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The Forgotten Cousin in Freshwater Community Ecology: Tidal Freshwater Wetlands

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THE FORGOTTEN COUSIN IN FRESHWATER

COMMUNITY ECOLOGY:

TIDAL FRESHWATER

WETLANDS

By

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A THESIS

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Thesis Advisor: Dr. Hamish S. Greig

An Abstract of the Thesis Presented
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Tidal freshwaters are unique in their placement in the landscape, forming where freshwater riverine flows are sufficient to overwhelm the saline water of the incoming tide, but not strong enough to suppress tidal water-height fluctuations. Tidal freshwaters and their wetlands have been overlooked by freshwater and marine researchers alike; neither discipline considers tidal freshwaters to fall under their purview. Invertebrate communities in tidal freshwaters are thought to be species depauperate; the consensus is that they support fewer taxa than nearby non-tidal freshwaters, but little is known about how these communities are structured. This study investigated how tidal hydrology, an atypical suite of environmental conditions for a freshwater habitat, influences benthic invertebrate community and trophic structure. A comparison was made between tidal freshwater wetlands, at three tidal heights (low, mid, high), and nearby non-tidal freshwater wetlands that varied in their hydrology (temporary and permanent).

Tidal freshwater wetlands generally had lower invertebrate richness and abundance than non-tidal freshwater wetlands. However, tidal freshwater wetlands contributed a large proportion

(~25%) of unique taxa to the local species pool suggesting that these wetlands may be important for supporting regional biodiversity. Communities were more strongly differentiated between wetlands of different tidal height than between hydrologically isolated inland wetlands.

Both invertebrate community structure and trophic structure exhibited zonation across the tidal height gradient. Low tidal height wetlands were typified by high abundances of a few dominant taxa, which were smaller-bodied on average than taxa found at higher tidal heights. High tidal height wetlands supported communities with more-evenly distributed abundances and supported more large-bodied invertebrates. Overall, invertebrate biomasses (body size x abundance) were greatest at wetlands of intermediate tidal height (mid) as were the biomasses of detritivorous and predatory invertebrates.

The tidal hydrology of tidal freshwater wetlands controls a suite of abiotic and biological drivers of community structure. Desiccation risk varies with tidal height due to variable inundation times. Likewise, the risk of predation (by fishes) appears to be linked to the time available for foraging during high tide. The reduction in diversity, invertebrate body size, and biomass at low tidal heights may be driven by fish predation, as these patterns are commonly observed in non-tidal freshwaters. Fish may have less access to higher tidal heights, which means larger invertebrate mesopredators could be released from predation pressure. Invertebrate biomasses at the highest tidal heights may be limited by a combination of limited foraging time (short inundation periods), high temperatures and desiccation risk, and by top-down control by *terrestrial* predators that utilize the marshes at low tide. Further work is needed to elucidate the relative importance and interactive effects of the abiotic and biological drivers that a likely responsible for the distinct zones of community structure and trophic structure observed across the tidal height gradient in this study.

Tidal freshwaters exhibit strong environmental gradients in a condensed geographic area and are amenable to manipulation. The broad range of abiotic and biological conditions found in tidal freshwaters may make them ideal study systems for answering broader questions in community ecology.

for Granny Snaddon

Daddylanglegs, flees, flechs, minnie-mony-feet
Emerteens an wyvers fechtin fur a seat
Foggy bummers, butteries, ettercaps and slugs
Snailies, slaters, a heeze o ither bugs
Pairtyin wi midgies wi a forkietail as cook
At the hornygollach's pairty ye cud either sting or sook!

[Tipulids, dipterans, siphonapterans, myriapods
Formicids and arachnids fighting for a seat
Bombus, lepidopterans, odonates and slugs
Snails, isopods, a swarm of other 'bugs'
Partying with *Culicoides*, with a dermapteran as cook
At the creepy-crawly's party, you could either sting or suck!]

The Hornygollach's Pairty
(Sheena Blackhall)

ACKNOWLEDGEMENTS

Special thanks go to Hamish Greig for being a supportive, flexible, and understanding advisor. He let me run with the idea of studying tidal freshwaters and their invertebrates and supported the development of a novel research project in a novel system, which definitely had the potential to go pear-shaped. Hamish worked hard with me on the many funding applications I submitted, usually returning multiple drafts on a tight schedule, and always found ways to improve my manuscripts and presentation style, from which I benefitted greatly.

