diss/SD ratio = 1 or higher and which decreased over winter. “nc” or no change represents taxa with a Diss/SD ratio < 1. “0” represents taxa which were absent and so a comparison was not possible. Full site names are in Table 2.1; Year 1 is for December 2009 to March 2010, and Year 2 for December 2010 to March 2011. Similar results were observed when population change over winter was analyzed using ANOVA (see Table A1.3 in Appendix 1).

Site	Year	Capitellidae	Cirratulidae	Spionidae	Phyllodocidae	Nereididae	Nephtyidae	<i>Macoma</i> spp.	Ostracoda	Copepod a	<i>C. volutator</i>
SP	1	+	+	+	-	0	nc	-	-	+	nc
SP	2	+	+	-	+	0	nc	+	-	+	-
AV	1	-	nc	-	nc	nc	nc	nc	nc	+	nc
AV	2	-	-	nc	-	0	nc	nc	-	-	-
MC	1	0	nc	nc	nc	nc	nc	nc	nc	-	-
MC	2	nc	-	-	-	nc	nc	nc	nc	-	-
MN	1	nc	nc	-	nc	nc	nc	-	nc	nc	-
MN	2	nc	nc	nc	-	nc	nc	nc	nc	-	-
PC	1	nc	0	-	-	nc	nc	+	nc	nc	-
PC	2	nc	nc	-	-	-	-	nc	nc	nc	-
GA	1	nc	nc	-	-	nc	nc	-	-	-	-
GA	2	nc	nc	-	-	nc	nc	+	-	nc	-
DF	1	nc	nc	-	+	nc	nc	-	-	+	-
DF	2	nc	nc	+	-	nc	nc	nc	-	+	-
MP	1	nc	+	+	+	nc	nc	-	-	+	+
MP	2	nc	-	nc	+	nc	nc	+	nc	nc	-

Table 2.6: Summary of BEST (BIO-ENV, Spearman correlation coefficient) results comparing the over-winter proportional change in the infaunal community to a selection of winter variables in Bay of Fundy mudflats in 2010-2011. a) Correlation with each single winter variable; b) correlation for the ten best combinations of winter variables. “Selection of variables” in b) refer to the “variable number” in a). Note that with multivariate data sets, a negative correlation does not represent a negative relationship, but rather no relationship.

a) Single winter variables			b) Combinations of winter variables		
Variable name	Variable number	Correlation	Selection of variables	Number of variables	Correlation
Scour Depth Variance	1	0.70	1, 3	2	0.87
Average Scour Depth	2	0.69	1-3	3	0.86
Scour Density Variance	3	0.63	1-4	4	0.86
Average Scour Density	4	0.62	1-5	5	0.85
Drift Ice Cover Variance	5	0.49	1, 3, 4	3	0.85
Pre-winter Average aRPD Depth	6	0.21	2, 3	2	0.83
Average Drift Ice Cover	7	0.09	1, 2, 4, 5	4	0.82
Average Crust Ice Cover	8	-0.04	1-4, 6	5	0.82
Crust Ice Cover Variance	9	-0.19	1-3, 5	4	0.82
Average Air Temperature	10	-0.24	1-4, 11	5	0.82
Air Temperature Variance	11	-0.26			
Wind Exposure	12	-0.29			
Over-winter aRPD Depth Change	13	-0.31			
Pre-winter aRPD Depth Variance	14	-0.32			
Minimum Air Temperature	15	-0.4			

Table 2.7: Summary of RELATE (Spearman correlation coefficient) results examining the correlation between pre- and post-winter densities for each taxon in Bay of Fundy mudflats in 2010-2011. Significant correlations are bolded. Note that a negative correlation value with a multivariate data set does not represent a negative relationship, but rather no relationship.

Taxon	Correlation	<i>p</i>
Nephtyidae	0.43	0.02
Phyllodocidae	0.20	0.16
<i>C. volutator</i>	0.06	0.35
Nereididae	0.05	0.39
Ostracoda	-0.01	0.46
Capitellidae	-0.02	0.48
Copepoda	-0.24	0.87
Spionidae	-0.26	0.98
Cirratulidae	-0.29	0.92
<i>Macoma</i> spp.	-0.29	0.93

Chapter 3: Relative importance of biotic and abiotic forces on the composition and dynamics of a soft-sediment intertidal community

3.1 Abstract

Top-down, bottom-up, middle-out and abiotic factors are usually viewed as main forces structuring biological communities, although assessment of their relative importance, in a single study, is rarely done. We quantified, using multivariate methods, association between abiotic and biotic (top-down, bottom-up and middle-out) factors and infaunal population and community variation on intertidal mudflats in the Bay of Fundy, Canada, over two years. We observed a significant relationship between infaunal communities/populations and biotic as well as abiotic factors. Abiotic and middle-out factors were of intermediate importance, while top-down and bottom-up factors were of relatively minor importance. Spatial structural factors like site and plot accounted for most of the variation. We suggest that community and population structure were relatively uncoupled from biotic and abiotic factors in this system because of high concentrations of resources (benthic diatoms and detrital organic matter), as in resource-pulse ecosystems, that sustain high densities of infauna and limit exploitative competition. Further, we hypothesize that the infaunal community at a mudflat primarily reflects stochastic spatial events, namely a “first come, first served” process. We observed differences in patterns for the relative importance of factors among taxa, as well as between taxa and the community, suggesting that community-level analyses may obscure patterns/associations of less common taxa due to the overwhelming

patterns/associations of more abundant taxa. Whether or not this represents a serious limitation of multivariate analyses at the community level must be further evaluated. The methods used here are applicable to any system of interest, and usage in a variety of systems may reveal general patterns in the relative importance of forces that structure communities.

3.2 Introduction

Ecologists have long debated the factors that structure biological communities (Rosemond et al. 1993, Snelgrove and Butman 1994, Menge 2000, Levinton and Kelaher 2004). Abiotic factors, such as salinity or temperature, coupled with the variations in tolerance or preference organisms exhibit for these factors (Stillman 2002, Lu et al. 2008, Ghasemi et al. 2014), exert an obvious influence on biological communities (Kelaher et al. 2001, Ferguson et al. 2013, Ghasemi et al. 2014). Biotic factors can also affect community composition and spatiotemporal dynamics. Some communities are controlled via predation in a top-down manner (Heck and Valentine 2007, Hughes et al. 2014, Johnson et al. 2014), while others are driven by availability of resources in a bottom-up manner (Davis et al. 2014, Schuldt et al. 2014, van den Hoff et al. 2014). In reality, most communities are likely influenced by a combination of top-down and bottom-up forces (Bracken et al. 2014, Greenville et al. 2014, Springer and van Vliet 2014, Vinuela et al. 2014). Further complicating matters is the role of middle-out variables, such as mid-trophic level predators, often referred to as mesopredators (Prugh et al. 2009). These animals, frequently omnivores (Comitato and Ambrose Jr 1985, Ambrose Jr 1991), can exert a strong structuring pressure upon biological

communities (Elmhagen and Rushton 2007, Quijón and Snelgrove 2008, Greenville et al. 2014).

Complementary studies focussed on determining patterns in community structure and dynamics, and on evaluating processes underlying community patterns are needed to fully understand the relative importance of structuring forces. Manipulative experiments are excellent at determining whether processes are occurring within an ecosystem, but are less efficient at quantifying how these processes interact to produce patterns at larger scales. This is because manipulative experiments are logistically constrained to a limited number of variables (Underwood 1996), and cannot manipulate the full suite of *in situ* conditions (Dayton 1971, Connolly 1994, Hamilton 2000, Cheverie et al. 2014, Johnson et al. 2014). This results in manipulative studies often focusing on only biotic or only abiotic factors (Snelgrove and Butman 1994, Hughes et al. 2014, van den Hoff et al. 2014). Survey-based methods measuring correlation, not cause and effect as in manipulative experiments, can include more variables than manipulative experiments and study them over a broader spatiotemporal scale in conditions not altered by experimenters. Mensurative methods are thus complimentary to manipulative experiments, and they enable one to assess the relative importance of different processes on pattern generation at scales much greater than what can be manipulated (Underwood et al. 2000, McGarigal and Cushman 2002, Ze-Hao 2004).

The infaunal community of the intertidal mudflats in the Bay of Fundy, Canada, exhibits moderate complexity and is an ideal system in which to investigate the relative importance of biotic and abiotic factors to community and population variation. The community appears to be structured by a combination of top-down and bottom-up forces

(Ólafsson et al. 1994, Hamilton et al. 2006, Cheverie et al. 2014). Potential bottom-up forces include highly productive populations of benthic diatoms, which form the base of this food web (Hargrave et al. 1983, Trites et al. 2005, Gerwing et al. 2015a). Diatom production is supplemented by high inputs of detrital organic matter (Stuart et al. 1985, Gerwing et al. 2015a), likely from local saltmarshes (Gordon Jr et al. 1986). Potential top-down forces include epibenthic predators such as benthic fish (McCurdy et al. 2005), the mudsnail *Nassarius obsoletus* (a.k.a. *Ilyanassa obsoleta*; Drolet et al. 2013a), and shorebirds (Hamilton et al. 2006, Cheverie et al. 2014). In addition, infaunal polychaete omnivores such as Phyllodocidae, Nereididae, and Nephtyidae (Fauchald and Jumars 1979, Pagliosa 2005, Jumars et al. 2014, Gerwing et al. 2015a) may represent strong middle-out forces (Ambrose Jr 1984b, Commito and Ambrose Jr 1985, Ambrose Jr 1991). Finally, abiotic factors such as particle size of sediments (Meadows 1964b), exposure time to air (Cranford et al. 1985), and dissolved oxygen content in sediments (Ferguson et al. 2013) may also be exerting structuring influences.

The goal of our paper was to quantify the relative importance of biotic (top-down, middle-out, bottom-up) and abiotic factors to community and population variation. We intensively sampled biotic and abiotic variables of eight mudflats spanning the entire upper Bay of Fundy over two years. The detailed information pertaining to the spatiotemporal variation in these variables can be found in Gerwing et al. (2015a). We then used a multivariate empirical modelling method (PRIMER; Clarke and Gorley 2006) to relate independent variables to the biological community. Our study thus contributes to our understanding of patterns in the mudflat community, and complements earlier studies focussed on process. More generally, the methods utilized

here when applied to other systems will not only expand the understanding of forces that structure biological communities, but also provide insight on how and why the relative importance of these variables may change.

3.3 Methods

3.3.1 Study sites

Our eight intertidal mudflats (termed “sites”) in the Bay of Fundy, Atlantic Canada, consisted of Mary’s Point (MP), Daniels Flats (DF), Grande Anse (GA), Pecks Cove (PC) and Minudie (MN) located in Chignecto Bay, and Moose Cove (MC), Avonport (AV) and Starrs Point (SP) located in Minas Basin ((Figure 2.1). Details of the biotic and abiotic characteristics of these sites can be found in Gerwing et al. (2015a), Gerwing et al. (2013), and Bringloe et al. (2013).

3.3.2 Mudflat sampling

3.3.2.1 Biota

Over two years, 2009-2011, we sampled mudflats every 3 weeks from June-August, and every 6-8 weeks from October-May. Sampling rounds (Round) occurred at approximately the same time each year (± 1 week). For random stratified sampling at each mudflat, we established two transects perpendicular to the low waterline, each divided into 4 equal zones based upon intertidal distance across-shore. This effectively represented 8 strata per mudflat. More details of the sampling scheme can be found in Gerwing et al. (2015a).

For mudflat infauna, we randomly selected one sampling location (1 m²; hereafter termed “plot”) per zone, for a total of 8 plots per site and an overall total of 1021 plots. Note that we actually sampled the biota (but not the abiotic variables; see below) at 3 randomly selected plots per zone per transect (Gerwing et al. 2015a); preliminary analysis indicated that population and community patterns were similar when the dataset was reduced to 1 plot per zone. Hence, we utilized the subset of our data in which each plot contained all biotic and abiotic measurements. At each plot, a 7-cm diameter corer was pushed into the sediment as deep as possible (5-10 cm; until hard bottom or the end of the corer was reached). Within 12 h of collection, samples were passed through a 250-µm sieve (Crewe et al. 2001) to retain all life stages of benthic macrofauna, as well as large meiofauna, and preserved in 95% ethanol. We quantified densities of *Corophium volutator*, *Macoma* spp., Copepoda, Ostracoda and Polychaetes (identified to family; Gerwing et al. (2015a)).

For each plot, we determined concentration of chlorophyll *a*, an indicator of diatom abundance, in the top 2-3 mm of the sediment, as in Coulthard and Hamilton (2011). We estimated the proportion of the plot covered in shorebird footprints, which were generated primarily by Semipalmated Sandpipers (*Calidris pusilla*), the most abundant shorebird species in this area (Hicklin 1987). This is a good indication of sandpiper habitat use (Robar and Hamilton 2007), and of foraging activity within a plot since sandpipers spend the majority of their time foraging while on the mudflats (MacDonald et al. 2012). We counted the numbers of *N. obsoletus* snails and fish feeding traces (hereafter termed “fish bites”) in each plot (see Risk and Craig (1976) and McCurdy et al. (2005) for images of fish bites and identification criteria).

3.3.2.2 Abiotic variables and sediment properties

We calculated an index of exposure time (time out of water) for each plot as: $1 - [\text{plot distance (m) from shore} / \text{total transect distance (m)}]$. Transects extended from the landward start of the mudflat to the highest low water line (and were 700-1800 m long, depending on the size of the mudflat). In each plot, we evaluated penetrability of sediment by dropping a metal rod (15 cm long, 1.9 cm diameter, 330 g) from 0.74 m above the substratum. The depth (mm) that the rod penetrated into the sediment was recorded (Kennedy 2012). We measured depth of the apparent redox potential discontinuity (aRPD), an index of the general sediment dissolved oxygen content (Gerwing et al. 2015b), to the nearest 0.5 cm in the void left in the sediment following removal of the 7-cm diameter core for infaunal sampling (Gerwing et al. 2013). We determined additional sediment properties by collecting one sediment sample (corer: 3-cm diameter, 5-cm deep) from each plot, and quantified organic matter content, water content and volume-weighted mean particle size in the top 1 cm of the sediment, as in Gerwing et al. (2015a).

3.3.3 Data analysis

3.3.3.1 Environmental factors associated with community structure

All data analyses were conducted using the statistical program PRIMER with the PERMANOVA (Permutational Multivariate Analysis of Variance) add-on (McArdle and Anderson 2001). We used a PERMANCOVA, a multivariate analysis of covariance, to determine which of our covariates (Abiotic: air exposure, mean particle size, water

content, sediment penetrability, aRPD depth; Biotic top-down: percent cover of sandpiper footprints, density of *N. obsoletus*, density of fish bite; Biotic bottom-up: chlorophyll *a* concentration, organic matter content) were associated with the spatiotemporal variation of the infaunal community. We also quantified variance components, the proportion of the multivariate variation accounted for by each variable (Searle et al. 1992, Anderson et al. 2008). The infaunal community included: *Macoma* spp., *C. volutator*, Copepoda, Ostracoda, and polychaetes (Capitellidae, Spionidae, Cirratulidae, Nereididae, Nephtyidae, and Phyllodocidae). A resemblance matrix of the infaunal densities was calculated using Bray-Curtis coefficients, and a dummy variable of 1 to deal with plots with no infauna (Clarke et al. 2006). Taxa densities were fourth root transformed to improve assessment of rare and common taxa on community structure (Clarke and Gorley 2006). All covariates were normalized prior to analysis to handle measurements with different units and scales (e.g., μm , number m^{-2}). Mean particle size, chlorophyll *a* concentration, density of fish bites, and density of *N. obsoletus* were fourth root transformed prior to normalization to correct skewed distributions (Clarke and Ainsworth 1993). Middle-out polychaetes (Phyllodocidae, Nereididae, and Nephtyidae) were omitted as covariates in this infaunal community analysis since they were part of that community. Beyond the covariates, Round (8 levels per year) was included as a fixed factor, while Year (2 levels) and Site (8 levels) were included as random factors. Year, Round, Site, and Plot (i.e., the lowest level of replication) are hereafter referred to as structural factors. We used $\alpha = 0.05$ for the community analysis, and tested homogeneity of slopes by examining the interaction between structural variables and covariates. Non-significant interactions with covariates

were removed from the model, and significant interactions with covariates were interpreted as contributing to the proportion of the community variation accounted for by the involved covariate (Anderson et al. 2008). Since we used Type I sums of squares and our dataset was mildly unbalanced (data from only 3 plots were missing), we repeated the PERMANCOVA with the various independent variables entered in different orders and verified that variable order within the model did not alter results (Clarke and Gorley 2006, Anderson et al. 2008). Finally, covariates and structural variables that did not account for any variation in the multivariate data cloud were removed or pooled, respectively (Fletcher and Underwood 2002).

3.3.3.2 Environmental factors associated with individual taxa

To evaluate the variables associated with population densities of individual taxa, a resemblance matrix was constructed for each taxon (density data fourth-root transformed, Bray-Curtis coefficients, and a dummy variable). We used the same covariates as detailed for the community analysis, and we added middle-out polychaetes as covariates for the taxon-specific analyses. Phyllodocidae, Nereididae, and Nephtyidae were fourth-root transformed prior to normalization when used as covariates. We conducted PERMANCOVAs as detailed above, and repeated them to test for the possible effect of order of independent variables; variable order only affected the statistical results for one taxon (Nephtyidae), but did not change the general interpretation for that taxon. To correct for possible inflation of family-wise error rates in these multiple taxon-specific analyses, we used $\alpha = 0.01$ (Kelaher et al. 2001). We calculated Pearson's univariate correlation coefficient between the density of each taxon and each of its significant covariates.

3.4 Results

3.4.1 Environmental factors associated with community structure

Structural factors accounted for the majority of the observed infaunal community variation (~79%; Table 3.1). Spatial factors (plots 37% and sites 32%) accounted for most of this variation, while temporal factors (year and round) accounted for a significant, but small proportion of the variation. Bottom-up factors also contributed significantly to community variation, although chlorophyll *a* concentration (a bottom-up factor) only accounted for ~1% of the variation. Top-down factors accounted for ~6% of the variation. Of the top-down predators, *N. obsoletus* (and interactions involving *N. obsoletus*) accounted for the largest proportion of the variation (4.7%), while sandpipers (0.4%) and fish bites (1.1%) accounted for a minority of the variation (Table 3.1). Abiotic covariates accounted for 11% of the community variation. Air exposure (and interactions involving it) accounted for the most (~9%), while mean particle size (and interactions involving it) accounted for a small proportion of the variation (~2%). nMDS and bubble plots exhibiting spatiotemporal change in community composition, as well as which taxa and abiotic factors are associated with these groupings can be found in Appendix 2.

3.4.2 Environmental factors associated with individual taxa

Similar to the community analysis, structural factors (particularly spatial factors) accounted for the majority of the variation in taxon-specific analyses (Table 3.2).

Abiotic, bottom-up, middle-out, and top-down covariates accounted for a smaller proportion of the variation; however, the pattern of significant variables and the proportion of the variation they accounted for varied among taxa, and with the community analysis. Middle-out covariates were associated with many of our taxa, and they accounted for a relatively large amount of the variation, especially for our sessile polychaetes (Capitellidae, Spionidae, and Cirratulidae; 12-21%).

3.5 Discussion

3.5.1 Relative contribution of biotic, abiotic, and structural factors to mudflat community structure

As in other systems, the infaunal community of the Bay of Fundy mudflats was influenced by top-down (Hughes et al. 2014, Johnson et al. 2014), bottom-up (van den Hoff et al. 2014, Vinuela et al. 2014), and abiotic factors (Kelahe et al. 2001, Ghasemi et al. 2014). Our study agrees with past experimental studies in the Bay of Fundy, which found that both top-down and bottom-up forces influenced mudflat communities (Hamilton et al. 2006, Cheverie et al. 2014). However, these past studies were conducted on a smaller spatiotemporal scale than ours, and so only tested the effects of these factors on spatially and temporally localized processes. Two strengths of our study are the broad spatiotemporal scale, and the multitude of factors examined concomitantly, both of which allow us to investigate the relationship between these factors and patterns in community structure. We observed that, although significant, top-down and bottom-up factors accounted for only a small fraction of the community variation. This suggested that infaunal community structure may be relatively decoupled

from both top-down and bottom-up factors in this type of habitat. Instead, structural factors accounted for the majority (~79%) of the community variation. These factors may reflect stochastic events; for example, temporal factors may be related to interactions between time of year (seasons: temperature, photoperiod) and weather patterns (Scholz and Liebezeit 2012, Drolet et al. 2013b). The influence of the spatial factor Site (at the scale of kilometres) may be related to processes such as larval supply (Weersing and Toonen 2009), post-settlement dispersal (Pilditch et al. 2015), unmeasured site features (e.g. hydrodynamic patterns or shelter from tides/waves; Williams et al. 2013), or their interaction. Sediment type (particle size), typically an important site-level feature in soft-sediment studies (Flach 1992a, Snelgrove and Butman 1994, Woodin et al. 2010, Ghasemi et al. 2014), would not have been greatly influential in our study because we had a small range of sediment types among our silt-dominated mudflats (Gerwing et al. 2015a). The variation among plots (at the spatial scale of tens of meters) may be a result of fine-scale interactions such as intra- and interspecific interactions among infauna (Flach 1992a, b, Flach and Beukema 1995, Woodin et al. 2010, Drolet et al. 2013a). Overall, the mudflat infaunal community may reflect a “first come, first served” situation, as described in community succession models (Connell and Slatyer 1977) and discussed further below.

Community dynamics that are uncoupled from top-down predation (i.e., where predation, even when common, has a minor influence on measured phenomenon) have been observed before in resource-pulse ecosystems. In these situations, resource-driven increases in prey numbers are so large that predators exert little influence upon density of prey species (Letnic and Dickman 2010, Greenville et al. 2014, Vinuela et al. 2014).

We propose that the annual bloom in benthic diatoms observed during spring/summer in our system (Hargrave et al. 1983, Gerwing et al. 2015a) acts as a resource pulse, resulting in such an increase in infaunal density (Gerwing et al. 2015a) that top-down predation has little lasting effect. Further, while predators such as shorebirds may have substantial short-term impacts on certain taxa, the mortality is likely compensatory in nature (sensu Pöysä 2004). Seasonal declines in many invertebrates occur regularly in this region (Gerwing et al. 2015c), so predators are consuming soon-to-die individuals. Therefore, the effect of such predation on the community as a whole may be minor. Indeed, Hamilton et al. (2006) suggested that although foraging by sandpipers coincided with large declines in *Corophium volutator*, much of this mortality would have occurred anyway. In addition, our epibenthic predators are intraguild predators, feeding upon multiple trophic levels (Cranford 1988, McCurdy et al. 2005, Coffin et al. 2012, Quinn and Hamilton 2012). Feeding on multiple trophic levels may result in negligible suppression of prey species (Finke and Denno 2005), and thus explain the relatively low proportion of community variation accounted for by epibenthic predators in our system.

Although we propose that top-down effects in our mudflat system were largely neutralized by a superabundance of resources, it should be noted that benthic chlorophyll *a* concentration (a measure of diatom abundance) accounted for only a small proportion of the infaunal community variation and sediment organic matter content was not significant. Thus, community structure and dynamics may also be relatively uncoupled from bottom-up factors. Ample resources should not necessarily be interpreted as bottom-up control of a system, at least not in the sense that resources tightly influence community structure and dynamics. The high primary productivity on

mudflats during spring and summer (Schelske and Odum 1961, Hargrave et al. 1983, Gerwing et al. 2015a) likely limits the importance of exploitation competition, as in resource-pulse ecosystems (Letnic and Dickman 2010, Greenville et al. 2014, Vinueza et al. 2014). Indeed, Drolet et al. (2013a) found no evidence of intraspecific competition among the highly abundant *C. volutator* in our mudflat system, and attributed this to the presence of ample resources. The high amount of resources observed for the majority of the year on our mudflats may be above the threshold required to sustain infaunal populations that minimize the impact of predation as well as to limit exploitative competition. When food is relatively low in late fall to mid-winter (Drolet et al. 2013b, Gerwing et al. 2015a), top-down predators are mostly absent (Gerwing et al. 2015a), and infauna are low in density and relatively inactive (Drolet et al. 2013b, Gerwing et al. 2015a, Gerwing et al. 2015c), so bottom-up factors would not greatly influence community structure (see also Gerwing et al. 2015b for an analysis focused on over-winter patterns). We thus suggest that high levels of resources on mudflats limit the controlling influence and thus the relative importance of bottom-up forces.

Strong relationships between abiotic factors and community/population densities have been well documented in previous studies (Meadows 1964b, Flach 1992a, Snelgrove and Butman 1994, Woodin et al. 2010, Ghasemi et al. 2014). However in our study, measured abiotic factors (air exposure, and mean particle size, penetrability, water content and oxygen content of sediment) accounted for just 11% of the variation in the infaunal community. Of the abiotic variables we examined, air exposure (i.e., time emersed) accounted for the largest proportion of the community variation (~9%). This suggests that the infaunal community exhibited across-shore zonation, an observation

previously reported for *Macoma balthica* on Bay of Fundy mudflats (Cranford et al. 1985). Zonation is likely a result of differential exposure tolerance (Stillman 2002) and is common but subtle on intertidal mudflats (Peterson 1991, Dyer et al. 2000, Bertness 2007). While abiotic factors accounted for more of the community variation than biotic factors, both accounted for less than structural variables. The relatively low importance of abiotic factors may be partially related to the limited variability in conditions observed among our mudflats. In addition, high resource concentrations, as in resource-pulse ecosystems, can lower the influence of abiotic factors by attracting animals to habitats or patches with abiotic characteristics that would normally preclude occupancy (Rose and Leggett 1989, Connolly 1994). This may be occurring in our system, since we have observed high densities of *C. volutator* in sandy-mud patches rich in chlorophyll *a* (Gerwing et al. 2015a), despite this animal's tendency to avoid areas of relatively coarse sediments (Meadows 1964b, c, 1967). Indeed, Meadows (1964a) observed that *C. volutator* can settle after a swimming event on sandy sediments, but avoided settling there if the sand was treated to remove biofilm.

In sum, intertidal mudflats have high primary productivity (Schelske and Odum 1961, Hargrave et al. 1983, Field et al. 1998, Bertness 2007), as well as muted temperature, desiccation and salinity stresses compared to other intertidal habitats (Nybakken and Bertness 2005, Bertness 2007). Mudflats have less competition for space than rocky shores or salt marshes, given the three-dimensional aspect of the substrate (Dayton 1971, Bertness 1991, Nybakken and Bertness 2005, Bertness 2007), and have a low angle of repose and are often expansive, which contributes to diffuse predation pressure by mobile predators (Ambrose Jr 1991, Nybakken and Bertness 2005, Bertness 2007,

Cheverie et al. 2014). Therefore, mudflats may be viewed as a relatively benign environment for organisms adapted to living in mud. We hypothesize that mudflat community structure and dynamics are mainly reflective of “first come, first served” taxa (Sutherland 1974, Connell and Slatyer 1977, Bertness 2007). Inputs of larvae (for species with a dispersive larval phase) and movement by juveniles and adults (Drolet et al. 2012, Bringloe et al. 2013, Pilditch et al. 2015), may be important at the spatial scale of sites. In a review of population variability versus reproductive mode, Ólafsson et al. (1994) concluded that larval availability (recruitment limitation) was not a dominant determinant of community structure of macro-invertebrates in marine soft sediments, but rather that post-settlement factors, such as predation, competition, physical disturbance, and resource availability were more important. Recent work by Pilditch et al. (2015) suggests that dispersal by juveniles and adults (also a post-settlement factor), which is characterized by continued, frequent, small-scale movements over long periods and can dominate meta-community dynamics, may be particularly important in soft-sediment communities. Further, once established, residents may resist colonization by new dispersing individuals (Ambrose Jr 1984a, Loeuille and Leibold 2008). This combined thinking is in line with our findings; we found that (i) predation, resources and abiotic factors had significant but minor relationships with intertidal infaunal community variation, (ii) the community was resilient (Figure S2 in Online Resource, Gerwing et al. 2015b), and (iii) some large-scale spatial factor was strongly associated with community variation. At the smaller spatial scale (among plots) identified to also be important in our study, sediment-animal relations and inter- and intraspecific interactions (Ambrose Jr 1984a, Flach 1992a, Beukema and Flach 1995, Flach 1996,

Woodin et al. 2010) may be dominating. In future studies, we are interested in testing whether pre-emptive competition may be an important structuring force of mudflat infaunal communities.

3.5.2 Patterns at the taxon level, and assessment of middle-out forces

Similar to other systems, most taxa were influenced by a combination of abiotic (Ghasemi et al. 2014), top-down (Johnson et al. 2014), bottom-up (Vinueza et al. 2014), and middle-out factors (Elmhagen and Rushton 2007, Quijón and Snelgrove 2008, Prugh et al. 2009). As in our community analysis, the majority of the spatiotemporal variation of each taxon was accounted for by structural factors (Table 3.2). However, not only was there a different pattern in the importance of independent variables among taxa, but also between taxa and the community as a whole (Tables 3.1 and 3.2). For instance, the community level analysis suggested that sediment water and organic matter content were not associated with community variation. However, taxon-specific analyses revealed that water content was associated with Spionidae densities, and organic matter with copepod densities. Further, variance components (%) varied substantially, indicating that individual taxa were sometimes more and sometimes less connected to abiotic, top-down, and bottom-up factors than the community as a whole, or other taxa. In all cases though, these factors accounted for a relatively small proportion of the spatiotemporal variation of individual taxa (Table 3.2).

Generally, middle-out polychaetes accounted for a relatively large proportion of population variation when compared to top-down and bottom-up factors (Table 3.2). The association between sessile infauna (Capitellidae, Spionidae, and Cirratulidae) and

mesopredators was often relatively high, likely because sessile animals cannot easily avoid predation (Ambrose Jr 1991) or bioturbation (DeWitt and Levinton 1985).

However, the influence of middle-out predators was still limited compared to structural variables, perhaps as a result of low mesopredators densities (Gerwing et al. 2015a).

Nevertheless, even if mesopredator density had been higher, intraguild predation would likely have resulted in limited suppression of prey species (Finke and Denno 2005), since these polychaetes are omnivores (Fauchald and Jumars 1979, Pagliosa 2005, Jumars et al. 2014).

We also observed positive and negative correlations between predators (top-down predators and mesopredators) and prey densities (Table 3.2). Negative effects of predators on prey have been well documented (Hamilton et al. 2006, Prugh et al. 2009, Cheverie et al. 2014). Positive associations between some infauna and predators (Table 3.2) may be the result of predators aggregating in areas or times of high prey densities (Norkko and Bonsdorff 1996, Hamilton et al. 2003), predator and prey densities co-varying with a third factor, or competitive release (Sharpe and Chapman 2014). More work is required on top-down predators and mesopredators of intertidal mudflats at different spatial and temporal scales to explain the variety of correlations they had with prey species.

3.5.3 Implications of different results for community and taxon-specific analyses

The methods used in our paper can be applied to any system to quantify the relative importance of various potential structuring forces. In our paper, the variation in patterns reported between taxa, even taxa performing similar ecological roles, for example

Cirratulidae and Spionidae, (Fauchald and Jumars 1979, Pagliosa 2005, Jumars et al. 2014), suggests that generalizations cannot always be made. Thus, the relative importance of structuring variables should be investigated for all taxa of interest within a community. Murray et al. (2014) arrived at a similar conclusion when they observed that species sharing traits cannot always be aggregated into the same functional group. Furthermore, differences between taxon-specific and community patterns must be addressed. Empirically modelling the community as a whole offers a useful method to understand community spatiotemporal dynamics. However, one drawback of this community-level analytic approach is that associations between individual taxa and structuring variables can be obscured. Spasojevic and Suding (2012), in their examination of plant community functional diversity, also observed that multivariate analyses obscured key relationships which were subsequently identified by analysing individual traits (abiotic filtering, above-ground competition, etc.). Sturaro et al. (2014), in a multivariate analysis of biological assemblages of seagrass meadows, observed limited community variation at their coarser spatial scales (equivalent in scale to our community-level analysis), but strong variations in density and biomass at finer spatial scales. Therefore, analysis at broader scales may obscure fine-grained associations. Continued work is required to better understand processes at different scales, as well as to evaluate whether community models that overlook less common taxa due to the influence of more common taxa are useful. In many situations, less common taxa may exert such a minor influence on the community that the community approach is applicable. In other situations, community-level models which obscure factors that influence key but less common taxa, such as ecosystem engineers (Mermillod-Blondin

and Rosenberg 2006, Caliman et al. 2013), may fail to quantify essential interactions. It is also likely that the answer to this question varies between biological systems and the features of the system investigated.

3.5.4 Conclusions

Previous studies in Bay of Fundy intertidal mudflats observed significant effects of top-down, bottom-up, and abiotic factors on infaunal dynamics (Hamilton et al. 2006, Cheverie et al. 2014). These manipulative experiments were instrumental in illuminating variables that operate within this ecosystem. However, such experiments could not clarify the relative importance of these variables. In other words, manipulative experiments are excellent at identifying processes, but less efficient at determining how multiple processes interact to form larger patterns. Although correlational, the broad spatiotemporal sampling and statistical analysis presented in our study helped elucidate patterns and the relative importance of different structuring variables upon the ecosystem. Specifically, we found that while spatiotemporal variation of infauna were statistically related to top-down, middle-out, bottom-up and abiotic factors, the majority of the observed variation was accounted for by structural variables (site, plot). This suggests that the infaunal communities and populations are relatively uncoupled from measured biotic and abiotic factors. This is likely a result of high concentrations of resources, as in resource-pulse ecosystems, sustaining high densities of infauna as well as limiting exploitative competition. Based on our results and known features of mudflats, we now hypothesize that the infaunal community at a mudflat primarily reflects stochastic events, namely an assemblage of taxa that first recruit onto the mudflat.

The methods and result of our study can be applied to any system of interest. The multivariate analysis presented here demonstrates a method to quantify (and not simply rank) the associations between multiple variables and community or population patterns in a single model. Such methods are useful at elucidating which fine scale processes dominate to create broad scale patterns. However, the considerable variation in importance of the independent variables observed not only among taxa, but also between taxa and the community analysis, urges caution. Similar taxa may be affected by different combinations of factors. Moreover, taxon-specific trends may be overlooked when the community is modelled as a whole. Management plans or conceptual models that include only the factors influencing the community may overlook key taxa-specific relationships, possibly risking their effectiveness. More work is required to determine how this issue limits the usefulness of multivariate analyses of community patterns. Regardless, the methods utilized here will, when applied to other systems, expand our understanding of the variables and processes that structure biological communities, as well as provide insight on how and why the relative importance of these variables changes.

3.6 Chapter 3 acknowledgements

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Table 3.1: PERMANCOVA determining which of the covariates and structural variables were associated with the infaunal community change over space and time for Bay of Fundy mudflats in 2009-2011. We used 996-999 unique permutations. Significant *p* values are in bold. Only interactions between structural variables and covariates that were significant are presented. The detailed data are in Gerwing et al. (2015a).

Variable Type	Source	df	MS	Pseudo-F	<i>p</i>	Variance component (%)
Abiotic	Exposure	1	68215	98.35	0.001	4.37
	Exposure x Round	7	1651	2.91	0.001	0.57
	Exposure x Site	7	7541	13.49	0.001	3.87
	Particle Size	1	18872	1.21	0.358	0.23
	Particle Size x Round	7	2250	2.83	0.001	0.85
	Particle Size x Site	7	1477	2.46	0.001	1.10
	Penetrability	1	11842	1.44	0.241	0.38
	aRPD Depth	1	8884	1.43	0.264	0.23
	aRPD Depth x Site	7	1041	1.57	0.036	0.32
Biotic: Top-down	Sandpiper					
	Footprints	1	8468	4.28	0.002	0.42
	<i>N. obsoletus</i>	1	68222	9.04	0.001	4.30
	<i>N. obsoletus</i> x Site	7	1053	1.82	0.005	0.35
	Fish Bites	1	5071	3.10	0.02	0.24
	Fish Bites x Year	1	2090	3.52	0.003	0.34
	Fish Bites x Site	7	1533	2.35	0.001	0.53
Biotic: Bottom-up	Organic Matter	1	33715	1.41	0.277	1.24
	Chlorophyll <i>a</i>	1	23870	3.06	0.017	1.09
Structural	Year	1	6879	2.55	0.077	0.68
	Round	7	10280	3.60	0.001	4.68
	Site	7	52501	31.44	0.001	31.59
	Year x Round	7	1253	1.32	0.147	0.39
	Year x Site	7	1484	2.67	0.001	1.29
	Round x Site	49	1048	1.14	0.178	0.65
	Year x Round x Site	49	926	1.67	0.001	3.58
	Residual (a.k.a. Plot)	834	556			36.71
	Total	1020				

Table 3.2: Summary results of the PERMANCOVAs determining which covariates were associated with each taxon's spatiotemporal variation for Bay of Fundy mudflats in 2009-2011. Values represent the percent of the variation accounted for by each independent variable (i.e., variance components). The sign in parenthesis represents the nature (+/-) of the Pearson's correlation coefficient between the response taxon's density and that variable. Empty cells represent independent variables which did not account for any of the variation (in this situation, covariates were removed from the models, and structural factors were pooled). na = not appropriate; for the analysis of Phyllodocidae, Nereididae or Nephtyidae, the middle-out covariate for that taxon was not used. We used 996-999 unique permutations. * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$; however, only terms with ** and *** are interpreted. The detailed data are in Gerwing et al. (2015a).

Variable Type	Variable	<i>C. volutator</i>	Ostracoda	Copepoda	<i>Macoma</i> spp.	Capitellidae	Spionidae	Cirratulidae	Phyllodocidae	Nereididae	Nephtyidae
Abiotic	Exposure	0.28 (-)**	1.89 (+)***		12.55 (+)***	0.38 (+)***	4.36 (-)***	0.65 (+)***	0.40 (+)*	4.48 (+)***	12.18 (-)***
	Exposure x Round	1.45***						1.68***			
	Exposure x Site	4.41***	0.99**		4.04***	3.64***	3.44***	5.25***		0.03***	4.79***
	Particle Size			2.43 (-)**							
	Particle Size x Site										2.22***
	Water Content						3.17 (-)**				
	Water Content x Site										2.79***
	Penetrability		2.75 (+)*								
Biotic: Top-down	aRPD Depth	1.92 (-)**		0.59 (+)*							
	aRPD Depth x Site	1.95***									
	Sandpiper Footprints	0.98 (+)***								0.56 (-)*	
	<i>N. obsoletus</i>		2.04 (+)*			3.25 (+)**			2.77 (+)***		
	<i>N. obsoletus</i> x Site		0.83**				1.47***				1.09***
	Fish Bites	0.33 (+)*			0.21 (-)*		0.71**				
	Fish Bites x Year										
	Fish Bites x Site	2.13***									
Biotic: Middle-out	Nereididae	4.13 (+)***	6.11 (-)*		6.81 (+)***	5.02 (-)**	0.97 (-)*			na	
	Nereididae x Site			1.43***				2.09***		na	
	Nephtyidae			3.26 (-)*			0.51 (+)*				na
	Nephtyidae x Site					3.00***		4.05***			na
	Phyllodocidae		3.92 (+)*	3.79 (+)***		9.18 (+)**	9.82 (+)***	13.44 (+)***	na		
Biotic: Bottom-up	Phyllodocidae x Site	2.28***		1.08**			1.19***	1.39***	na		
	Organic Matter			4.82 (+)**			2.71 (-)*				
	Organic x Round	0.99**									
Structural	Chlorophyll <i>a</i>	1.15 (-)*				4.32 (+)**		3.62 (+)**			
	Year			1.41*							
	Round	6.29***	1.06*		2.19**			3.44***	2.15**	5.82***	
	Site	17.27***	29.49***	11.49***	9.72***	28.51***	5.37*	24.83***	12.01***	23.02***	23.47***
	Year x Round			1.75*							
	Year x Site		1.09**	0.89*			1.95**				
	Round x Site	4.29***			3.11***		7.84***		2.49*	2.23***	
	Year x Round x Site			5.85***							
	Residual	50.09	45.30	58.97	59.05	41.59	54.45	36.58	76.24	61.31	52.38

Chapter 4: Lines in the mud: diet reconstruction using next-generation sequencing increases the known ecosystem usage by a shorebird

4.1 Abstract

Molecular scatology and next-generation sequencing identified previously unknown linkages among ecosystems in the diet of Semipalmated Sandpipers (*Calidris pusilla*) in the Bay of Fundy, Canada. During their annual migratory stopover, sandpipers consumed a wider range of prey items than previously thought, demonstrating that they are generalist foragers. Our analysis identified several novel prey items, indicating that sandpipers consume prey from marine (pelagic and intertidal), freshwater, and terrestrial ecosystems. Connections between sandpipers and freshwater as well as terrestrial ecosystems were previously unknown. Current conservation efforts directed towards sandpipers focus on beach and intertidal habitats. However, adequate protection of sandpipers may need to consider freshwater and terrestrial systems as well. Not only do these systems represent an understudied component of sandpiper diet, but they may also represent potential pathways for the consumption of toxic chemicals.