And lastly, I'd like to thank my family, especially Jess Haghkerdar, an excellent scientist and supportive partner who helps me with everything I do in life and constantly makes me a better, happier ecologist and general human being. I couldn't do anything I do without her support and advice.

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CHAPTER 1:

AN INTRODUCTION TO TIDAL FRESHWATERS AND THEIR WETLANDS

<u>Tidal freshwaters</u>

Formation

Tidal freshwaters occur in estuaries with riverine flows that are sufficiently strong to maintain salinity levels below 0.5 ‰ while still permitting upstream tidal movement and fluctuations in water height (Odum et al. 1984). The denser salt water of the incoming tide is forced downwards by strong freshwater flows, and the incoming tide pushes large volumes of freshwater upwards—creating uniquely freshwater intertidal zones. Tidal freshwater conditions are more likely to occur in highly-stratified (or "salt-wedge") estuaries (Figure 1.1), where there is a sharp distinction between fresh and saline water, but are thought to occur to some extent in the upper reaches of most estuaries with high freshwater inputs (McLusky 1993). Tidal freshwaters are also common in rivers that produce large deltaic landforms where sediment or geology restricts the inflow of saline tidal waters (Hoitink and Jay 2016). Barendregt and Swarth (2013) posit that tidal freshwater conditions can only form and be maintained in the estuaries of rivers where seasonal mean low discharge is greater than 10% of the maximum discharge, otherwise excessive saline intrusion would occur during periods of low flow. In such cases, tidal freshwater conditions are unlikely to form in tropical or Mediterranean climates where precipitation patterns and river discharge values vary greatly by season (Barendregt and Swarth 2013).
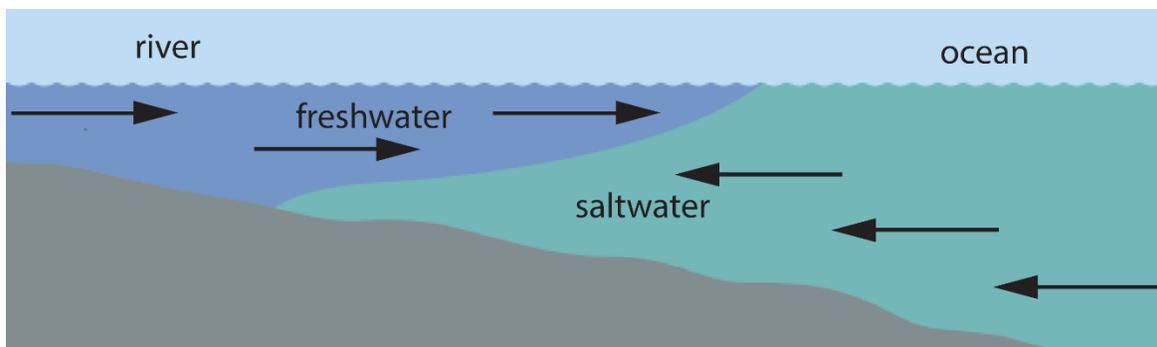
Figure 1.1. Diagrammatic representation of a "salt-wedge" estuary. Sharp color boundaries suggest little or no mixing of saltwater and freshwater.

Classification

The study of tidal freshwaters has likely been hampered by a lack of clear definitions or confusing synonymies (McLusky 1993; Elliott and McLusky 2002; Barendregt et al. 2009a). Additionally, the lack of clear consensus on what an estuary is, where it begins or ends, and how they should be classified, has meant tidal freshwaters have often been neglected. For clarity, this thesis will use the definitions outlined in McLusky (1993) (see Table 1.1. for details). To wit, tidal freshwaters are found between the head of tide (the highest upstream point reached by tides) and the upper limit of intrusion by saline water that causes water salinity to exceed 0.5 ‰.

Table 1.1. Classification of estuarine divisions and salinity definitions. Table adapted from McLusky (1993)].