4.2 Introduction

Molecular scatology, the use of molecular techniques to identify prey DNA in faecal samples, is a non-invasive tool used to elucidate diet (Deagle et al. 2009). Using PCR (polymerase chain reactions) techniques, this method can identify minute quantities of prey DNA in faecal samples, often revealing previously unknown prey items (Bowser et

al. 2013). As an organism's diet influences every aspect of its biology, understanding diet is essential for conservation/management plans (Fryxell et al. 2014). As such, molecular scatology has strong applications in conservation science.

The decline of most North American shorebirds due to anthropogenic influences has led to the suggestion that many species face increased extinction risks (Bart et al. 2007, Galbraith et al. 2014). The goal of our paper was to examine the diet of a declining shorebird, the Semipalmated Sandpiper (*Calidris pusilla*), during its fall migratory stopover in the Bay of Fundy, Canada. Due to its importance to sandpiper survival, areas within the Bay of Fundy have been designated as a part of the Western Hemisphere Shorebird Reserve Network (Shepherd and Boates 1999). Historical studies using stomach content analysis suggested that while in the Bay of Fundy, sandpipers foraged preferentially upon a single, but abundant, prey species, the amphipod *Corophium volutator* (Hicklin and Smith 1979, 1984). However, recent work using stable isotope analysis and visual observations has shown that this shorebird consumes a broader range of mudflat prey items than previously thought (MacDonald et al. 2012, Quinn and Hamilton 2012). To advance our understanding of feeding by Semipalmated Sandpipers in the Bay of Fundy, we use molecular scatology to identify the range of prey items.

4.3 Materials and methods

4.3.1 Study sites and sample collection

We collected faecal samples of Semipalmated Sandpipers in summer 2010 on three intertidal mudflats in the upper Bay of Fundy, Canada (Figure 2.1): Avonport (AV), Grande Anse (GA), and Mary's Point (MP), both early (AV: 3 Aug, GA: 2 Aug, MP: 5

Aug) and late (AV: 22 Aug, GA: 23 Aug, MP: 23 Aug) in the sandpiper's stopover period (Hicklin 1987). Mudflats were chosen because they are visited by sandpipers every year. Given the potentially short time (estimated at ~ 20-30 min) it takes food to transit sandpiper digestive tracts (Pienkowski et al. 1983, Tsipoura and Burger 1999), faecal samples were collected approximately 1-2 h after sandpipers ceased roosting and were foraging on the mudflat. Prior to collection, foraging sandpipers were observed from a distance until they naturally relocated; we then moved to where the birds had been and immediately collected, with sterilized tweezers, 50 fresh faecal samples (the brown digested matter at the center and on top of the uric acid), being attentive to not touch the mudflat surface with the tweezers. Immediately after collection, a faecal sample was stored in 95% ethanol and within 12 h frozen until DNA extraction.

4.3.2 Primer design and DNA preparation

DNA extracted from feces is often highly degraded (Kohn and Wayne 1997, Deagle et al. 2006) and since molecular analyses based on a single locus result in highly variable coverage of diet composition (Bowser et al. 2013), we used universal primer pairs that target short fragments (130-300 bp) of two mitochondrial genes (*COI*: (Meusnier et al. 2008); and *16S*: (Deagle et al. 2007)). We used a pooled massively parallel sequencing (MPS) approach described by Puritz et al. (2012). To facilitate the recovery and identification of sequences obtained from individual fecal samples, we included a 10 base multiplex identifier (MID) tag between the Lib-L 454 sequencing adapter (26bp plus a 4bp signal calibration key) and the universal primer (*16S* or *COI*) in our custom engineered forward and reverse primers. Fecal samples can contain significant amounts of DNA from the host species due to the sloughing of cells from the digestive tract

(Shehzad et al. 2012). However, we did not attempt to block the amplification of the host DNA during PCR, because several species of shorebirds forage on the mudflats and we used the traces of host DNA to verify and link the fecal samples to shorebird species. Details of the primer design, including the MID tags used, can be found in Bowser et al. (2013).

Ethanol was removed from the fecal samples by decanting following 30 min of centrifugation at 4°C. DNA was extracted with QIAamp DNA Stool Mini Kit (QIAGEN, ON, Canada) following the manufacturer's protocol. Samples with small amounts of fecal material were eluted with 75-100µl of buffer AE instead of the recommended 200µl. DNA was stored in 2ml microcentrifuge tubes at -20°C until used for *16S* and *COI* gene amplification.

4.3.3 454 library preparation

Amplification of fecal DNA with *16S* MID-tagged sequencing primers was achieved in 20µl reactions containing 5µl undiluted template fecal DNA, 0.2mM dNTP (New England Biolabs, NEB, ON, Canada), 1X bovine serum albumin (BSA; NEB, ON, Canada), 5mM MgSO₄ (Life Technologies, ON, Canada), 0.5µM of each primer (Integrated DNA Technologies, IDT, IA, USA), 1X High Fidelity Buffer (Life Technologies, ON, Canada), and 1 unit of Platinum® *Taq* DNA Polymerase High Fidelity (Life Technologies, ON, Canada). Thermocycling protocol for *16S* began at 94°C for 2 min followed by 35 cycles of 94°C for 30s, 55°C for 30s, and 68°C for 45s, with a final extension of 68°C for 5 min (C-1000™ Thermal Cycler, Bio-Rad, ON, Canada). Amplification with *COI* followed similar component and cycling conditions

as the *16S*, but the annealing temperature was dropped to 45°C. Successful amplification of individual PCR samples was verified by electrophoresis in 1.5% agarose and visualized under UV light using SYBR Safe (Life Technologies, ON, Canada). Amplicons were purified using the QIAEX II Gel Extraction Kit (QIAGEN, ON, Canada) and the concentration was determined with dsDNA BR Assays on a Qubit 2.0 Fluorometer (Life Technologies, ON, Canada). Samples with amplicon concentrations <1ng/µl were re-amplified using the same PCR conditions. Finally, the pooled library was prepared by combining 20ng of each of the *16S* and *COI* amplicons and concentrating to 35ng/µl in 150 PCR-grade H₂O using the DNA Clean & ConcentratorTM-100 (ZYMO RESEARCH, CA, USA). The library was sequenced unidirectionally on half a pico titre plate using the Roche GS-FLX (454) platform at the Genome Quebec Innovation Centre (McGill University, Montreal, Quebec, Canada).

4.3.4 454 data sorting and MOTU identification

Raw reads (DNA sequences) were imported to the CLC genomics workbench (QIAGEN, ON, Canada) for downstream sequence analyses. The library was first sorted by MID tag and then by locus based the first 5 bases of the primer (GACGA for *16S*; TCCAC for *COI*). Following the trimming of the MID Tag and primers, reads were discarded if: 1) there were more than 2 ambiguous nucleotides, 2) had a minimum quality score >0.01 (equivalent to a Phred score of 20), and 3) they were <30 nucleotides. Duplicate reads were removed to increase the representation of unique reads. Faecal samples containing DNA from shorebirds other than Semipalmated Sandpipers were omitted from analysis (16,836 avian DNA sequences were detected and 54 faecal samples were omitted).

The reads were assembled into contigs using the default *de novo* assembly parameters. Both contigs and singletons were considered as ‘molecular operational taxonomic units’ (MOTUs) and were searched in the nucleotide database of the National Center for Biotechnology Information (NCBI, USA) using the basic local alignment search tool for nucleotide (BLASTn) through the CLC GW. We used the following criteria to identify candidate species in the fecal DNA samples: 1) 50 nucleotide minimum length of query sequence, 2) 90% minimum fraction on length consensus between top hit and query sequences, 3) 90% minimum identity between top hit and query sequences, 4) and 60 minimum bit score of top hit sequence. Finally, the identification of each MOTU was accomplished by matching the top-hit *16S* or *COI* MOTU with 69,614 genus and 305,936 species that were registered to taxonomy database of the NCBI as of July 2014.

4.3.5 Identification of *Corophium volutator* in faecal samples

Although our main goal was to assess the breadth of the sandpiper’s diet, we also wanted to confirm the importance of *Corophium* as a prey item for this species. Both empirical and bioinformatics analyses indicated a mismatch between the *COI* primers and the sequence in *Corophium volutator*. However, there was an adequate match with the *16S* primers but the public database did not contain *Corophium spp.* *16S* sequences and our BLASTn searches failed to identify *Corophium* in any fecal sample. To probe our library further, we sequenced the short universal *16S* from 7 different *Corophium volutator* DNA extractions and constructed our own species-specific reference sequence for this locus. Using the same settings in CLC GW described above, we aligned all demultiplexed and quality-trimmed *16S* reads and *16S* MOTUs (contigs + singletons) to our *C. volutator 16S* consensus. As a result, we found 67 of the 1,775 *16S* contigs and

867 of the 6,146 *16S* singletons (11.8% of the 7,896 *16S* MOTUs) matched to the *16S* consensus, positively identifying >100 fecal samples as containing *Corophium* DNA.

4.3.6 Prey bins

To ease interpretation, DNA sequences were placed into the following bins: Diatoms: all diatoms. Insecta Diptera: all flies. Insecta: Caddisflies, Mayflies, and Damselflies. Insecta Other Terrestrial: ants, aphids, beetles, true bugs, butterflies, mosquitos, moths, spittlebugs, wasps, booklice, and unknown insects. Insecta Other Marine: intertidal insects and marine lice. Arachnida: spiders, ticks, and tickspiders. Crustacea Amphipoda *Corophium volutator*: *C. volutator*. Crustacea Amphipoda Other: *Gammarus* spp., *Eurythenes* spp., and *Ischyrocerus* spp. Crustacea Ostracoda: all ostracods. Crustacea Copepoda: all copepods. Crustacea Other: krill, sand fleas, crabs, cladocerans, and unknown crustaceans. Annelida: Polychaetes, oligochaetes, and unknown annelids. Bivalvia: all clams. Gastropoda: all snails. Nemertea: all ribbon worms. Cnidaria and Ctenophoran: all hydrozoans, cnidarians and ctenophores. Fish: all fish. Nematoda: all nematodes.

4.3.7 Data analysis

Data from both *16S* and *COI* loci were combined to maximize prey identification (not all samples amplified for both loci; Table 4.1). Frequency of occurrence (FOO; number of faecal samples a prey item appeared in divided by total number of samples) was calculated for each prey bin.

4.4 Results

The pooled library, generated 389,328 total reads, of which 118,253 unique high quality sequences were used for analysis (after excluding samples with DNA from shorebirds other than Semipalmated Sandpipers as well as low quality reads; Table 4.2). We assembled 7,921 and 26,189 unique MOTUs from the *16S* and *COI* data, respectively. BLASTn analysis of these data identified 131 unique prey taxa. Surprisingly, Semipalmated Sandpipers consumed a variety of prey items (Table 4.3), not only from marine (intertidal and pelagic) systems, but also freshwater, and terrestrial ecosystems. The most common prey item, other than diatoms, was *C. volutator*, whose frequency of occurrence among times and mudflats ranged from 18-96%. We observed several prey items not previously identified for sandpipers in the Bay of Fundy: arachnids, crabs, bivalves, several terrestrial and freshwater insect species, fish (likely eggs or juveniles), and cnidarians/ctenophores. FOO of prey items as well as the number of prey items varied over time and space.

4.5 Discussion

Faecal samples from Semipalmated Sandpipers contained a wide variety of prey items (Table 3). Historic interpretation of stomach content analyses suggested that sandpipers foraged preferentially upon *C. volutator* in this region (Hicklin and Smith 1979), and we did observe *C. volutator* in the majority of sandpiper faecal samples. However, this does not suggest selection or preference, since *C. volutator* is often the dominant resident of these mudflats (Gerwing et al. 2015a). A high FOO of the most common prey item in sandpiper diet would be expected if sandpipers are generalist foragers.

This study expanded our understanding of sandpiper diet by adding terrestrial, freshwater and pelagic species to the list of potential prey, links not previously quantified for this species. Further, we observed several prey items (arachnids, terrestrial and freshwater insect species, crabs, bivalves, fish, and cnidarians/ctenophores) not previously identified as prey. While the proportion of sandpiper diet they comprise is still unknown, our results suggest that sandpipers are consuming freshwater and terrestrial prey items, as well as intertidal prey items. This may suggest that sandpipers will be resilient to changes in their environments, as diet generalists are more resistant to changing environmental conditions than specialists (Colles et al. 2009).

Our analysis identified diatoms in all samples, and there is evidence that sandpipers consume diatoms in this system (MacDonald et al. 2012, Quinn and Hamilton 2012); biofilm has been identified as a major diet component in numerous other small-bodied sandpipers (Kuwae et al. 2012). However, we cannot exclude the possibility that diatom contamination occurred when feces contacted the sediment. Therefore, while our results are consistent with other studies with respect to diatom consumption, they should not be viewed as an independent confirmation. In addition, nematodes may or may not represent actual prey items. Nematodes may represent free living species, or parasites (McCurdy et al. 1999), and a more complete reference library of parasitic and free living nematode DNA sequences in this region is required to clarify this.

The observed connections between Semipalmated Sandpipers and marine (pelagic and intertidal), freshwater, and terrestrial ecosystems raise the possibility that disturbances or contamination of prey in any of these systems may affect sandpipers. The marine influences on sandpipers is well understood, but the link with terrestrial and freshwater

ecosystems is novel. While the strength of this link is unclear, we may need to consider multiple ecosystems when attempting to protect Semipalmated Sandpipers, and other shorebirds with similar ecologies. Not only do these ecosystems represent a currently understudied component of sandpiper diet, but contaminated prey items may originate from freshwater (Kraus et al. 2014), terrestrial (Hallmann et al. 2014), or marine systems (Simmons et al. 2014). Therefore, bioaccumulation of harmful chemicals may be occurring as sandpipers forage upon prey items found in the conflux of terrestrial, marine, and freshwater systems. However, it should be pointed out that molecular scatology is limited by the presence/absence data it produces, as well as the reference databank available for comparison. Therefore, the magnitude of the relationships observed here requires further investigation.

How these non-traditional prey items were incorporated into sandpiper diet is currently unknown, and more study is required. Freshwater prey items (mayflies, caddisflies, and damselflies), however, may have washed onto the mudflats through small streams that discharge into the Bay of Fundy. Sandpipers also frequently forage near these streams in the upper intertidal area, potentially picking up such items before reaching the mudflats. Terrestrial prey items, on the other hand, are probably consumed opportunistically during roosting (TG Gerwing Personal Observation) or as birds are moving off the beach toward mudflats as the tide starts to recede. Pelagic prey items (Atlantic herring, flounder, unknown fish, cnidarians/ctenophores) likely represent eggs (or the smallest juveniles), along with detrital remains deposited on the mudflats as the tide recedes, and then consumed opportunistically by sandpipers.

4.5.1 Conclusion

Current conservation plans for Semipalmated Sandpipers revolve around protecting beach and intertidal habitat, as exemplified by the Western Hemisphere Shorebird Reserve Network's conservation priorities (www.whsrn.org/). Our results suggest that protecting only beaches or mudflats may be inadequate. Terrestrial and freshwater habitats may contribute to sandpiper diet and thus may represent potential sources of contamination. Future conservation plans associated with Semipalmated Sandpipers in the Bay of Fundy should not only consider protecting traditional foraging and roosting habitat, but also the surrounding terrestrial environment, and freshwater waterways. Given our findings, we recommend the use of molecular scatology in other systems to investigate diet and potential conservation challenges for similar species.

4.6 Chapter 4 acknowledgements

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Table 4.1: Summary of the number of successful amplifications of prey DNA in faecal samples of Semipalmated Sandpiper (*Calidris pusilla*) from three intertidal mudflats in the Bay of Fundy, Canada, in 2010. For *16S* and *COI*, and the two loci combined.

Site	Sample Date		Sample Size					
			<i>16S</i>		<i>COI</i>		Combined	
	Early	Late	Early	Late	Early	Late	Early	Late
AV	03 Aug	22 Aug	29	20	23	20	30	26
GA	02 Aug	23 Aug	26	8	23	5	28	24
MP	05 Aug	23 Aug	29	24	21	13	33	23

Table 4.2: Total number of reads (% total) and number of Molecular Operational Taxonomic Units (MOTUs) identified by the analysis of the 389,328 raw reads sequenced from the pooled library for prey items in feces of Semipalmated Sandpiper (*Calidris pusilla*) sampled in August 2010 from three intertidal mudflats in the Bay of Fundy, Canada.

Locus	Reads Remaining After Filtering		<i>de novo</i> Assembly		
	Demultiplexing (MID tags)	Quality Control, Duplicate Removal	Contigs	Singletons	Total MOTUs
<i>16S</i>	138,418	32,280	1,775	6,146	7,921
<i>COI</i>	235,675	85,973	9,095	17,094	26,189
Total	374,093 (96.1%)	118,253 (30.4%)			

Table 4.3: Frequency of occurrence (%) of prey items in feces of Semipalmated Sandpiper (*Calidris pusilla*), identified by the combination of two DNA loci (the mitochondrial *COI* and *16S*), from three intertidal mudflats in the Bay of Fundy in 2010. Total represents the frequency of occurrence pooled over sites and times. Sample sizes are indicated in Table 4.1.