Estuary division	Tidal	Salinity (‰)	Venice System (1958)
River	Non-tidal	< 0.5	Limnetic
Head	The highest point reached by tides	< 0.5	
Tidal fresh	Tidal	< 0.5	Limnetic
Upper	Tidal	0.5-5	Oligohaline
Inner	Tidal	5-18	Mesohaline
Middle	Tidal	18-30	Polyhaline
Lower	Tidal	25-30	Polyhaline
Mouth	Tidal	> 30	Euhaline

Global distribution and research attention

No global inventory of tidal freshwaters currently exists (Barendregt et al. 2009), although Barendregt and Swarth (2013) list rivers globally that tidal freshwater conditions are likely to occur in, based on freshwater discharge. Like most branches of ecological research, tidal freshwaters have been most intensively studied in North America and Western Europe, and are thought to occur in almost all large river estuaries, excluding those in Mediterranean climates (Odum et al. 1984; Barendregt et al. 2009a). In the southern hemisphere, tidal freshwaters have been studied in Argentina, Uruguay, Australia, and South Africa (Barendregt et al. 2009). In addition to those areas listed in the above reviews, I have found evidence of tidal freshwater conditions occurring in China (Bai et al. 2012), Nigeria (Adesalu and Nwankwo 2008), New Zealand (Wilding et al. 2012), India (David 1954), Papua New Guinea (Georges et al. 2008), and Indonesia (Sassi and Hoitink 2013). This selection of studies found during a relatively cursory review indicate that tidal freshwaters are more broadly distributed than currently thought.

Tidal freshwaters have received relatively little research attention compared with their neighboring ecosystem types. A simple comparison of keyword searches on Web of Science (searches performed July 7th 2016) clearly demonstrates the research bias. Scientists interested in hydrodynamic freshwaters have given more research attention to temporary or ephemeral systems [(*temporary* OR *ephemeral*) AND *freshw** = 1910 hits] over tidal freshwaters ["*tidal fresh**" OR "*fresh* tidal*" = 715 hits]. Estuarine scientists too tend to study brackish systems [*estuar** AND (*brackish* OR *oligohaline*) = 2270 hits] more often than freshwater portions of the estuary [*estuar** AND ("*tidal fresh**" OR "*fresh* tidal*") = 432 hits]. McLusky (1994) wryly offered the following reasoning why tidal freshwaters are little-studied: "freshwater scientists have traditionally ceased their activities once the river became tidal, and marine (and estuarine) scientists, like many

animals, migrated into estuaries from the nearshore marine waters and once the number of animal species reached a minimum level, at about 5 ‰ salinity, have often ceased their activities". Despite the consensus on the ecological importance of ecotones in a landscape (Décamps and Naiman 1990), many ecologists have never even heard of tidal freshwaters (personal observation; Barendregt and Swarth (2013))

Conclusion

Currently, no reliable data exist for the distribution or extent of tidal freshwaters in northern New England but this cursory review has generated useful preliminary information that can be built upon by future spatial analyses. Understanding where tidal freshwater wetlands occur in northern New England and their extent will be an important for predicting wetland responses to climate change scenarios. This is especially critical in the northeastern United States as increasing storm frequency and river flooding events (Armstrong et al. 2012) and accelerating sea-level rise (Hay et al. 2015) could potentially imperil these tidal freshwater areas on two fronts. This thesis will investigate the role of hydrology in structuring the benthic communities of tidal freshwater wetlands and discuss how altered hydrological conditions, as forecasted by climate change scenarios, might influence these communities. I will also discuss how these potential changes in community structure might affect how tidal freshwater wetland ecosystems function. Furthermore, this work will serve to highlight the unique ecology of tidal freshwaters and their potential utility for addressing key questions in theoretical community ecology.

Tidal freshwater wetlands

Wetlands in tidal freshwaters host a diverse suite of annual and perennial freshwater wetland plants, and associated fauna (Swarth and Kiviat 2009; Van den Bergh et al. 2009). Moreover, daily tidal height changes prevents many wetlands in tidal freshwaters from freezing in winter, providing critically important staging grounds for migratory waterfowl, nursery sites for anadromous fishes, and year-round forage for furbearers and grazing mammals (Swarth and Kiviat 2009). Furthermore, tidal freshwater wetlands (TFWs) provide vital ecosystem services for coastal communities, such as supporting pollinators, water purification and wastewater treatment, and the sequestration of nutrients, heavy metals, and carbon (Simpson et al. 1983).

Our understanding of tidal freshwater wetlands (TFWs) as an ecosystem type in North America has been synthesized several times in the last 50 years, notably in Good et al. (1978), Odum et al. (1984), Odum (1988), Mitsch and Gosselink (2000), and Barendregt et al. (2009a). Despite these syntheses, we still have a poor understanding of the distribution and extent of TFWs in North America, and no systematic spatial surveys or predictive analyses have been conducted.

TFWs can be found on all North American coastal areas except along the Arctic Ocean coastline (Hall 2009). Odum et al. (1984) were the first to attempt to estimate the total acreage of TFWs by state, and this treatise is still the main reference for their distribution and extent in North America. Odum et al. (1984) stated that TFWs are most common along the eastern U.S. seaboard from Florida to southern New England TFWs and provided estimates of their coverage for each state. Additionally, extensive TFWs can be found on the large river systems of the Sacramento-San Joaquin and Columbia on the west coast (Barendregt and Swarth 2013), and in the Mississippi tidal deltas on the Gulf Coast (Mitsch and Gosselink 2000). It is likely that the coverage of TFW in Alaska is greater than in the contiguous United States combined, but there are no reliable

estimates of their total extent (Hall 2009). The occurrence and ecological significance of TFWs has been noted across North America—it is surprising then that their total extent and distribution is still relatively unknown.

Tidal freshwater wetlands in northern New England

What information we do have on the tidal freshwater portions of estuaries and their wetlands in New England comes from data reported tangentially in studies with a different primary focus (i.e. not wetlands), or from anecdotal sources. Jury et al. (1994), reporting on data collected during the National Oceanographic and Atmospheric Administration's (NOAA) Estuarine Living Marine Resources project, state that tidal freshwater *conditions* were observed in 13 estuaries in northern New England, from Passamaquoddy Bay, ME to the Merrimack River, MA, (Table 1.2) but noted that the majority of the tidal freshwater areas were small with little wetland coverage. Odum et al. (1984) had no data for Maine nor New Hampshire but reported an estimate of 400 ha of TFW for Massachusetts (on the North and Merrimack Rivers). Leck and Crain (2009) published revised estimates for northeastern states in the U.S. (MA 419 ha; RI 43 ha; CT 1409 ha) and provided the first estimates for the extent of TFW in Maine (990 ha) and New Hampshire (~20 ha), but admit that these estimates are from anecdotal sources. Leck et al. (2009) who included data from Field et al. (1991) give a total estimate of 1295 ha of TFW for all five coastal New England states. Our lack of understanding of the extent of TFWs in New England is perhaps perfectly exemplified by these wildly different estimates from two studies with the same lead author, published in the same volume (Leck and Crain 2009 and Leck et al 2009)!

Table 1.2. Summary of occurrence data for tidal freshwater portions of some New England estuaries. Remarks in quotations are taken directly from Jury et al. (1994). Linear distances in parentheses are rough estimates made on the descriptions given by Jury et al. (1994) except for Penobscot Bay/River, where additional information was taken from Weitkamp et al. (2014) and Albert (2008).

State/Estuary	Tidal freshwater extent
Maine	
Passamaquoddy Bay	"present"
Englishman/Machias Bays	"present"
Narraguagus Bay	"present"
Blue Hill Bay	"present"
Penobscot Bay/River	from South Brewer to Veazie Dam (~16 km)
Muscongus Bay	"present"
Damariscotta River	"quite small"
Sheepscot River	"from Head Tide Village to Bailey Pt." (~24 km)
Kennebec/Androscoggin Rivers	"from Chops Pt. to Augusta Dam" (~39 km)
Casco Bay	"present"
Saco Bay	"present"
New Hampshire	
Great Bay	"present"
Massachusetts	
Merrimack River	"from Haverhill to Pow Pow River" (~10 km)

Tidal freshwater wetlands of Maine

In Maine, TFWs can be found in the Kennebec river estuary, in Merrymeeting Bay (Köster et al. 2007); in the upper reaches of the Saco River estuary (Feurt and Morgan 2015); and fringing the Penobscot River from Veazie to Brewer (personal observation). Merrymeeting Bay is the confluence of the Kennebec and five other rivers that collectively drain one third of Maine's water and is the largest tidal freshwater ecosystem north of the Chesapeake Bay region, with an area of over 4000 hectares, much of which is vegetated (Lichter et al. 2006).

The TFWs of Merrymeeting Bay are of prime conservation interest as they provide the largest staging ground in the northeast for migratory waterfowl; the only area of nursery habitat for all of Maine's 10 anadromous fishes, including the federally endangered shortnose sturgeon (*Acipenser brevirostrum*); and support a highly diverse assemblage of freshwater plant species,

many being federally or globally rare or endangered (Lichter et al. 2006). Swan Island, a National Wildlife Management Area in northern reaches of Merrymeeting Bay was where data for the following two chapters (Chapters Two and Three) were collected.