Prey Bin	Total	Avonport		Grande Anse		Mary's Point	
		03-Aug	22-Aug	02-Aug	23-Aug	05-Aug	23-Aug
Diatoms	100	100	100	100	100	100	100
Insecta Diptera	16.5	10.0	15.4	3.7	0	33.3	4.3
Insecta: Caddisflies, Mayflies, and Damselflies	10.4	16.7	19.2	14.8	0	54.5	0
Insecta Other Terrestrial	13.4	10.0	15.4	14.8	0	9.1	17.4
Insecta Other Marine	7.3	3.3	0	0	0	21.2	0
Arachnida	6.7	0	11.5	7.4	8.3	0.0	13.0
Crustacean Amphipoda	85.4	83.3	65.4	96.3	95.8	18.2	91.3
<i>Corophium volutator</i>							
Crustacean Amphipoda Other	6.7	3.3	3.8	0	4.2	33.3	21.7
Crustacean Ostracoda	7.9	3.3	0	0	0	12.1	4.3
Crustacean Copepoda	7.3	13.3	3.8	7.4	0	84.8	4.3
Crustacean Other	12.2	3.3	15.4	11.1	8.3	9.1	26.1
Annelida	18.9	13.3	11.5	14.8	8.3	6.1	21.7
Bivalvia	8.5	36.7	7.7	0	0	3.0	0
Gastropoda	31.1	73.3	46.2	3.7	0	9.1	21.7
Cnidaria and Ctenophora	9.8	13.3	11.5	3.7	0	3.0	8.7
Fish	16.5	26.7	30.8	7.4	8.3	12.1	17.4
Nemertea	1.8	0	0	0	0	6.1	4.3
Nematoda	1.2	0	0	0	0	33.3	0

Chapter 5: General discussion

In my thesis, I quantified interactions that structure a soft-sediment infaunal community, utilizing ecological, statistical, and molecular techniques. I investigated eight intertidal mudflats spanning the entire upper Bay of Fundy, Canada. Study sites were sampled every 3-8 weeks over two years (2009-2011), and I quantified the density of 10-15 taxa (macrofauna and large meiofauna), as well as 6-10 abiotic environmental variables.

While a web of connections was observed both within and among biotic and abiotic factors, the structuring influence of these factors on the infauna was relatively minor. Moreover, quantification of Semipalmated Sandpiper diet using 454-pyrosequencing revealed a broad range of prey items, and further elucidated connections between terrestrial, marine (pelagic and intertidal), and freshwater ecosystems.

5.1 Relative importance of structuring forces of the infauna community

Models investigating factors that structure benthic communities focus on environmental conditions (abiotic factors), resource availability, competition, predation, physical disturbance, and supply of propagules. (Underwood and Fairweather 1989, Menge et al. 1997, Ghasemi et al. 2014). My thesis quantified the structuring influence of many of these forces upon an infaunal community. Specifically, Chapter 2 investigated the role of winter stressors (wind, ice presence and scour, dissolved oxygen content in the sediment, temperature) on over-winter community and taxa-specific change. The infaunal community appeared to be relatively resilient to winter stressors, and over-winter change appeared to be simply a component of annual patterns of infaunal

variation (Gerwing et al. 2015a), such as those investigated in Chapter 3. Chapter 3 examined the structuring influence of biotic (top-down, middle-out, bottom-up) and abiotic (sediment penetrability, particle size, water content, exposure, apparent redox potential discontinuity (aRPD) depth) factors to community and taxa-specific spatiotemporal variation year-round. Similar to Chapter 2, these factors accounted for only a small portion of the community variation. Instead, structural factors (~79%) such as spatial variables at a broad (kilometres, Site: ~32%) and fine scale (10's of metres, Plot: ~37%) accounted for the majority of observed variation. When examined together in both Chapters 2 and 3, the factors that strongly influenced the infaunal community were unmeasured characteristics, predominantly spatial and associated with sites and plots.

That the biotic and abiotic factors examined in my thesis accounted for such a minor proportion of infaunal variation, therefore likely exerting a minor structuring influence upon the system, was surprising, since past studies have observed these factors substantially impacting similar systems (Ambrose Jr 1984a, 1991, Ólafsson et al. 1994, Todd 1998). Winter stressors (Strasser et al. 2001, Thieltges et al. 2004, Büttger et al. 2011), other abiotic factors (Stillman 2002, Lu et al. 2008, Ghasemi et al. 2014), top-down predation (Heck and Valentine 2007, Hughes et al. 2014, Johnson et al. 2014), bottom-up resource availability (Davis et al. 2014, Schuldt et al. 2014, van den Hoff et al. 2014), and middle-out mesopredators (Elmhagen and Rushton 2007, Quijón and Snelgrove 2008, Greenville et al. 2014) have all been observed to exert a controlling influence upon other systems. Specifically for the Bay of Fundy, winter stressors (Drolet et al. 2013b), as well as top-down and bottom-up forces (Hamilton et al. 2006, Cheverie

et al. 2014), have been observed to influence mudflat communities. However, past studies operated on a much finer spatiotemporal scale (at one or two sites, for short periods), suggesting that the impacts of these factors may be localized in time and space. My thesis quantified the relative importance of these variables over a broader spatiotemporal scale, suggesting that these factors have a minor influence upon this ecosystem as a whole. The dichotomy between fine and coarse-grained studies suggests that caution is required when extrapolating the results of investigations, including manipulative experiments, conducted at fine spatiotemporal grains. Manipulative experiments are excellent at determining whether processes are occurring within an ecosystem, but are less efficient at quantifying how multiple processes interact to produce patterns at larger spatiotemporal scales. Even well-constructed manipulative experiments are logistically constrained to a small number of variables (Underwood 1996), cannot manipulate the full suite of *in situ* conditions, and are limited in their investigations of how relationships change over broad spatial and temporal scales (Dayton 1971, Connolly 1994, Hamilton 2000, Cheverie et al. 2014, Johnson et al. 2014). Therefore, a holistic understanding of the structuring role of a factor will rely upon both fine-grained manipulative, and coarse-grained mensurative studies. Fine-grained investigations assess direct cause and effect, quantifying the nature of this process locally. Coarse-grained mensurative studies, on the other hand, place this process into the context of the ecosystem, quantifying its relative importance with respect to other processes, and examining how this varies over time and space. In other words, mensurative studies conducted at broad spatiotemporal scales relate local

processes together, elucidating general patterns that structure entire ecosystems across broad spatiotemporal scales.

Upon considering my combined results, the mudflat infaunal community may reflect a “first come, first served” paradigm, as described in community succession models (Connell and Slatyer 1977). More specifically, the influence of dispersal ability and fecundity of infauna (commonly called supply-side ecology) may be the predominant structuring force in this system (Underwood and Fairweather 1989, Todd 1998, Hughes et al. 2000, Dahms et al. 2014). Under this scenario, presence/absence and density of infauna are directly related to supply of larvae for species with a dispersive larval phase, and juveniles and adults for species undergoing active or passive movement later in their life cycle (Sutherland 1974, Connell and Slatyer 1977, Bertness 2007, Pilditch et al. 2015). If the dominant force driving community structure is supply of individuals, operating in conjunction with pre-emptive competition (Tilman 1994), I would expect to observe no constancy in numbers of species, patterns of resource usage, and rates or intensities of structuring processes over space (Underwood and Fairweather 1989), but a fair amount of resilience over time. More work is needed; however, the results of Chapters 2 and 3 and Gerwing et al. (2015a) could be interpreted to support this. Furthermore, relatively random settlement of larvae, or arrival of juveniles or adults due to hydrodynamics (Underwood and Fairweather 1989, Hughes et al. 2000, Weersing and Toonen 2009, Dahms et al. 2014, Pilditch et al. 2015) would explain the high proportion of community and population variation accounted for by the site and plot factors in my models (Table 3.1). In a review of population variability versus reproductive mode, Ólafsson et al. (1994) concluded that larval availability (recruitment limitation) was not

likely the dominant determinant of community structure in soft-sediment habitats, rather post-settlement factors were more important. Recent work by Pilditch et al. (2015) suggests that post-settlement dispersal by juveniles and adults, which is characterized by continued, frequent, small-scale movements over long periods and can dominate meta-community dynamics, may be particularly important in soft-sediment communities. Studies on *C. volutator* in the Bay of Fundy suggest that substantial movement by adults and juveniles, within and between mudflats, may be occurring (Drolet et al. 2012, Bringloe et al. 2013, Macfarlane et al. 2013) on the mudflats I studied. Small-scale movements occurring within sites may explain the large proportion of the community variation accounted for by the plot term in my analysis. The large proportion of the variation accounted for by the site term suggests that larval, juvenile, and adult supply to sites is also important. Table 3.1 showed that the plot and site terms account for equal proportions (31-37%) of the community variation, suggesting that their influence upon this system may be of similar strength. Future studies should attempt to further explore the importance of these spatial-related factors in structuring the infaunal community of the Bay of Fundy.

5.2 Semipalmated Sandpipers as top-down predators

In Chapter 3, I postulated that as our top-down predators, including Semipalmated Sandpipers, are omnivores, intraguild predation would result in limited suppression of prey species (Finke and Denno 2005). This may partially explain the relatively low importance of top-down predation in the soft-sediment system. This postulate was further supported by the broad range of sandpiper prey items observed in Chapter 4. Not

only did sandpipers consume numerous intertidal prey items, but they also consumed prey items from the pelagic, terrestrial, and freshwater water ecosystems. Such a broad diet would further act to lessen the influence sandpipers exert upon the intertidal infaunal community via top-down predation. Conversely, numerous studies, mostly on *C. volutator*, have suggested that sandpiper predation may decrease prey populations and potentially alter prey behaviour (Boates and Smith 1979, Boates and Smith 1989, Matthews et al. 1992, Boates et al. 1995, McCurdy et al. 2000). However, the actual impacts sandpipers have upon infaunal residents is currently unclear due to: the breadth of sandpiper diet, as shown in Chapter 4, MacDonald et al. (2012) and Quinn and Hamilton (2012), coupled with high prey densities (Gerwing et al. 2015a), the minor proportion of infaunal community variation shorebirds accounted for (Chapter 3), the short period of time sandpipers are present on these mudflats (Hicklin 1987), and the natural mortality experienced by infauna populations during and after shorebird occupancy (Gerwing et al. 2015c). More work conducted at both fine and coarse spatiotemporal scales is required to further investigate the role sandpipers play in this system.

5.3 Thesis limitations and recommendations for future studies

It is unclear how applicable the findings of Chapter 3 are to other systems, including other soft-sediment systems. Numerous studies have observed that the biotic and abiotic factors investigated in this study exert a controlling influence upon other systems (Ambrose Jr 1984a, Commito and Ambrose Jr 1985, Ambrose Jr 1991, Ólafsson et al. 1994, Todd 1998). The macrotidal nature of the Bay of Fundy (Desplanque and

Mossman 2004a, Shaw et al. 2010) represents an exceptional habitat, controlled by unique assortment of biological and abiotic factors. For instance, and unlike other soft-sediment systems along the Atlantic coast, the macrotides of the Bay of Fundy erodes local cliffs to such a degree that sediment load in the water (Haralampides and Rodriguez 2006) is too high for large filter feeders to survive. This results in an infaunal community mostly devoid of large filter feeders such as clams or mussels (Dashtgard et al. 2014). It is possible that the infaunal communities of the Bay of Fundy mudflats are dominated to a greater degree by tidal factors (potentially explaining the high proportion of the community variation accounted for by the site and plot term) than other systems. Because of the particular conditions present in the Bay of Fundy, it is unclear if studies adopting my methods in other systems would observe the same trends, or if biotic and abiotic variables would account for a higher proportion of the community variation. More studies are required, utilizing similar methods in different habitats, to determine how applicable the findings of my thesis are.

A potential limitation of Chapter 3 is the coarse, within-site spatial grain (1 plot per stratum), which may be too coarse to detect fine-grained spatial trends in biotic or abiotic variables. This is unlikely to have greatly impacted my findings because, as detailed in Chapter 3, the analyzed dataset is a subset of another dataset, with increased spatial resolution: $n = 3$ plots per stratum, therefore 12 plots per transect, and 24 plots per site. Preliminary analyses revealed little difference in results between the two datasets; therefore, I conducted analyses on the coarser dataset ($n = 1$ per stratum) which included both biotic and abiotic factors.

Chapters 2 and 3 are mensurative in nature, and unlike manipulative experiments, these analyses identify correlations, not cause and effect. A potential compromise is to nest manipulative studies within a mensurative framework. More specifically, to conduct fine-grained manipulative studies at multiple sampling locations, or sites, along a gradient of environmental factors (Thrush et al. 2000). Previously, manipulative studies have been conducted on this infaunal community in the Bay of Fundy, often incorporating gradients of biotic or abiotic variables such as predation or resource availability (Hamilton et al. 2006, Coffin et al. 2008, Drolet and Barbeau 2009, Drolet et al. 2009, Cheverie et al. 2014); however, these experiments have been limited in both space and time. Future studies utilizing manipulative experiments at multiple study sites, across gradients of environmental factors (such as sandpiper predation), may help elucidate the controlling influence, across broad spatiotemporal scales, of top-down, bottom-up, and abiotic factors on the intertidal mudflats of the Bay of Fundy.

Beyond investigating larval supply to a site, and effects of post-settlement dispersal on the Bay of Fundy intertidal mudflats, more work is required on identifying our broad taxonomic groupings (polychaete families, Ostracoda, Copepoda) to species level. It is likely that numerous cryptic species exist within these broad groupings, especially within polychaete families (Carr 2011, Carr et al. 2011). Closely related species with similar morphologies can exhibit different environmental tolerances, and influence the environment in divergent ways (Vismann 1990). Queirós et al. (2013) observed that even closely related species can influence sediment in different ways via bioturbation. Further, Murray et al. (2014) concluded that while it is possible to group species into broad functional groups, membership varies by the ecosystem function examined, and

groupings do not correspond well to species taxonomy. Therefore, a greater understanding of the diversity and identity of species would enable a deeper understanding of the interactions between and within biotic and abiotic factors in the Bay of Fundy intertidal mudflats. Low taxonomic resolution for some taxa may have resulted in my failing to quantify species-specific responses to winter stressors, as well as top-down, bottom-up, and abiotic structuring forces. Increasing taxonomic resolution would have improved the ability of these analyses to accurately represent species-specific responses, and how these responses aggregated into ecosystem wide patterns. Similarly, reanalysis of Chapters 2 and 3 utilizing biomass (Bringloe et al. 2013) could offer further insights into how biotic and abiotic factors influence the infaunal community. Finally, the bioturbation of benthic infauna is understudied in the Bay of Fundy. A study similar to Queirós et al. (2013) is needed to quantify bioturbation potential of individual Bay of Fundy infauna species.

Chapter 2 was limited by the different scales of investigation for biota (plot) and winter stressors (site via aerial surveys). Different scales of investigation were necessary as I was only able to visit a single mudflat each day, and ice conditions varied greatly day to day. Therefore, to obtain an accurate understanding of winter conditions throughout the Bay of Fundy, aerial surveys of every site within one tidal cycle were required. Unfortunately, this resulted in a disconnect between the scale of collection for biotic data and for winter stressor data. If ice presence, ice scour, and temperature data had been assessed at each plot and directly related to the infauna of that patch, a stronger relationship may have been observed between winter stressors and infauna changes over-winter. However, the effect this had upon Chapter 2 is likely small, given the

minor population decreases (as well as increases and no changes) observed over winter. Regardless, future studies may want to combine aerial surveys to assess winter conditions at broad scales, with quantification of winter stressors at a small number of focal sites to assess direct correlations at the scale of a plot between winter stressors and the infaunal community.

My investigation of winter stressors was only conducted over a single, relatively mild winter, and severe winters would likely have a much stronger impact upon intertidal residents (Crisp 1964, Armonies et al. 2001, Strasser et al. 2001, Büttger et al. 2011). While it is impossible to predict winter severity, future studies should investigate the impact of winter stressors on infaunal communities over several years in order to elucidate how different degrees of winter severity (ice presence and ice scour, temperature) alter the findings reported in Chapter 2. Such an understanding would help clarify the average impact of winter stressors upon coastal systems in temperate regions.

With regards to Semipalmated Sandpiper diet, I suggest a study similar to Chapter 4, but conducted on a finer temporal scale. Our samples were collected shortly after sandpipers left the roost, so terrestrial and freshwater prey items were more likely to be detected. Collecting samples over the course of a tidal cycle would not only quantify the full spectrum of prey items, but produce a more accurate representation of sandpiper diet and how it varies over a tidal cycle. Investigating sandpiper diet at a larger number of sites, and more frequently during their visit in the Bay of Fundy would also help elucidate how the diet of this species varies over time and space. Future studies would also benefit from increased resolution of prey items. This is only possible if prey DNA is compared to a more in-depth reference library of prey items found in the Bay of

Fundy. Currently online DNA reference libraries such as GenBank and Barcode of Life are underrepresented with regards to Bay of Fundy infauna. Creation of such a reference library should be the goal of any future studies attempting to use 454-pyrosequencing to determine sandpiper diet in the Bay of Fundy.

Another potential limitation of Chapter 4 is related to the power of the selected method of diet assessment. Molecular scatology can often detect the prey items of prey items, a phenomenon referred to as secondary consumption (Deagle et al. 2005, Barrett et al. 2007, Deagle et al. 2007, Pompanion et al. 2011). It is therefore possible that some prey items may have been detected indirectly; however, I suggest that secondary consumption did not greatly bias these results. Prey at low trophic levels (diatoms and the invertebrates that consume them, such as copepods) would be more likely to be detected through secondary consumption because they are food for higher consumers (annelids). However, these taxa are already well established in the diets of sandpipers (Baker 1977, Hicklin and Smith 1979, 1984, Quinn and Hamilton 2012). Further, when the FOO of lower level consumers like copepods was high (Table 4.3), the FOO of the most likely sources of secondary consumption, annelids, were low. Lastly, some of the more unusual prey items (e.g., insects, bivalves, snails) are unlikely to have been consumed, except perhaps as detritus, by animals that sandpipers commonly eat. While it is likely that secondary consumption did occur (Sheppard et al. 2005), it is unlikely to have greatly biased my results.

Finally, a potential limitation of this thesis is the manner in which study sites (intertidal mudflat) were selected. Site selection was based primarily upon silty mudflats visited by Semipalmated Sandpipers in the past, had *Corophium volutator* populations in the past,

and secondarily on a history of sites being studied and on accessibility. In practice, this resulted in mudflats with more coarse sediment (sandier sediments) being excluded from my study. Future studies could include sites spanning a broader range of sediment types (particle size) to determine if the observations reported in this thesis are representative of general tidal flats within the Bay of Fundy.

5.4 Implications of the work

Chapters 2 and 3 investigated the influence of winter stressors, as well as biotic and abiotic factors, year-round, upon community and taxa-specific spatiotemporal variation. The low relative importance of the investigated factors contributes to our theoretical understanding of the forces which structure this, and by extension, other ecosystems. Further, the statistical methods presented in Chapter 3 are easily adaptable to other systems, and their use in a range of environments would facilitate comparisons of results. These methods also allowed me to use the entire infaunal community as a response variable, as well as numerous biological and abiotic independent variables, over a broad spatiotemporal scale. Including the entire community and numerous independent variables, analyzed across a broad spatiotemporal scale, offers a model which produces a more complete understanding of how the relative importance of structuring factors varies over time and space, as well as among systems. Finally, statistical analyses which allow for partitioning of variation between structuring processes represents a useful method in investigating the relative importance of these processes (Menge 1991, Borcard et al. 1992). However, the use of the PERMANOVA (multivariate ANOVA) framework provided by the program PRIMER, utilized in

Chapter 3, allowed me to adequately model the spatial and temporal structure of my data set. Therefore, when I investigated the relative importance of biotic and abiotic factors in this model, the analysis takes into account – or controls for – my sampling structure (site, plot, round) (Clarke 1993, Anderson et al. 2008, Clarke et al. 2008). By controlling for these factors, the actual importance of the variables of interest can be more clearly assessed.

Chapter 4 quantified Semipalmated Sandpiper diet and concluded that sandpipers were foraging as generalists, consuming marine, terrestrial and freshwater prey. This suggests that sandpipers are relatively resilient to changes in their environments, as diet generalists are more resistant to changing environmental conditions than specialist species (Colles et al. 2009). Given the connections between sandpipers and these ecosystems, future studies should consider these systems as contributing to sandpiper diet. Moreover, these systems may represent not only sources of prey, but also potential sources of contaminants. While it comes as no surprise that the intertidal region is influenced by freshwater and terrestrial systems – transport of nutrients, detritus, contaminants, and sediments – the connections observed here make an implicit link between these systems and sandpipers foraging in the Bay of Fundy. Expansion of conservation strategies beyond beaches and mudflats may be necessary for this species. With respect to methodology, I found that molecular scatology and next generation sequencing were powerful tools to examine the diet of a single species, as well as the interactions occurring within and between ecosystems. More accurate measures of diet components and ecological interactions will greatly improve our ability to not only understand the ecosystems around us, but also to manage and protect them. Finally,

Chapters 3 and 4 suggest that sandpipers are exerting a minor structuring influence upon these intertidal systems, contradicting several previous studies (Boates and Smith 1979, Boates and Smith 1989, Matthews et al. 1992, Boates et al. 1995, McCurdy et al. 2000). More studies, conducted at fine and coarse spatiotemporal scales along environmental gradients, are required to clarify the role sandpipers play in structuring this intertidal community.