CHAPTER 2:

ZONATION AND DIVERSITY PATTERNS OF BENTHIC COMMUNITIES IN TIDAL FRESHWATER WETLANDS

<u>Introduction</u>

A central tenet of community ecology is that species diversity and community organization are governed by the tradeoffs that species face between gradients of environmental and biological selection pressures (Kneitel and Chase 2004; Violle et al. 2010). Tradeoffs occur when the traits that increase a taxon's fitness along one axis of stress (e.g. herbivory or predation pressure) negatively impact fitness along another axis (e.g. shade tolerance or drought resistance) (Lubchenco 1980; Schiesari et al. 2006). These tradeoffs are key for determining a taxon's persistence in a community because traits that allow a species to persist in one habitat may exclude it from another with different conditions. Tradeoffs promote speciation and maintain diversity patterns along habitat gradients in almost all ecological systems (Connell 1961; McPeek 1996; Kraft et al. 2008), especially those where there is a strong, sustained environmental selection pressure exerted on a community that results in species with specialized functional or life history traits (Stearns 1976). However, we know little about what happens when the trade-offs that promote and structure diversity break down or are reconfigured by novel environments or species interactions that are outwith the evolutionary history of a community.

In non-tidal freshwaters, tradeoffs structure community membership and diversity patterns along gradients of habitat permanence and predation pressure (Figure 2.1). Small ephemeral ponds that dry frequently are physiologically harsh environments that do not support large-bodied top predators (Wiggins et al. 1980; Vanschoenwinkel et al. 2013); abiotic stress therefore drives

community structure and species traits in temporary freshwaters. Larger ponds or lakes that do not dry up are more likely to support top predators, which exert a strong selective pressure on lower trophic levels and supplant environmental variability as the main driver of community structure. This tradeoff between habitat permanence and predation pressure is the key driver of community structure and function in freshwaters (Batzer and Wissinger 1996; Wellborn et al. 1996; Schriever 2015) and has led to adaptive radiation (within families and genera) to fill vacant niches along the gradient (Wellborn et al. 1996; Stoks and McPeek 2003a; Wissinger et al. 2006).
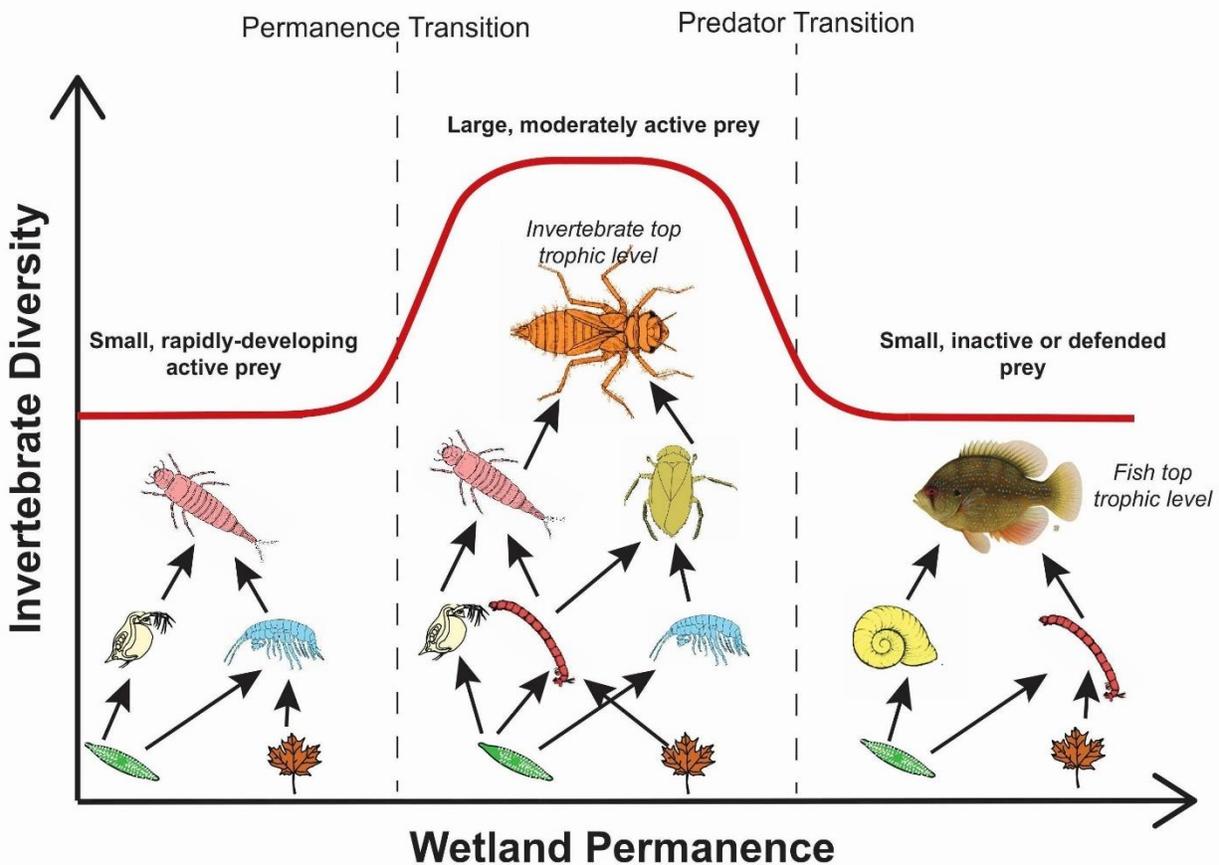
Figure 2.1. Hypothetical relationship between freshwater wetland permanence and invertebrate community structure. When wetland permanence is low (shallow waterbodies that dry frequently and/or unpredictably) then invertebrate community structure is governed mainly by physiological tolerances to harsh abiotic conditions. As habitat permanence increases and physiological stressors relax, larger predatory invertebrates are able to persist in the community. Once habitats are sufficiently permanent to allow fish to colonize, predation pressure—a biotic driver supplants abiotic stress as the main driver of invertebrate community structure. This idea is modified after Wellborn et al. (1996).