The need for informed ecological management and conservation will increase as human-related climate change (Barange et al. 2014) and habitat degradation/fragmentation (Fahrig 2003) are predicted to have increasingly negative impacts on both ecosystems and the natural resources we rely upon. Management and conservation efforts will be more successful if we understand the ecological interactions that structure our ecosystems. The interactions (top-down, bottom-up, abiotic, middle-out) studied in this thesis, when contrasted with similar interactions from other systems (Tilman 1996, Gage and Cooper 2005, Bracken et al. 2014), could offer general insights into the types of processes, and their relative importance, that structure biological communities. However, between-study variation in methods limits our ability to compare studies and synthesize general theories. The methods presented in Chapters 3 and 4 are easily applicable to studies conducted in any ecosystem, potentially allowing comparison between studies. Increasing our understanding of the relative importance of these interactions in structuring individual ecosystems, as well as general processes spanning multiple systems, will help provide us with the information needed to not only predict variation in natural systems, but also how human impacts may cascade through

these ecosystems. Such an increased understanding may enable us to potentially prevent or remediate future degradation of our ecosystems.

Literature Cited

- Aller, R. C., and J. Y. Aller. 1998. The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *Journal of Marine Research* **56**:905-936.
- Altieri, A. H. 2008. Dead zones enhance key fisheries species by providing predation refuge. *Ecology* **89**:2808-2818.
- Altieri, A. H., and J. D. Witman. 2006. Local extinction of a foundation species in a hypoxic estuary: integrating individuals to ecosystem. *Ecology* **87**:717-730.
- Ambrose Jr, W. G. 1984a. Influence of residents on the development of a marine soft-bottom community. *Journal of Marine Research* **42**:633-654.
- Ambrose Jr, W. G. 1984b. Influences of predatory polychaetes and epibenthic predators on the structure of a soft-bottom community in a Maine estuary. *Journal of Experimental Marine Biology and Ecology* **81**:115-145.
- Ambrose Jr, W. G. 1991. Are infaunal predators important in structuring marine soft-bottom communities? *American Zoologist* **31**:849-860.
- Anderson, M., R. N. Gorley, and R. K. Clarke. 2008. Permanova+ for Primer: Guide to Software and Statistical Methods. PRIMER-E Ltd, Plymouth, United Kingdom.
- Armonies, W., E. Herre, and M. Sturm. 2001. Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. *Helgolander Marine Research* **55**:170-175.
- Ayling, A. 1981. The role of biological disturbance in temperate subtidal encrusting communities. *Ecology*:830-847.
- Baker, M. 1977. Shorebird food habits in the eastern Canadian Arctic. *Condor* **79**:56-62.
- Barange, M., G. Merino, J. L. Blanchard, J. Scholtens, J. Harle, E. H. Allison, J. I. Allen, J. Holt, and S. Jennings. 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change*.
- Barbeau, M., and L. Grecian. 2003. Occurrence of intersexuality in the amphipod *Corophium volutator* (Pallas) in the upper Bay of Fundy, Canada. *Crustaceana*:665-679.
- Barbeau, M., L. Grecian, E. Arnold, D. Sheahan, and D. Hamilton. 2009. Spatial and Temporal Variation in the Population Dynamics of the Intertidal Amphipod *Corophium volutator* in the Upper Bay of Fundy, Canada. *Journal of Crustacean Biology* **29**:491-506.
- Barnes, D. 1995a. Sublittoral epifaunal communities at Signy Island, Antarctica. I. The ice-foot zone. *Marine Biology* **121**:555-563.
- Barnes, D. 1995b. Sublittoral epifaunal communities at Signy Island, Antarctica. II. Below the ice-foot zone. *Marine Biology* **121**:565-572.
- Barnes, D. K. 1999. The influence of ice on polar nearshore benthos. *Journal of the Marine Biological Association of the UK* **79**:401-407.
- Barrett, R. T., K. C. J. Camphuysen, T. Anker-Nilssen, J. W. Chardine, R. W. Furness, S. Garthe, O. Hüppop, M. F. Leopold, W. A. Montevecchi, and R. R. Veit. 2007. Diet studies of seabirds: a review and recommendations. *Ices Journal of Marine Science* **64**:1675-1691.

- Bart, J., S. Brown, B. Harrington, and R. I. G. Morrison. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? *Journal of Avian Biology* **38**:73-82.
- Baum, J. K., and B. Worm. 2009. Cascading top - down effects of changing oceanic predator abundances. *Journal of Animal Ecology* **78**:699-714.
- Belt, K. M., S. W. Cole, and R. A. Scrosati. 2009. Intertidal barnacles as indicators of the intensity of scour by sea ice. *Marine Ecology Progress Series* **381**:183-187.
- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society* **57**:289-300.
- Berke, S. K., V. Cruz, and R. W. Osman. 2009. Sublethal predation and regeneration in two onuphid polychaetes: patterns and implications. *The Biological Bulletin* **217**:242-252.
- Bertness, M. D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. *Ecology* **72**:138-148.
- Bertness, M. D. 2007. *Atlantic shorelines: natural history and ecology*. Princeton University Press Princeton, Princeton, NJ.
- Beukema, J. J. 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. *Netherlands Journal of Sea Research* **13**:203-223.
- Beukema, J. J. 1991. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. *Journal of Experimental Marine Biology and Ecology* **153**:97-113.
- Beukema, J. J. 1992. Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters. *Marine Ecology Progress Series* **83**:157-165.
- Beukema, J. J., and R. Dekker. 2003. Redistribution of spat-sized *Macoma balthica* in the Wadden Sea in cold and mild winters. *Marine Ecology Progress Series* **265**:117-122.
- Beukema, J. J., and E. C. Flach. 1995. Factors controlling the upper and lower limits of the intertidal distribution of two *Corophium* species in the Wadden Sea. *Marine Ecology Progress Series* **125**:117-126.
- Beukema, J. J., P. J. C. Honkoop, and R. Dekker. 1998. Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. *Hydrobiologia* **375**:23-34.
- Bleakney, J. S. 1972. Ecological implications of annual variation in tidal extremes. *Ecology*:933-938.
- Boates, J. S., M. R. Forbes, M. Zinck, and N. McNeil. 1995. Male amphipods (*Corophium volutator* [Pallas]) show flexible behaviour in relation to risk of predation by sandpipers. *Ecoscience. Sainte-Foy* **2**:123-128.
- Boates, J. S., and P. Smith. 1979. Length-weight relationships, energy content and the efforts of predation on *Corophium volutator* (Pallas)(Crustacea: amphipoda). *Proceedings of the Nova Scotian Institute of Science* **29**.
- Boates, J. S., and P. C. Smith. 1989. Crawling behaviour of the amphipod *Corophium volutator* and foraging by Semipalmated Sandpipers, *Calidris pusilla*. *Canadian Journal of Zoology* **67**:457-462.

- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**:1045-1055.
- Bowser, A. K., A. W. Diamond, and J. A. Addison. 2013. From Puffins to Plankton: A DNA-based analysis of a Seabird food chain in the Northern Gulf of Maine. *Plos One* **8**:e83152.
- Bracken, M. E. S., R. E. Dolecal, and J. D. Long. 2014. Community context mediates the top-down versus bottom-up effects of grazers on rocky shores. *Ecology* **95**:1458-1463.
- Bringloe, T. T., D. Drolet, M. A. Barbeau, M. R. Forbes, and T. G. Gerwing. 2013. Spatial variation in population structure and its relation to movement and the potential for dispersal in a model intertidal invertebrate. *Plos One* **8**:e69091.
- Büttger, H., G. Nehls, and S. Witte. 2011. High mortality of Pacific oysters in a cold winter in the North-Frisian Wadden Sea. *Helgoland Marine Research* **65**:525-532.
- Caliman, A., L. S. Carneiro, J. J. Leal, V. F. Farjalla, R. L. Bozelli, and F. A. Esteves. 2013. Biodiversity effects of ecosystem engineers are stronger on more complex ecosystem processes. *Ecology* **94**:1977-1985.
- Carr, C. M. 2011. Polychaete diversity and distribution patterns in Canadian marine waters. *Marine Biodiversity*:1-15.
- Carr, C. M., S. M. Hardy, T. M. Brown, T. A. Macdonald, and P. D. N. Hebert. 2011. A Tri-Oceanic Perspective: DNA Barcoding Reveals Geographic Structure and Cryptic Diversity in Canadian Polychaetes. *Plos One* **6**:e22232.
- Chambers, J. Q., R. I. Negron-Juarez, D. M. Marra, A. Di Vittorio, J. Tews, D. Roberts, G. H. Ribeiro, S. E. Trumbore, and N. Higuchi. 2013. The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proceedings of the National Academy of Sciences* **110**:3949-3954.
- Cheverie, A. V., D. J. Hamilton, M. R. S. Coffin, and M. A. Barbeau. 2014. Effects of shorebird predation and snail abundance on an intertidal mudflat community. *Journal of Sea Research* **92**:102-114.
- Christensen, B., A. Vedel, and E. Kristensen. 2000. Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N. virens*) polychaetes. *Marine Ecology Progress Series* **192**:203-217.
- Clarke, K. R. 1993. Non - parametric multivariate analyses of changes in community structure. *Australian journal of ecology* **18**:117-143.
- Clarke, K. R., and M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**:205-205.
- Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6: user manual/tutorial Primer-E Ltd, Plymouth, United Kingdom.
- Clarke, K. R., P. J. Somerfield, and M. G. Chapman. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* **330**:55-80.

- Clarke, K. R., P. J. Somerfield, and R. N. Gorley. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* **366**:56-69.
- Coffin, M. R. S., M. A. Barbeau, D. J. Hamilton, and D. Drolet. 2012. Effect of the mud snail *Ilyanassa obsoleta* on vital rates of the intertidal amphipod *Corophium volutator*. *Journal of Experimental Marine Biology and Ecology* **418**:12-23.
- Coffin, M. R. S., D. Drolet, D. J. Hamilton, and M. A. Barbeau. 2008. Effect of immersion at low tide on distribution and movement of the mud snail, *Ilyanassa obsoleta* (Say), in the upper Bay of Fundy, eastern Canada. *Journal of Experimental Marine Biology and Ecology* **364**:110-115.
- Colles, A., L. H. Liow, and A. Prinzing. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters* **12**:849-863.
- Commuto, J. A., and W. G. Ambrose Jr. 1985. Multiple trophic levels in soft-bottom communities. *Marine Ecology Progress Series* **26**:289-293.
- Conlan, K., H. Lenihan, R. Kvitek, and J. Oliver. 1998. Ice scour disturbance to benthic communities in the Canadian High Arctic. *Marine Ecology Progress Series* **166**:1-16.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Connolly, R. M. 1994. The role of seagrass as preferred habitat for juvenile *Sillaginodes punctata* (cuv. & val.)(Sillaginidae, Pisces): habitat selection or feeding? *Journal of Experimental Marine Biology and Ecology* **180**:39-47.
- Coulthard, M. E., and D. J. Hamilton. 2011. Effects of *Ilyanassa obsoleta* (Say) on the abundance and vertical distribution of *Corophium volutator* (Pallas) on mudflats of the upper Bay of Fundy. *Journal of Experimental Marine Biology and Ecology* **397**:161-172.
- Cranford, P., D. Peer, and D. Gordon. 1985. Population dynamics and production of *Macoma balthica* in Cumberland Basin and Shepody Bay, Bay of Fundy. *Netherlands Journal of Sea Research* **19**:135-146.
- Cranford, P. J. 1988. Behaviour and ecological importance of a mud snail (*Ilyanassa obsoleta*) population in a temperate macrotidal estuary. *Canadian Journal of Zoology* **66**:459-466.
- Crewe, T. L., D. J. Hamilton, and A. W. Diamond. 2001. Effects of mesh size on sieved samples of *Corophium volutator*. *Estuarine, Coastal and Shelf Science* **53**:151-154.
- Crisp, D. 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *The Journal of Animal Ecology* **33**:165-210.
- Dahms, H.-U., L.-C. Tseng, and J.-S. Hwang. 2014. Marine Invertebrate Larval Distribution at the Hydrothermal Vent Site of Gueishandao. *Journal of Marine Science and Technology* **22**:67-74.
- Dashtgard, S. E., N. J. Pearson, and M. K. Gingras. 2014. Sedimentology, ichnology, ecology and anthropogenic modification of muddy tidal flats in a cold-temperate environment: Chignecto Bay, Canada. *Geological Society, London, Special Publications* **388**:229-245.

- Davis, B., C. Mattone, and M. Sheaves. 2014. Bottom-up control regulates patterns of fish connectivity and assemblage structure in coastal wetlands. *Marine Ecology Progress Series* **500**:175-186.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological monographs* **41**:351-389.
- De Goeij, P., P. C. Luttikhuisen, J. Van der Meer, and T. Piersma. 2001. Facilitation on an intertidal mudflat: the effect of siphon nipping by flatfish on burying depth of the bivalve *Macoma balthica*. *Oecologia* **126**:500-506.
- Deagle, B., N. Gales, K. Evans, S. Jarman, S. Robinson, R. Trebilco, and M. Hindell. 2007. Studying seabird diet through genetic analysis of faeces: a case study on macaroni penguins (*Eudyptes chrysolophus*). *Plos One* **2**:831.
- Deagle, B., D. Tollit, S. Jarman, M. Hindell, A. Trites, and N. Gales. 2005. Molecular scatology as a tool to study diet: analysis of prey DNA in scats from captive Steller sea lions. *Molecular Ecology* **14**:1831-1842.
- Deagle, B. E., J. P. Eveson, and S. N. Jarman. 2006. Quantification of damage in DNA recovered from highly degraded samples – a case study on DNA in faeces. *Frontiers in Zoology* **3**:11.
- Deagle, B. E., R. Kirkwood, and S. N. Jarman. 2009. Analysis of Australian fur seal diet by pyrosequencing prey DNA in faeces. *Molecular Ecology* **18**:2022-2038.
- Desplanque, C., and D. J. Mossman. 2004a. Tides and their seminal impact on the geology, geography, history, and socio-economics of the Bay of Fundy, Eastern Canada. *Atlantic Geology* **40**:178-203.
- Desplanque, C., and D. J. Mossman. 2004b. Tides and their seminal impact on the geology, geography, history, and socio-economics of the Bay of Fundy, eastern Canada. *Atlantic Geology* **40**:1-130.
- DeWitt, T. H., and J. S. Levinton. 1985. Disturbance, emigration, and refugia: How the mud snail, *Ilyanassa obsoleta* (Say), affects the habitat distribution of an epifaunal amphipod, *Microdeutopus gryllotalpa* (Costa). *Journal of Experimental Marine Biology and Ecology* **92**:97-113.
- Diaz, R. J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* **321**:926-929.
- Drolet, D., and M. Barbeau. 2009. Diel and Semi-lunar Cycles in the Swimming Activity of the Intertidal, Benthic Amphipod *Corophium volutator* in the Upper Bay of Fundy, Canada. *Journal of Crustacean Biology* **29**:51-56.
- Drolet, D., M. A. Barbeau, M. R. S. Coffin, and D. J. Hamilton. 2009. Effect of the snail *Ilyanassa obsoleta* (Say) on dynamics of the amphipod *Corophium volutator* (Pallas) on an intertidal mudflat. *Journal of Experimental Marine Biology and Ecology* **368**:189-195.
- Drolet, D., T. T. Bringloe, M. R. S. Coffin, M. A. Barbeau, and D. J. Hamilton. 2012. Potential for between-mudflat movement and metapopulation dynamics in an intertidal burrowing amphipod. *Marine Ecology Progress Series* **449**:197-209.
- Drolet, D., M. R. S. Coffin, M. A. Barbeau, and D. J. Hamilton. 2013a. Influence of intra-and interspecific interactions on short-term movement of the amphipod *Corophium volutator* in varying environmental conditions. *Estuaries and Coasts* **36**:1-11.

- Drolet, D., K. Kennedy, and M. A. Barbeau. 2013b. Winter population dynamics and survival of the intertidal mudflat amphipod *Corophium volutator* (Pallas). *Journal of Experimental Marine Biology and Ecology* **441**:126-137.
- Dyer, K. R., M. C. Christie, and E. W. Wright. 2000. The classification of intertidal mudflats. *Continental Shelf Research* **20**:1039-1060.
- Elmhagen, B., and S. P. Rushton. 2007. Trophic control of mesopredators in terrestrial ecosystems: top - down or bottom - up? *Ecology Letters* **10**:197-206.
- Everitt, D., G. Poore, and J. Pickard. 1980. Marine benthos from Davis station, eastern Antarctica. *Australian Journal of Marine and Freshwater Research* **31**:829-836.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*:487-515.
- Fauchald, K., and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* **17**:193-284.
- Ferguson, N., C. R. White, and D. J. Marshall. 2013. Competition in benthic marine invertebrates: the unrecognized role of exploitative competition for oxygen. *Ecology* **94**:126-135.
- Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* **281**:237-240.
- Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* **8**:1299-1306.
- Flach, E. C. 1992a. Disturbance of benthic infauna by sediment-reworking activities of the lugworm *Arenicola marina*. *Netherlands Journal of Sea Research* **30**:81-89.
- Flach, E. C. 1992b. The influence of four macrozoobenthic species on the abundance of the amphipod *Corophium volutator* on tidal flats of the Wadden Sea. *Netherlands Journal of Sea Research* **29**:379-394.
- Flach, E. C. 1996. The influence of the cockle, *Cerastoderma edule*, on the macrozoobenthic community of tidal flats in the Wadden Sea. *Marine Ecology* **17**:87-98.
- Flach, E. C., and J. J. Beukema. 1995. Density-governing mechanisms in populations of the lugworm *Arenicola marina* on tidal flats. *Oceanographic Literature Review* **42**.
- Fletcher, D. J., and A. J. Underwood. 2002. How to cope with negative estimates of components of variance in ecological field studies. *Journal of Experimental Marine Biology and Ecology* **273**:89-95.
- Folke, C., S. R. Carpenter, B. Walker, M. Scheffer, T. Chapin, and J. Rockström. 2010. Resilience thinking: integrating resilience, adaptability and transformability. *Ecology and Society* **15**:20.
- Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology & Evolution* **28**:86-92.
- Fraser, E. D., A. J. Dougill, W. E. Mabee, M. Reed, and P. McAlpine. 2006a. Bottom up and top down: Analysis of participatory processes for sustainability indicator identification as a pathway to community empowerment and sustainable environmental management. *Journal of Environmental Management* **78**:114-127.

- Fraser, E. D. G., A. J. Dougill, W. E. Mabee, M. Reed, and P. McAlpine. 2006b. Bottom up and top down: Analysis of participatory processes for sustainability indicator identification as a pathway to community empowerment and sustainable environmental management. *Journal of Environmental Management* **78**:114-127.
- Fryxell, J. M., A. R. Sinclair, and G. Caughley. 2014. *Wildlife Ecology, Conservation, and Management*. John Wiley & Sons, Chichester, West Sussex, UK.
- Gage, E., and D. Cooper. 2005. Patterns of willow seed dispersal, seed entrapment, and seedling establishment in a heavily browsed montane riparian ecosystem. *Botany* **83**:678-687.
- Galbraith, H., D. W. DesRochers, S. Brown, and J. M. Reed. 2014. Predicting vulnerabilities of North American Shorebirds to climate change. *Plos One* **9**:e108899.
- Gerwing, T. G., A. M. Allen Gerwing, D. Drolet, M. A. Barbeau, and D. J. Hamilton. 2015a. Spatiotemporal variation in biotic and abiotic features of eight intertidal mudflats in the Upper Bay of Fundy, Canada. *NorthEastern Naturalist* **In Press**.
- Gerwing, T. G., A. M. Allen Gerwing, D. Drolet, M. A. Barbeau, and D. J. Hamilton. Accepted. Spatiotemporal variation in biotic and abiotic features of eight intertidal mudflats in the Upper Bay of Fundy, Canada. *NorthEastern Naturalist* **In Press**.
- Gerwing, T. G., A. M. Allen Gerwing, D. Drolet, D. J. Hamilton, and M. A. Barbeau. 2013. Comparison of two methods of measuring the depth of the redox potential discontinuity in intertidal mudflat sediments. *Marine Ecology Progress Series* **487**:7-13.
- Gerwing, T. G., A. M. Allen Gerwing, D. J. Hamilton, and M. A. Barbeau. 2015b. Apparent redox potential discontinuity (aRPD) depth as a relative measure of sediment oxygen content and habitat quality. *International Journal of Sediment Research* **30**:74-80.
- Gerwing, T. G., D. Drolet, M. A. Barbeau, D. J. Hamilton, and A. M. Allen Gerwing. 2015c. Resilience of an intertidal infaunal community to winter stressors. *Journal of Sea Research* **97**:40-49.
- Ghasemi, A. F., J. C. Clements, M. Taheri, and A. Rostami. 2014. Changes in the quantitative distribution of Caspian Sea polychaetes: Prolific fauna formed by non-indigenous species. *Journal of Great Lakes Research* **40**:692-698.
- Gillet, P., M. Mouloud, C. Mouneyrac, P. Simo, and F. Gilbert. 2012. Preliminary Data on the Bioturbation Activity of *Hediste diversicolor* (Polychaeta, Nereididae) from the Loire Estuary, France. *The Open Marine Biology Journal* **6**:53-56.
- Gilmurray, M., and G. Daborn. 1981. Feeding relations of the Atlantic silverside *Menidia menidia* in the Minas Basin, Bay of Fundy. *Marine Ecology Progress Series*.
- Gordon Jr, D. C., and C. Desplanque. 1983. Dynamics and environmental effects of ice in the Cumberland Basin of the Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* **40**:1331-1342.
- Gordon Jr, D. C., P. D. Keizer, G. R. Daborn, P. Schwinghamer, and W. L. Silvert. 1986. Adventures in holistic ecosystem modelling: the Cumberland Basin ecosystem model. *Netherlands Journal of Sea Research* **20**:325-335.

- Gordon Jr, D. C., P. D. Keizer, P. Schwinghamer, and G. R. Daborn. 1987. Ecological evaluation of the Cumberland Basin ecosystem model. *Continental Shelf Research* **7**:1477-1482.
- Greenville, A. C., G. M. Wardle, B. Tamayo, and C. R. Dickman. 2014. Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. *Oecologia* **175**:1349-1358.
- Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* **109**:323-334.
- Gunderson, L. H. 2000. Ecological resilience--in theory and application. *Annual Review of Ecology and Systematics*:425-439.
- Günther, C.-P. 1992. Dispersal of intertidal invertebrates: a strategy to react to disturbance of different scales? *Netherlands Journal of Sea Research* **30**:45-56.
- Gutt, J. 2001. On the direct impact of ice on marine benthic communities, a review. *Polar Biology* **24**:553-561.
- Hallmann, C. A., R. P. Foppen, C. A. van Turnhout, H. de Kroon, and E. Jongejans. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature*.
- Hamilton, D. J. 2000. Direct and indirect effects of predation by common eiders and abiotic disturbance in an intertidal community. *Ecological monographs* **70**:21-43.
- Hamilton, D. J., M. A. Barbeau, and A. W. Diamond. 2003. Shorebirds, mud snails, and *Corophium volutator* in the upper Bay of Fundy, Canada: predicting bird activity on intertidal mud flats. *Canadian Journal of Zoology* **81**:1358-1366.
- Hamilton, D. J., A. W. Diamond, and P. G. Wells. 2006. Shorebirds, snails, and the amphipod *Corophium volutator* in the upper Bay of Fundy: top-down vs. bottom-up factors, and the influence of compensatory interactions on mudflat ecology. *Hydrobiologia* **567**:285-306.
- Haralampides, K., and A. Rodriguez. 2006. Erosional properties of the sediments in the Petitcodiac River estuary at Moncton, New Brunswick. *Canadian journal of civil engineering* **33**:1209-1216.
- Hargrave, B. T., N. J. Prouse, G. A. Phillips, and P. A. Neame. 1983. Primary production and respiration in pelagic and benthic communities at two intertidal sites in the upper Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* **40**:229-243.
- Heck, K. L., and J. F. Valentine. 2007. The primacy of top-down effects in shallow benthic ecosystems. *Estuaries and Coasts* **30**:371-381.
- Hicklin, P. W. 1987. The migration of shorebirds in the Bay of Fundy. *The Wilson Bulletin* **99**:540-570.
- Hicklin, P. W., and P. C. Smith. 1979. The diets of five species of migrant shorebirds in the Bay of Fundy. *Proceedings of the Nova Scotian Institute of Science* **29**:483-488.
- Hicklin, P. W., and P. C. Smith. 1984. Selection of foraging sites and invertebrate prey by migrant Semipalmated Sandpipers, *Calidris pusilla* (Pallas). *Canadian Journal of Zoology* **62**:2201-2210.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* **6**:324-337.

- Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. Johnson. 2001. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge university press Cambridge, United Kingdom and New York, NY, USA.
- Hughes, J. M., J. S. Stewart, J. M. Lyle, and I. M. Suthers. 2014. Top-down pressure on small pelagic fish by eastern Australian salmon *Arripis trutta*; estimation of daily ration and annual prey consumption using multiple techniques. *Journal of Experimental Marine Biology and Ecology* **459**:190-198.
- Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* **81**:2241-2249.
- Johnson, K. D., J. H. Grabowski, and D. L. Smee. 2014. Omnivory dampens trophic cascades in estuarine communities. *Marine Ecology Progress Series* **507**:197-206.
- Jones, L. A., and A. Ricciardi. 2014. The influence of pre - settlement and early post - settlement processes on the adult distribution and relative dominance of two invasive mussel species. *Freshwater Biology* **59**:1086-1100.
- Jones, N. 1952. The bottom fauna and the food of flatfish off the Cumberland coast. *The Journal of Animal Ecology* **21**:182-205.
- Jumars, P. A., K. M. Dorgan, and S. M. Lindsay. 2014. Diet of worms emended: an update of polychaete feeding guilds. *Annual Review of Marine Science* **7**:1-340.
- Kamermans, P., and H. J. Huitema. 1994. Shrimp (*Crangon crangon* L.) browsing upon siphon tips inhibits feeding and growth in the bivalve *Macoma balthica* (L.). *Journal of Experimental Marine Biology and Ecology* **175**:59-75.
- Kelaher, B. P., M. G. Chapman, and A. J. Underwood. 2001. Spatial patterns of diverse macrofaunal assemblages in coralline turf and their associations with environmental variables. *Journal of the Marine Biological Association of the UK* **81**:917-930.
- Kennedy, K. 2012. Population dynamics of the mudflat amphipod *Corophium volutator* in winter. MSc Thesis University of New Brunswick, Fredericton New Brunswick, Canada.
- Knight, R., and R. Dalrymple. 1976. Winter conditions in a macrotidal environment, Cobequid Bay. Nova Scotia. *Rev. Geogr. Montreal* **30**:65-85.
- Kohn, M. H., and R. K. Wayne. 1997. Facts from feces revisited. *Trends in Ecology & Evolution* **12**:223-227.
- Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**:269-271.
- Kraus, J. M., T. S. Schmidt, D. M. Walters, R. B. Wanty, R. E. Zuellig, and R. E. Wolf. 2014. Cross-ecosystem impacts of stream pollution reduce resource and contaminant flux to riparian food webs. *Ecological Applications* **24**:235-243.
- Kristensen, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* **426**:1-24.

- Kuwae, T., E. Miyoshi, S. Hosokawa, K. Ichimi, J. Hosoya, T. Amano, T. Moriya, M. Kondoh, R. C. Ydenberg, and R. W. Elner. 2012. Variable and complex food web structures revealed by exploring missing trophic links between birds and biofilm. *Ecology Letters* **15**:347-356.
- Letnic, M., and C. R. Dickman. 2010. Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews* **85**:501-521.
- Levin, L. A. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* **65**:1185-1200.
- Levinton, J. S., and B. P. Kelaher. 2004. Opposing organizing forces of deposit-feeding marine communities. *Journal of Experimental Marine Biology and Ecology* **300**:65-82.
- Loeuille, N., and M. A. Leibold. 2008. Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. *The American Naturalist* **171**:788-799.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. Grime, A. Hector, D. Hooper, M. Huston, D. Raffaelli, and B. Schmid. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804-808.
- Lu, L., J. Grant, and J. Barrell. 2008. Macrofaunal spatial patterns in relationship to environmental variables in the Richibucto estuary, New Brunswick, Canada. *Estuaries and Coasts* **31**:994-1005.
- MacDonald, E. C., M. G. Ginn, and D. J. Hamilton. 2012. Variability in foraging behavior and implications for diet breadth among semipalmated sandpipers staging in the upper Bay of Fundy. *Condor* **114**:135-144.
- Macfarlane, C. B., D. Drolet, M. A. Barbeau, D. J. Hamilton, and J. Ollerhead. 2013. Dispersal of marine benthic invertebrates through ice rafting. *Ecology* **94**:250-256.
- Matthews, S., J. Boates, and S. Walde. 1992. Shorebird predation may cause discrete generations in an amphipod prey. *Ecography* **15**:393-400.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82**:290-297.
- McCurdy, D., M. Forbes, and J. Boates. 2000. Male amphipods increase their mating effort before behavioural manipulation by trematodes. *Canadian Journal of Zoology* **78**:606-612.
- McCurdy, D. G., M. R. Forbes, and J. S. Boates. 1999. Evidence that the parasitic nematode *Skrjabinoclava manipulates* host *Corophium* behavior to increase transmission to the sandpiper, *Calidris pusilla*. *Behavioral Ecology* **10**:351.
- McCurdy, D. G., M. R. Forbes, S. P. Logan, D. Lancaster, and S. I. Mautner. 2005. Foraging and impacts by benthic fish on the intertidal amphipod *Corophium volutator*. *Journal of Crustacean Biology* **25**:558-564.
- McGarigal, K., and S. A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* **12**:335-345.
- Meadows, P. S. 1964a. Experiments on substrate selection by *Corophium* species: films and bacteria on sand particles. *Journal of Experimental Biology* **41**:499-511.

- Meadows, P. S. 1964b. Experiments on substrate selection by *Corophium volutator* (Pallas): depth selection and population density. *Journal of Experimental Biology* **41**:677-687.
- Meadows, P. S. 1964c. Substrate selection by *Corophium* species: the particle size of substrates. *The Journal of Animal Ecology* **33**:387-394.
- Meadows, P. S. 1967. Discrimination, previous experience and substrate selection by the amphipod *Corophium*. *The Journal of experimental biology* **47**:553.
- Menge, B., B. Daley, P. Wheeler, E. Dahlhoff, E. Sanford, and P. Strub. 1997. Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? *Proceedings of the National Academy of Sciences of the United States of America* **94**:14530.
- Menge, B. A. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* **146**:69-100.
- Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* **250**:257-289.
- Mermillod-Blondin, F., and R. Rosenberg. 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic Sciences* **68**:434-442.
- Meusnier, I., G. Singer, J. F. Landry, D. Hickey, P. Hebert, and M. Hajibabaei. 2008. A universal DNA mini-barcode for biodiversity analysis. *BMC genomics* **9**:214.
- Miller, K., C. Quine, and J. Hunt. 1987. The assessment of wind exposure for forestry in upland Britain. *Forestry* **60**:179.
- Murray, F., A. Douglas, and M. Solan. 2014. Species that share traits do not necessarily form distinct and universally applicable functional effect groups. *Marine Ecology Progress Series* **516**:23-34.
- Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**:1846-1850.
- Norkko, A., and E. Bonsdorff. 1996. Altered benthic prey - availability due to episodic oxygen deficiency caused by drifting algal mats. *Marine Ecology* **17**:355-372.
- Nozawa, Y., C.-H. Lin, and A.-C. Chung. 2013. Bathymetric variation in recruitment and relative importance of pre-and post-settlement processes in coral assemblages at Lyudao (Green Island), Taiwan. *Plos One* **8**:e81474.
- Nybakken, J. W., and M. D. Bertness. 2005. *Marine biology: an ecological approach*. 6th edition. Harper & Row New York.
- Ólafsson, E. B., C. H. Peterson, and W. G. Ambrose Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre-and post-settlement processes. *Oceanography and Marine Biology: an annual review* **32**:65-109.
- Pacala, S. W., and M. Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *The American Naturalist* **152**:729-737.

- Pagliosa, P. R. 2005. Another diet of worms: the applicability of polychaete feeding guilds as a useful conceptual framework and biological variable. *Marine Ecology* **26**:246-254.
- Partridge, V. 2001. Influence of ice cover on sediment temperature and implications for intertidal benthic invertebrates on a Bay of Fundy mudflat. Pages 14-16 in *Workshop on River Ice*.
- Passarelli, C., C. Hubas, A. Nicolas Segui, J. Grange, and T. Meziane. 2012. Surface adhesion of microphytobenthic biofilms is enhanced under *Hediste diversicolor* (OF Müller) trophic pressure. *Journal of Experimental Marine Biology and Ecology* **438**:52-60.
- Peck, L., and L. Bullough. 1993. Growth and population structure in the infaunal bivalve *Yoldia eightsi* in relation to iceberg activity at Signy Island, Antarctica. *Marine Biology* **117**:235-241.
- Petersen, M. E. 1999. Reproduction and development in Cirratulidae (Annelida: Polychaeta). *Hydrobiologia* **402**:107-128.
- Peterson, C. H. 1991. Intertidal zonation of marine invertebrates in sand and mud. *American Scientist* **79**:236-249.
- Peterson, C. H., S. R. Fegley, C. M. Voss, S. R. Marschhauser, and B. M. VanDusen. 2013. Conservation implications of density-dependent predation by ghost crabs on hatchling sea turtles running the gauntlet to the sea. *Marine Biology* **160**:629-640.
- Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology*:393-418.
- Pienkowski, M. W., P. N. Ferns, N. C. Davidson, and D. H. Worrall. 1983. Balancing the budget: measuring the energy intake and requirements of shorebirds in the field. Pages 29-56 in P. R. Evans, J. D. Goss-Custard, and W. G. Hale, editors. *Coastal waders and wildfowl in winter*. Cambridge University Press, Cambridge.
- Pilditch, C. A., S. Valanko, J. Norkko, and A. Norkko. 2015. Post-settlement dispersal: the neglected link in maintenance of soft-sediment biodiversity. *Biology letters* **11**:20140795.
- Pompanon, F., B. E. Deagle, W. O. C. Symondson, D. S. Brown, S. N. Jarman, and P. Taberlet. 2011. Who is eating what: diet assessment using next generation sequencing. *Molecular Ecology*.
- Pöysä, H. 2004. Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid? *Oikos* **104**:612-615.
- Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. *BioScience* **59**:779-791.
- Puritz, J. B., J. A. Addison, and R. J. Toonen. 2012. Next-generation phylogeography: a targeted approach for multilocus sequencing of non-model organisms. *Plos One* **7**:e34241.
- Queirós, A. M., S. N. R. Birchenough, J. Bremner, J. A. Godbold, R. E. Parker, A. Romero - Ramirez, H. Reiss, M. Solan, P. J. Somerfield, and C. Colen. 2013. A bioturbation classification of European marine infaunal invertebrates. *Ecology and Evolution* **3**:3958-3985.

- Quijón, P. A., and P. V. Snelgrove. 2008. Trophic complexity in marine sediments: new evidence from the Gulf of St. Lawrence. *Marine Ecology Progress Series* **371**:85-89.
- Quine, C., and I. White. 1994. Using the relationship between rate of tatter and topographic variables to predict site windiness in upland Britain. *Forestry* **67**:245.
- Quinn, J. T., and D. J. Hamilton. 2012. Variation in diet of Semipalmated Sandpipers (*Calidris pusilla*) during stopover in the upper Bay of Fundy, Canada. *Canadian Journal of Zoology* **90**:1181-1190.
- Quintana, C. O., E. Kristensen, and T. Valdemarsen. 2013. Impact of the invasive polychaete *Marenzelleria viridis* on the biogeochemistry of sandy marine sediments. *Biogeochemistry* **115**:95-109.
- Rayner, M. J., M. E. Hauber, M. J. Imber, R. K. Stamp, and M. N. Clout. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences* **104**:20862-20865.
- Reise, K., editor. 1991. Mosaic cycles in the marine benthos. Springer, Berlin, Heidelberg, New York, New York, USA.
- Risk, M. J., and H. D. Craig. 1976. Flatfish feeding traces in the Minas Basin. *Journal of Sedimentary Research* **46**:411-413.
- Robar, N. D. P., and D. J. Hamilton. 2007. A method for estimating habitat use by shorebirds using footprints. *Waterbirds* **30**:116-123.
- Rodriguez, A. 2005. Erosional properties of the sediments in the Peticodiac River Estuary at Moncton, NB. MSc Thesis. University of New Brunswick, Fredericton, New Brunswick, Canada
- Rose, G. A., and W. C. Leggett. 1989. Interactive effects of geophysically-forced sea temperatures and prey abundance on mesoscale coastal distributions of a marine predator, Atlantic Cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**:1904-1913.
- Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* **74**:1264-1280.
- Rosenberg, R., H. C. Nilsson, and R. J. Diaz. 2001. Response of benthic fauna and changing sediment redox profiles over a hypoxic gradient. *Estuarine, Coastal and Shelf Science* **53**:343-350.
- Schelske, C. L., and E. P. Odum. 1961. Mechanisms maintaining high productivity in Georgia estuaries. Pages 75-80 in *Proceedings of the Gulf and Caribbean Fisheries Institute*.
- Scholz, B., and G. Liebezeit. 2012. Microphytobenthic dynamics in a Wadden Sea intertidal flat—Part II: Seasonal and spatial variability of non-diatom community components in relation to abiotic parameters. *European Journal of Phycology* **47**:120-137.
- Schuldt, A., M. Baruffol, H. Bruelheide, S. Chen, X. Chi, M. Wall, and T. Assmann. 2014. Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests. *Oecologia* **176**:171-182.
- Scrosati, R., and L. K. Eckersley. 2007. Thermal insulation of the intertidal zone by the ice foot. *Journal of Sea Research* **58**:331-334.

- Scrosati, R., and C. Heaven. 2006. Field technique to quantify intensity of scouring by sea ice in rocky intertidal habitats. *Marine Ecology Progress Series* **320**:293-295.
- Searle, S. R., G. Casella, and C. E. McCulloch. 1992. Variance components. John Wiley & Sons, New York, USA.
- Sharpe, D. M., and L. J. Chapman. 2014. Niche expansion in a resilient endemic species following introduction of a novel top predator. *Freshwater Biology* **59**:2539-2544.
- Shaw, J., C. L. Amos, D. A. Greenberg, C. T. O'Reilly, D. R. Parrott, and E. Patton. 2010. Catastrophic tidal expansion in the Bay of Fundy, Canada. *Canadian Journal of Earth Sciences* **47**:1079-1091.
- Shehzad, W., T. Riaz, M. A. Nawaz, C. Miquel, C. Poillot, S. A. Shah, F. Pompanon, E. Coissac, and P. Taberlet. 2012. Carnivore diet analysis based on next - generation sequencing: application to the leopard cat (*Prionailurus bengalensis*) in Pakistan. *Molecular Ecology* **21**:1951-1965.
- Shepherd, P., and J. Boates. 1999. Effects of a commercial baitworm harvest on Semipalmated Sandpipers and their prey in the Bay of Fundy Hemispheric Shorebird Reserve. *Conservation Biology* **13**:347-356.
- Sheppard, S., J. Bell, K. Sunderland, J. Fenlon, D. Skervin, and W. Symondson. 2005. Detection of secondary predation by PCR analyses of the gut contents of invertebrate generalist predators. *Molecular Ecology* **14**:4461-4468.
- Simmons, D., M. McMaster, E. Reiner, L. Hewitt, J. Parrott, B. Park, S. Brown, and J. Sherry. 2014. Wild fish from the Bay of Quinte Area of Concern contain elevated tissue concentrations of PCBs and exhibit evidence of endocrine-related health effects. *Environment International* **66**:124-137.
- Snelgrove, P. V. R., and C. A. Butman. 1994. Animal sediment relationships revisited-cause versus effect. *Oceanography and Marine Biology* **32**:111-177.
- Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* **100**:652-661.
- Springer, A. M., and G. B. van Vliet. 2014. Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. *Proceedings of the National Academy of Sciences* **111**:E1880-E1888.
- Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences* **99**:15497-15500.
- Stillman, J. H. 2002. Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, genus *Petrolisthes*. *Integrative and Comparative Biology* **42**:790-796.
- Strasser, M., and U. Pieloth. 2001. Recolonization pattern of the polychaete *Lanice conchilega* on an intertidal sand flat following the severe winter of 1995/96. *Helgolander Marine Research* **55**:176-181.
- Strasser, M., T. Reinwald, and K. Reise. 2001. Differential effects of the severe winter of 1995/96 on the intertidal bivalves *Mytilus edulis*, *Cerastoderma edule* and

- Mya arenaria* in the Northern Wadden Sea. *Helgoland Marine Research* **55**:190-197.
- Stuart, V., E. J. H. Head, and K. H. Mann. 1985. Seasonal changes in the digestive enzyme levels of the amphipod *Corophium volutator* (Pallas) in relation to diet. *Journal of Experimental Marine Biology and Ecology* **88**:243-256.
- Sturaro, N., G. Lepoint, S. Vermeulen, and S. Gobert. 2014. Multiscale variability of amphipod assemblages in *Posidonia oceanica* meadows. *Journal of Sea Research* **95**:258-271.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist*:859-873.
- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, and T. D. Lambert. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**:1923-1926.
- Thieltges, D. W., M. Strasser, J. E. van Beusekom, and K. Reise. 2004. Too cold to prosper—winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. *Journal of Experimental Marine Biology and Ecology* **311**:375-391.
- Thrush, S. F., J. E. Hewitt, V. J. Cummings, M. O. Green, G. A. Funnell, and M. R. Wilkinson. 2000. The generality of field experiments: interactions between local and broad-scale processes. *Ecology* **81**:399-415.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2-16.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:350-363.
- Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**:629-632.
- Todd, C. D. 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? *Hydrobiologia* **375/376**:1-21.
- Trites, M., I. Kaczmarska, J. M. Ehrman, P. W. Hicklin, and J. Ollerhead. 2005. Diatoms from two macro-tidal mudflats in Chignecto Bay, Upper Bay of Fundy, New Brunswick, Canada. *Hydrobiologia* **544**:299-319.
- Tsipoura, N., and J. Burger. 1999. Shorebird diet during spring migration stopover on Delaware Bay. *Condor* **101**:635-644.
- Underwood, A. J. 1996. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, New York, USA.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* **250**:97-115.
- Underwood, A. J., and P. G. Fairweather. 1989. Supply-side ecology and benthic marine assemblages. *Trends in Ecology & Evolution* **4**:16-20.
- van den Hoff, J., C. R. McMahon, G. R. Simpkins, M. A. Hindell, R. Alderman, and H. R. Burton. 2014. Bottom-up regulation of a pole-ward migratory predator population. *Proceedings of the Royal Society B: Biological Sciences* **281**.
- van Gils, J. A., C. Kraan, A. Dekinga, A. Koolhaas, J. Drent, P. de Goeij, and T. Piersma. 2009. Reversed optimality and predictive ecology: burrowing depth forecasts population change in a bivalve. *Biology letters* **5**:5-8.

- Vanschoenwinkel, B., F. Buschke, and L. Brendonck. 2013. Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. *Ecology*.
- Vinueza, L. R., B. A. Menge, D. Ruiz, and D. M. Palacios. 2014. Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos intertidal meta-ecosystem. *Ecological monographs* **84**:411-434.
- Vismann, B. 1990. Sulfide detoxification and tolerance in *Nereis (Hediste) diversicolor* and *Nereis (Neanthes) virens* (Annelida: Polychaeta). *Marine ecology progress series*. Oldendorf **59**:229-238.
- Walker, B. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* **9**:747-752.
- Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society* **9**:5.
- Weersing, K., and R. J. Toonen. 2009. Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology Progress Series* **393**:1-12.
- White, P., and S. Pickett, editors. 1985. Natural disturbance and patch dynamics: an introduction. Academic Press, Orlando, Florida, USA.
- Whitlatch, R., A. Lohrer, S. Thrush, R. Pridmore, J. Hewitt, V. Cummings, and R. Zajac. 1998. Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences. *Hydrobiologia* **375**:217-226.
- Williams, G. J., J. E. Smith, E. J. Conklin, J. M. Gove, E. Sala, and S. A. Sandin. 2013. Benthic communities at two remote Pacific coral reefs: effects of reef habitat, depth, and wave energy gradients on spatial patterns. *PeerJ* **1**:e81.
- Wilson Jr, W. 1983. The role of density dependence in a marine infaunal community. *Ecology* **64**:295-306.
- Wilson Jr, W. 1989. Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy. *Journal of Experimental Marine Biology and Ecology* **132**:221-245.
- Wilson Jr, W. H. 1991. The importance of epibenthic predation and ice disturbance in a Bay of Fundy mudflat. *Ophelia (Suppl. 5)* **507**:507-514.
- Woodin, S. A., D. S. Wethey, and N. Volkenborn. 2010. Infaunal hydraulic ecosystem engineers: cast of characters and impacts. *Integrative and Comparative Biology* **50**:176-187.
- Wu, Y., J. Chaffey, D. A. Greenberg, K. Colbo, and P. C. Smith. 2011. Tidally-induced sediment transport patterns in the upper Bay of Fundy: A numerical study. *Continental Shelf Research* **31**:2041-2053.
- Yeo. 1977. Animal-sediment relationships and the ecology of the intertidal mudflat environment, Minas Basin, Nova Scotia. MSc Thesis. McMaster University, Hamilton, Ontario, Canada.
- Ze-Hao, S. 2004. A review on the experimental approach in landscape ecology. *Acta Ecologica Sinica* **4**:1-17.

Appendix 1: Variation in winter variables and taxon-specific densities across eight intertidal mudflats in the Bay of Fundy, Canada

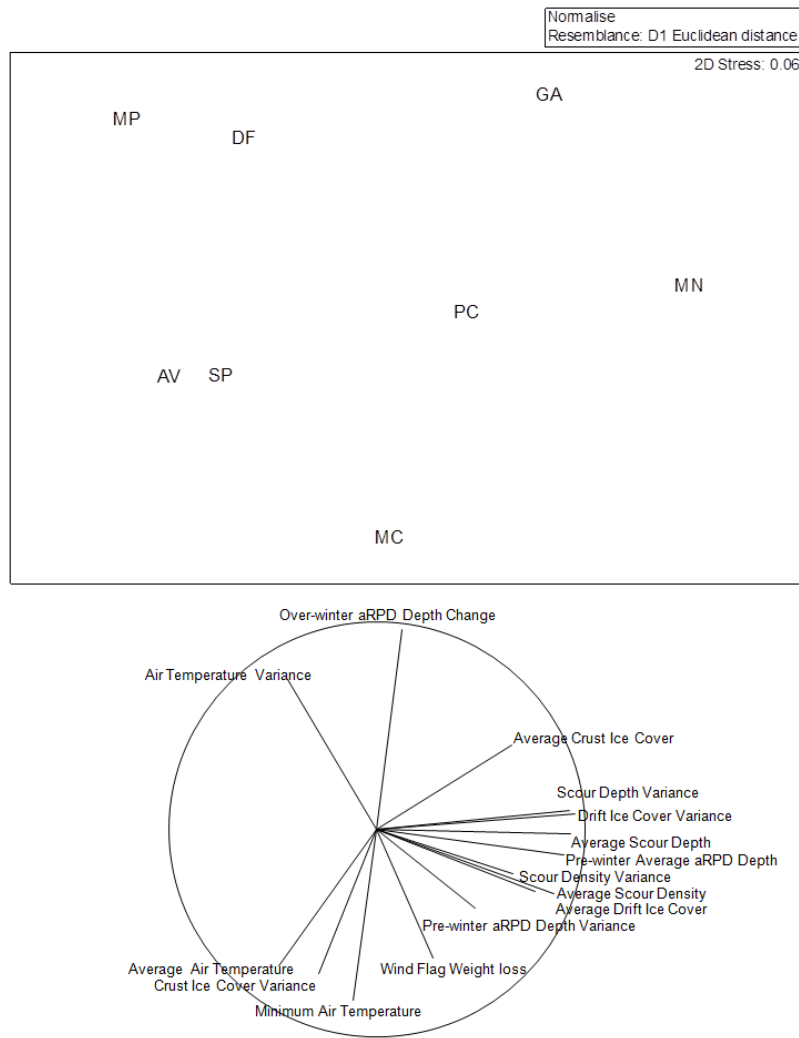


Figure A1.1: Non-metric multidimensional scaling (nMDS) plot of the intertidal mudflat sites based on winter variables in 2010-2011 [specifically, variables related to ice, ice scour, wind exposure (i.e., wind flag weight loss), air temperature, and the apparent redox potential discontinuity in the sediment (aRPD); see paper for an explanation of these winter variables]. Each symbol represents a site (see Table 2.1 in the paper for full site names). This plot resembles the geographic map of the sites (compare to Figure 2.1), suggesting that sites closer together are more similar to each other with regard to winter variables than sites further apart. The vector overlay beneath the nMDS plot represents correlations (Pearson correlation coefficients) between winter variables and nMDS axes. The vector for each winter variable shows the direction of increased value across the nMDS plot.

Table A1.1: A distance-based redundancy analysis (*dbRDA*) was used to determine the proportion of the multidimensional between-site variation that each winter variable (normalized) accounted for in winter 2010-2011. Variables not mentioned in the table (scour and wind exposure variables) did not account for a significant portion of the between-site variation. Scour variables were strongly correlated with drift ice variables (Pearson correlation coefficients = 0.75-0.93), which may explain why they were not highlighted in this analysis.

Variable	% Variation Fitted Model	Cumulative Variation (%)
Drift Ice Cover Variance	45.6	45.6
Crust Ice Cover Variance	26.4	72.0
Minimum Air Temperature	15.6	87.6
Average Drift Ice Cover	6.0	93.6
Average Air Temperature	3.6	97.2
Air Temperature Variance	1.7	98.9
Average Crust Ice Cover	1.0	99.9

Table A1.2: Results of ANOVAs (specifically, *p* values) for the effect of Site (8 mudflats), Season (pre- and post-winter) and Year (2009-2010 and 2010-2011) on density of infauna (# m⁻², data transformed using log₁₀ (datum +1) for all taxa, except *Corophium volutator*, which did not require any transformation) and taxa richness (# taxa per core; no data transformation). The factor of interest to assess if there is a significant over-winter change is Season and its interactions. This table supplements Figure 2.3 and Table 2.5. Total Density is the sum of all taxon-specific densities, and is an index for total over-winter change, independent of taxa specific trends. df = degrees of freedom in the numerator and denominator of the F-ratio. Interpretable and significant *p* values are in bold, while non-significant *p* values approaching significance are in italics. When the 3-way interaction (Site x Season x Year) was significant, separate analyses were done for each year. Results for the random effects of Transect(Site) and its interactions are not presented.

2009- 2011	Independent Variable	Site	Season	Year	Site x Season	Site x Year	Season x Year	Site x Season x Year
df		2,8	1,8	1,8	7,8	7,8	1,8	7,8
	Total Density	<i>0.083</i>	0.404	0.968	0.281	0.173	0.876	0.351
	Richness	0.246	0.958	0.001	0.384	0.430	0.801	0.715
	Phyllodocidae	0.001	0.013	0.041	0.038	0.029	0.211	0.313
	Cirratulidae	0.001	0.023	0.001	<i>0.084</i>	0.001	0.044	0.247
	Spionidae	0.002	0.060	0.160	0.007	0.003	0.638	0.007
	Nereididae	0.001	0.001	0.571	0.114	0.222	0.181	0.589
	Nephtyidae	0.001	0.241	0.010	0.027	0.015	0.637	0.246
	Capitellidae	0.001	0.689	0.007	0.034	0.121	0.001	0.002
	<i>Macoma</i> spp.	0.010	0.184	<i>0.094</i>	0.148	0.262	<i>0.097</i>	0.347
	Copepods	0.001	0.655	0.027	0.342	0.095	0.914	0.022
	Ostracods	0.001	<i>0.070</i>	0.264	0.647	0.291	0.989	0.558
	<i>C. volutator</i>	0.001	0.020	0.001	0.376	<i>0.057</i>	0.152	0.601
2009- 2010	Independent Variable	Site	Season	Site x Season				
df		7,8	1,8	7,8				
	Spionidae	0.022	0.277	0.001				
	Capitellidae	0.001	0.102	0.001				
	Copepods	0.002	0.716	0.047				
2010- 2011	Independent Variable	Site	Season	Site x Season				
df		7,8	1,8	7,8				
	Spionidae	0.011	0.568	0.162				
	Capitellidae	0.001	<i>0.060</i>	0.463				
	Copepods	0.003	0.555	0.030				

Table A1.3: Summary of ANOVA and Tukey's postoc test results (see Table A1.2 above) showing how different taxa change over winter in different years and sites. Richness is taxa richness, and Total is total density of infauna. This table supplements Figure 2.3 and Table 2.5. "0" represents a taxon not present, "+" a statistical increase in density over winter, "-" a statistical decrease in density over winter, and "nc" no statistical change over winter. Full site names are in Table 2.1; Year 1 is for December 2009 to March 2010, and Year 2 for December 2010 to March 2011.

Site	Year	Capitellidae	Cirratulidae	Spionidae	Phyllodocidae	Nereididae	Nephtyidae	Macoma	Ostracoda	Copepoda	<i>C. volutator</i>	Richness	Total
SP	1	+	+	+	nc	0	nc	nc	nc	nc	+	nc	nc
SP	2	+	nc	-	nc	0	nc	nc	nc	nc	-	nc	nc
AV	1	nc	-	nc	nc	-	nc	nc	nc	nc	+	nc	nc
AV	2	nc	nc	nc	nc	0	nc	nc	nc	nc	-	nc	nc
MC	1	0	+	nc	-	-	nc	nc	nc	nc	-	nc	nc
MC	2	nc	nc	nc	-	-	nc	nc	nc	nc	-	nc	nc
MN	1	nc	-	nc	-	+	nc	nc	nc	nc	-	nc	nc
MN	2	nc	nc	nc	-	-	nc	nc	nc	nc	-	nc	nc
PC	1	nc	0	nc	nc	-	nc	nc	nc	nc	-	nc	nc
PC	2	nc	nc	nc	nc	-	nc	nc	nc	nc	-	nc	nc
GA	1	nc	+	-	nc	-	nc	nc	nc	nc	-	nc	nc
GA	2	nc	nc	-	nc	+	nc	nc	nc	nc	-	nc	nc
DF	1	nc	+	nc	nc	-	nc	nc	nc	nc	-	nc	nc
DF	2	nc	nc	nc	nc	-	nc	nc	nc	nc	-	nc	nc
MP	1	nc	+	nc	nc	-	nc	nc	nc	nc	+	nc	nc
MP	2	nc	nc	nc	nc	-	nc	nc	nc	nc	-	nc	nc

Appendix 2: Supplemental information for: Relative importance of biotic and abiotic forces on the composition and dynamics of a soft-sediment intertidal community

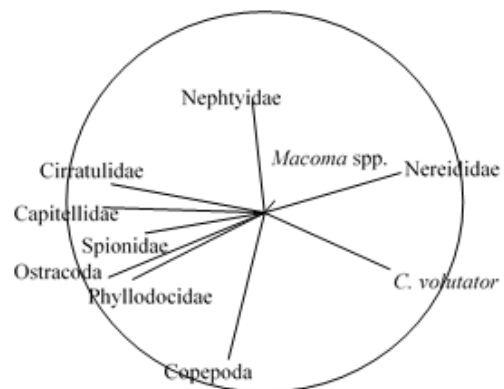
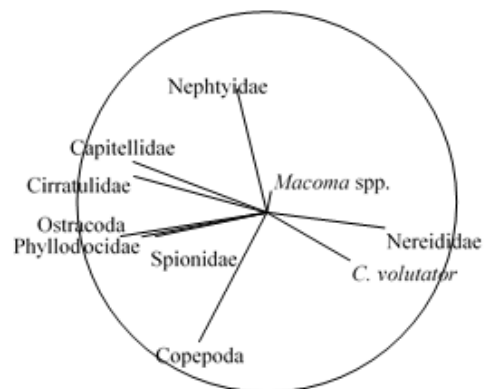
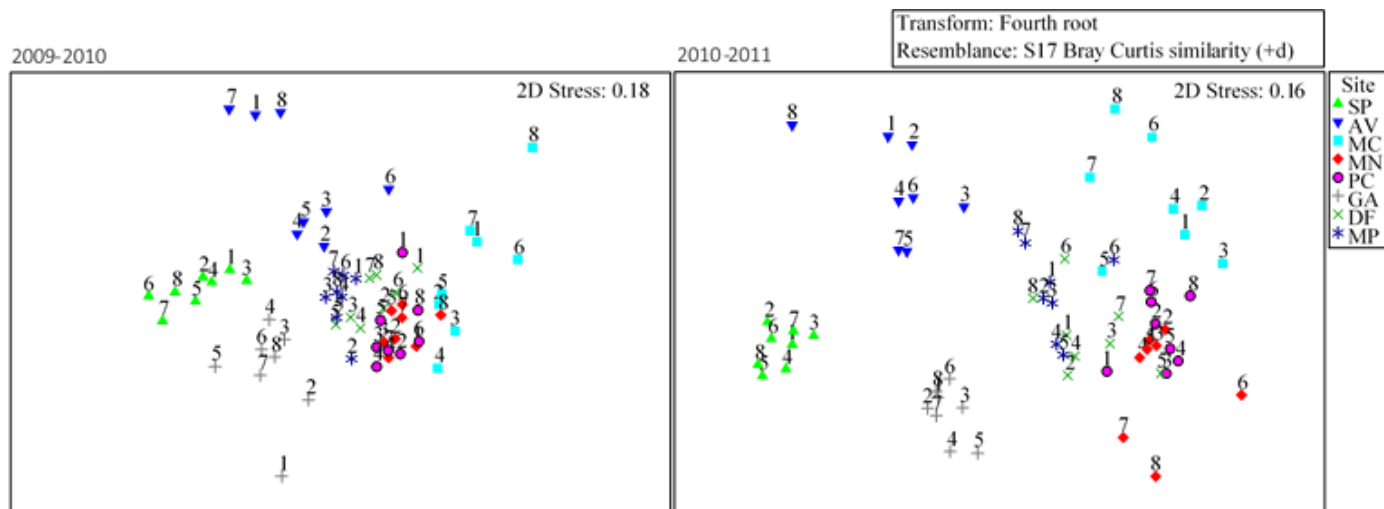


Figure A2.1: Non-metric multidimensional scaling (nMDS) plots of the infaunal community composition on eight intertidal mudflats (a.k.a. sites) in the upper Bay of Fundy, Canada, and eight sampling rounds per year over two years (2009-2011). Each symbol represents an average per combination of site and round. Round 1: early June, 2: late June, 3: mid-July, 4: early August, 5: late August/early September, 6: October, 7: December, 8: March. The stress is < 0.2 , indicating that the nMDS plots are adequate 2-dimensional representations of the multidimensional situation. Vector overlays beneath the nMDS plots represent Pearson correlations between taxa and nMDS axes; the vector of each taxon shows the direction of increased density across the nMDS plot. Detailed information of the population and community dynamics can be found in Gerwing et al. (2015a).

Curriculum Vitae

Education

July 2015: PhD, Biology. University of New Brunswick.

April 2009: Master of Science (*magna cum laude*), Natural Resources and Environmental Studies: Biology. University of Northern British Columbia.

April 2007: Bachelor of Science, Biology. University of Northern British Columbia.

June 2003: Dogwood (Top of class). Fort Nelson Secondary School

Awards

Outstanding Oral Presentation, Graduate Student. 44th Annual Benthic Ecology Meeting. 2015.

UNB Biology Department Demonstrator of the Year (Nominated). 2013/2014.

Marguerite and Murray Vaughan Graduate Fellowship. 2010-2013.

UNB President's Doctoral Tuition Award. 2009 – 2012.

UNBC Scholars Award. 2003 –2007.

BC Provincial Exam Scholarship. 2003.

Bronze Governor General's Award (Highest GPA in high school graduating class). 2003.

Duke Energy Award. 2003.

Lecturer Experience

Biology 3873. Ethology. 2014. University of New Brunswick.

Guest Lecturer Experience

Biology. 4641. Coastal Marine Ecology. 2011. 2012. 2013. 2014. 2015. University of New Brunswick.

Biology 2105. Research Foundations in Ecology and Population Biology. 2014. 2015. University of New Brunswick.

Teaching Assistant Experience

Biology 2812. Human Anatomy II. 2015. University of New Brunswick.

Biology 2903. Introductory Zoology. 2012, 2013. 2014. University of New Brunswick

Biology 2105. Research Foundations in Ecology and Population biology. 2012. 2014. 2015. University of New Brunswick.

Biology 1017. Introductory Biology II. 2010. University of New Brunswick.

Biology 1006. Introductory Biology I. 2009. University of New Brunswick.

Biology 102. Introductory Biology II. 2008. University of Northern British Columbia.

Biology 101. Introductory Biology I. 2007. University of Northern British Columbia.

Peer Reviewed Publications

Gerwing, T.G., Drolet, D., Barbeau, M.A., Hamilton, D.J., and Allen Gerwing, A.M. 2015. Resilience of an Intertidal Infaunal Community to Winter Stressors. Journal of Sea Research. 97. 40-49. DOI: 10.1016/j.seares.2015.01.001

Gerwing, T.G., Allen Gerwing, A.M., Hamilton, D.J., and Barbeau, M.A. 2015. Apparent Redox Potential Discontinuity (aRPD) Depth as a Relative Measure of Sediment Oxygen Content and Habitat Quality. International Journal of Sediment Research. 30. 74-80. DOI: [10.1016/S1001-6279\(15\)60008-7](https://doi.org/10.1016/S1001-6279(15)60008-7)

Gerwing. T.G., Allen Gerwing, A.M., Drolet, D., Hamilton, D.J., Barbeau, M.A. 2013. Comparison of Two Methods of Measuring the Depth of the Redox Potential Discontinuity in Intertidal Mudflat Sediments. Marine Ecology Progress Series. 487. 7-13.

Sizmur, T., Canário, J., Gerwing, T.G., Mallory, M.L., and O'Driscoll, N.J. 2013. Mercury and Methylmercury Bioaccumulation by Polychaete Worms is Governed by Feeding Ecology and Mercury Bioavailability in Coastal Mudflats. *Environmental Pollution*. 176. 18-25.

Bringloe, T.T., Drolet, D., Barbeau, M.A., Forbes, M., Gerwing, T.G. 2013. Spatial Variation in Population Structure and its Relation to Movement and Potential for Dispersal in a Model Intertidal Invertebrate. *Plos One*. DOI: <http://dx.plos.org/10.1371/journal.pone.0068329>

Gerwing, T.G., Johnson, C.J., and Alstrom-Rapaport, C. 2012. Factors Influencing Forage Selection by the North American Beaver (*Castor canadensis*). *Mammalian Biology*. 78. 79-86. DOI: <http://dx.doi.org/10.1016/j.mambio.2012.07.157>

Gerwing, T.G., Allen Gerwing, A.M., Rapaport, E., and Alstrom-Rapport, C. 2012. Sexual and Asexual Reproduction of *Salix sitchensis* and the Influence of Beaver (*Castor canadensis*) Herbivory on Reproductive Success. *ISRN Ecology*. DOI: 10.5402/2012/285748

Peer Reviewed Publications Accepted and In Press

Gerwing, T.G., Rash, J.A., Allen Gerwing, A.M., Bramble, B., and Landine, J. 2015. Perceptions and Incidence of Test Anxiety. *Canadian Journal for the Scholarship of Teaching and Learning*. Manuscript Number: 1249.

Gerwing, T.G., Allen Gerwing, A.M., Drolet, D., Barbeau, M.A., Hamilton, D.J. 2015. Spatiotemporal Variation in Biotic and Abiotic Features of Eight Intertidal Mudflats in the Upper Bay of Fundy, Canada. *Northeastern Naturalist*. Manuscript Number: N1354.

Peer Reviewed Publications: Submitted

Gerwing, T.G. Drolet, D. Hamilton, D.J. Barbeau, M.A. 2015. Relative Importance of Biotic and Abiotic Forces on the Composition and Dynamics of a Soft-Sediment Intertidal Community. Plos One. Manuscript Number: PONE-D-15-28913

Connon, H., Rash, J.A., Allen Gerwing, A.M., Bramble, B., and Landine, J., Gerwing, T.G. 2015. Instructor Perceptions of Test Anxiety. Canadian Journal for the Scholarship of Teaching and Learning. Manuscript Number: 1271.

Non-Peer Reviewed Publications

Gerwing, T.G., Rash, J.A., Allen Gerwing, A.M., Bramble, B., and Landine, J. 2013. The Perceived and Real Impact of Test Anxiety at UNB. Teaching Perspectives. Issue 18. St. Thomas University, Fredericton, New Brunswick, Canada. 13-15.

Gerwing, T.G., and Bramble, B. 2010. Teaching Assistant Training Manual for Civil Engineering. Center for Enhanced Teaching and Learning. University of New Brunswick, Fredericton, New Brunswick, Canada.

Gerwing, T.G. 2009. Reproductive Ecology of the Sitka Willow (*Salix sitchensis*). MSc Thesis. University of Northern British Columbia. Prince George BC Canada.

Gerwing, T.G. 2008. Basic Survival Tips for Marking and Grading. In: Ottery, G., and Foot, S. Editors. UNBC Teaching Assistant Manual. University of Northern British Columbia. Prince George BC Canada. 48-49.

Gerwing, T.G., and Owen, W. 2008. Teaching to Teach: The Need for a Course on Instructional Principles for Graduate Students. University of Northern British Columbia. Prince George BC Canada.

Invited Presentations

*Gerwing, T.G. 2015. Potential structuring factors of a soft sediment invertebrate community. Mount Allison University, Department of Biology Departmental Seminar. Mount Allison University, Sackville, New Brunswick, Canada.

*Gerwing, T.G. 2015. Potential structuring factors of a soft sediment invertebrate community. University of New Brunswick, Department of Biology Departmental Seminar. University of New Brunswick, Fredericton, New Brunswick, Canada.

*Gerwing, T.G., Allen Gerwing, A.M., Rash, J., Bramble, B., and Landine, J. 2014. Incidence and Perceptions of Text Anxiety at UNB. Presentation to UNB Faculty Association of Scholarship Teaching and Learning. University of New Brunswick, Fredericton, New Brunswick, Canada.

*Gerwing, T.G., Allen Gerwing, A.M., Rash, J., Bramble, B., and Landine, J. 2013. Test Anxiety: Understanding a Culturally Emerging Condition to Lessen its Impact. Presentation to Saint Thomas University Learning and Teaching Development Committee. Saint Thomas University, Fredericton, New Brunswick, Canada.

*Gerwing, T.G., Allen Gerwing, A.M., Rash, J., Bramble, B., and Landine, J. 2012. Perceptions of Test Anxiety. Graduate Research Conference: Invited Seminar Series. Fredericton, New Brunswick, Canada.

*Gerwing, T.G. 2008. Effective Marking Strategies. UNB Teaching Assistant Workshop. University of New Brunswick. Fredericton, New Brunswick, Canada

*Gerwing, T.G., and Allen Gerwing, A.M. 2011. Wildlife Ecology: Applying the Scientific Method to Understand Nature. Leo Hayes High School Science Club Guest Speaker Series. Leo Hayes High School. Fredericton, New Brunswick, Canada.

*Gerwing, T.G., *Allen Gerwing, A.M., Bramble, B., Rash, J., Landine, J. 2011. Perceptions of Test Anxiety: Preliminary Findings and Current Research Directions. Center for Enhanced Teaching and Learning Educational Colloquium. University of New Brunswick. Fredericton, New Brunswick, Canada.

*Gerwing, T.G. 2010. How to Mark Effectively. UNB Civil Engineer Teaching Assistant Training Seminar. University of New Brunswick. Fredericton, New Brunswick, Canada.

*Gerwing, T.G. 2010. How to Run a Laboratory Based Class Effectively. UNB Civil Engineer Teaching Assistant Training Seminar. University of New Brunswick. Fredericton, New Brunswick, Canada.

*Gerwing, T.G. 2009. Lecturing with PowerPoint: Tips, Tricks, and Time Savers. Centre for Teaching, Learning and Technology Workshop Series. University of Northern British Columbia. Prince George, British Columbia, Canada.

*Presenting author

Conference Presentations

*Gerwing, T.G., Drolet, D., Hamilton, D.J., Barbeau, M.A. 2015. Potential structuring factors of a soft sediment invertebrate community. 44th Annual Benthic Ecology Meeting. Laval University, Quebec City, Quebec. Awarded: Outstanding Oral Presentation, Graduate Student.

*Dixon, B., Barbeau, M.A., Gerwing, T.G. 2014. Population Dynamics of the Amphipod *Corophium volutator* on Mudflats in the Bay of Fundy Over a 14-Year Period. Atlantic Canada Coastal and Estuarine Science Society Annual Conference. St. Mary's University, Halifax, Nova Scotia, Canada.

*Bringloe, T.T., Drolet, D., Barbeau, M.A., Forbes, M.R., Gerwing, T.G. 2013. Spatial Variation in Population Structure and its Relation to Movement and Potential for Dispersal in a Model Intertidal Invertebrate. 52nd Annual Meeting of the Canadian Society of Zoologists, University of Guelph, Guelph, Ontario, Canada.

*Gerwing, T.G., Allen Gerwing, A. M., MacNeil, S., Drolet, D., Hamilton, D.J., and Barbeau, M.A. 2012. Nature and Possible Causes of the Annual Winter Die-Off of Benthic Invertebrates on Intertidal Mudflats in the Bay of Fundy, Canada. 19th Annual

Graduate Research Conference, University of New Brunswick, Fredericton, New Brunswick, Canada.

*Gerwing, T.G., Allen Gerwing, A. M., MacNeil, S., Drolet, D., Hamilton, D.J., and Barbeau, M.A. 2012. Winter is Coming: Species and Community Changes Over Winter in Bay of Fundy Intertidal Invertebrates. 51st Annual Meeting of the Canadian Society of Zoologists, Mount Allison University, Sackville, New Brunswick, Canada.

*Gerwing, T.G., Allen Gerwing, A.M., Rash, J.A., Bramble, B., *Landine, J. 2012. Fear of the Test: Incidence and Perceptions of Test Anxiety at UNB. Kaleidoscope: Teaching Showcase. University of New Brunswick, Fredericton, New Brunswick, Canada.

* Sizmur, T., Edmonds, S., Godfrey, A., Canário, J., Redden, A., Mallory, M., Gibson, G., Gerwing, T.G., and N., O'Driscoll. 2011. Impact of the Polychaete Worm *Nereis diversicolor* on Mercury Speciation in Intertidal Mudflats. Society of Environmental Toxicology and Chemistry North America 32nd Annual Meeting. Boston, Massachusetts, USA.

*Sizmur, T., Edmonds, S., Godfrey, A., Gerwing, T.G., Canário, J. and N., O'Driscoll. 2011. Interactions Between Mercury and Polychaete Worms in Intertidal Mudflats. Society of Environmental Toxicology and Chemistry UK Branch Annual Meeting. London, UK.

*Sizmur, T., Edmonds, S., Godfrey, A., Gerwing, T.G., Canário, J. and N., O'Driscoll. 2011. Interactions Between Mercury and Polychaete Worms in Intertidal Mudflats. The 9th BoFEP Bay of Fundy Science Workshop, Saint John, New Brunswick, Canada.

*Gerwing, T.G. 2008. Effective Marking Strategies. UNBC Annual Teaching Conference. University of Northern British Columbia. Prince George, British Columbia, Canada.

*Gerwing, T.G. 2008. Impact of Beavers on the Relative Success of Asexual and Sexual Reproduction in Riparian Willows. UNBC's 4th Annual Graduate Research Conference. University of Northern British Columbia. Prince George, British Columbia, Canada.

* Presenting author.

Non-Conference Presentations

*Gerwing, T.G. 2012. Changes in Community Structure and Taxa Density Over Winter on the Intertidal Mudflats. Coastal Soft Sediment Ecology Discussion Series. University of New Brunswick. Fredericton, New Brunswick, Canada.

*Gerwing, T.G. 2011. Understanding How *Corophium volutator* Burrow Depth is Related to Depth of Sediment and the Depth to the Anoxic Layer. *Corophium* Working Group of the Bay of Fundy Ecosystem Partnership. Mudflat Ecology Discussion Series. University of New Brunswick. Fredericton, New Brunswick, Canada.

*Gerwing, T.G. 2011. Preliminary Results on the Variation of the Depth to the Anoxic Sediment in Bay of Fundy Mudflats. *Corophium* Working Group of the Bay of Fundy Ecosystem Partnership. Mudflat Ecology Discussion Series. University of New Brunswick. Fredericton, New Brunswick, Canada.

*Gerwing, T.G. 2011. Winter Conditions on Nine Mudflats in the Bay of Fundy Canada. *Corophium* Working Group of the Bay of Fundy Ecosystem Partnership. Mudflat Ecology Discussion Series. University of New Brunswick. Fredericton, New Brunswick, Canada.

*Gerwing, T.G. 2011. A Preliminary Look at Biotic and Abiotic Factors on 9 Mudflats in the Bay of Fundy, Canada. *Corophium* Working Group of the Bay of Fundy Ecosystem Partnership. Mudflat Ecology Meeting. Mount Allison University. Sackville, New Brunswick, Canada.

*Gerwing, T.G. 2010. Spatial and Temporal Interactions of Intertidal Mudflat Ecosystems in the Upper Bay of Fundy. *Corophium* Working Group of the Bay of Fundy Ecosystem Partnership. Mudflat Ecology Meeting. Mount Allison University. Sackville, New Brunswick, Canada.

* Presenting author(s).

Poster Presentations

Gerwing, T.G., Allen Gerwing, A.M., Hamilton, D.J., *Barbeau, M.A. 2014. Apparent Redox Potential Discontinuity Depth as a Relative Measure of Sediment Oxygen Content. Atlantic Canada Coastal and Estuarine Science Society Annual Conference. St. Mary's University, Halifax, Nova Scotia, Canada.

*Dixon, B.V., Barbeau, M., Gerwing, T.G. 2013. Temporal and Spatial Variation in Population Density of the Mudflat Amphipod *Corophium volutator* in the Upper Bay of Fundy. Atlantic Canada Coastal and Estuarine Science Society. Centre for Geographic Sciences, Nova Scotia Community College Lawrencetown, Nova Scotia, Canada.

*Gerwing, T.G., Allen Gerwing, A. M., MacNeil, S., Drolet, D., Hamilton, D.J., and Barbeau, M.A. 2012. Comparing Two Methods of Measuring Depth to the Redox Potential Discontinuity in Intertidal Mudflat Sediments. 19th Annual Graduate Research Conference, University of New Brunswick, Fredericton, New Brunswick, Canada.

*Gerwing, T.G., Allen Gerwing, A. M., MacNeil, S., Drolet, D., Hamilton, D.J., and Barbeau, M.A. 2012. Comparing Two Methods of Measuring Depth to the Redox Potential Discontinuity in Intertidal Mudflat Sediments. 51st Annual Meeting of the Canadian Society of Zoologists, Mount Allison University, Sackville, New Brunswick, Canada.

Bringloe, T.T., *Drolet, D., Barbeau, M., Forbes, M.R., Gerwing, T.G. 2012. Informing Hypotheses About the Dispersal of the Amphipod *Corophium volutator*. 51st Annual Meeting of the Canadian Society of Zoologists, Mount Allison University, Sackville, New Brunswick, Canada.

*Gerwing, T.G., Drolet, D., Barbeau, M.A., and Hamilton, D.J. 2011. Quantifying Winter Conditions on Nine Mudflats in the Bay of Fundy, Canada. Atlantic Canada Coastal and Estuarine Science Society Annual Conference. St. Francis Xavier University. Antigonish, Nova Scotia, Canada.

*Gerwing, T.G., Drolet, D., Barbeau, M.A., and Hamilton, D.J. 2011. Quantifying Winter Conditions on Nine Mudflats in the Bay of Fundy, Canada. *Corophium* Working

Group of the Bay of Fundy Ecosystem Partnership. Mudflat Ecology Meeting. Mount Allison University. Sackville, New Brunswick, Canada.

*Barbeau, M.A., Hamilton, D.J., Murray, J., Kennedy, K., Gerwing, T.G., Drolet, D., and Haralampides, K. 2011. Temporal and Spatial Variation of Diatom Abundance (measured as chlorophyll *a* concentration) on Intertidal Mudflats in the Bay of Fundy, Canada. Trophic Significance of Microbial Biofilms in Tidal Flats Symposium. La Rochelle, France.

*Gerwing, T.G., and Alstrom-Rapaport, C. 2008. Analyzing if Forage Selection by Beavers is Based on Preference or Availability. UNBC Annual NRES Icebreaker. University of Northern British Columbia. Prince George. British Columbia. Canada.

*Gerwing, T.G., and Alstrom-Rapaport C. 2008. Influences of Beaver Browse on Willow Asexual Reproduction. British Columbia Protected Areas Research Forum. University of Northern British Columbia. Prince George. British Columbia. Canada.

* Presenting author.

Professional Membership

Atlantic Canada Coastal and Estuarine Science Society (ACCESS). Inducted 2011.

Corophium Working Group of the Bay of Fundy Ecosystem Partnership. Inducted: 2009.

Golden Key Society: Inducted 2004.

Professional Development

Haralampides, K. 2012. Theme Teaching Across the Curriculum. Kaleidoscope: Teaching Showcase.

Bramble, B. 2011. Critical Incidents in Teaching. Center for Enhanced Teaching and Learning. University of New Brunswick. Fredericton, New Brunswick, Canada.

DiBattista, D. 2011. Getting the Most Out of Multiple-Choice Questions. Saint Thomas University, Fredericton, New Brunswick, Canada.

Fuller, R. 2010. Students in Distress In-service. Counseling Services. University of New Brunswick. Fredericton, New Brunswick, Canada.

Collins, F., Lyon, D., and Briggs, B. 2010. Teaching First Year Courses. Subtle Changes, Sudden Results. Center for Enhanced Teaching and Learning. University of New Brunswick. Fredericton, New Brunswick, Canada.