In contrast to most freshwater systems, tidal freshwaters experience considerable water-level fluctuations daily and seasonally and are important forage areas for predatory fish (Rozas and Odum 1987; McIvor and Odum 1988; Nellis et al. 2007). Because fish can move with the tides, predation pressure in tidal freshwaters is consistently high, despite high environmental variability among zones of different tidal heights and the desiccation stress generated by twice-daily fluctuations in water level. Moreover, tidal freshwaters are a geologically transient habitat type, with coring dates indicating these habitats are typically less than 5,000 years old (Pasternack 2009), likely because of variable sea-level coupled with the unique geological features than promote the development of tidal freshwater zones. Thus, tidal freshwaters are unlikely to have exerted a consistent selection pressure on communities. The tradeoffs associated with key drivers of community structure – desiccation risk and fish predation – are therefore decoupled and novel compared with the evolutionary history of the vast majority of freshwater colonists in the landscape. Understanding how communities are structured in tidal freshwaters could shed light on how communities might organize in novel ecosystems, or when the main drivers of community structure are altered or reorganized; for example, through climate-driven changes in species' ranges (Alexander et al. 2016) or changes in the frequency or timing of natural disturbance regimes (Turner 2010).

Current understanding

Despite the unique ecology of tidal freshwaters and their potential to illuminate the tradeoffs that structure freshwater communities, our understanding of invertebrate communities in North America tidal freshwaters is sorely lacking. Of the combined 930 pages of the aforementioned five major syntheses of tidal freshwater ecology (Good et al. 1978; Odum et al. 1984; Odum 1988; Mitsch and Gosselink 2000; Barendregt et al. 2009a), invertebrate communities

are discussed on a total of 5 pages. Additionally, a recent international synthesis of the ecology of invertebrates in freshwater wetlands (Batzer and Boix 2016), which included many lesser-known habitat types, did not include any information on the invertebrates of tidal freshwater wetlands, hereafter TFWs.

Invertebrates in tidal freshwaters have been studied in Europe for almost a century (Hentschel 1923; Milne 1939; Caspers 1948). Hentschel (1923) concluded that tidal freshwaters represented a distinct biotope in the Elbe estuary, with a fauna that differed from non-tidal reaches upriver and more saline reaches downstream, and suggested that community structure was dictated by the rapid fluctuations in environmental conditions that accompany changes in tidal height (immersion, desiccation, current direction, temperature). More recent efforts have synthesized understanding of how these invertebrate communities could be structured, with some consensus that the distinct biotope observed in tidal freshwaters results from a combination of increased water residence time, changing flow direction, and high turbidity (Meire and Vincx 1993; McLusky 1994).

Research into the benthos of North American tidal freshwaters is more nascent. Yozzo and Diaz (1999) provide the only available dedicated review of the scant information on the ecology of North American tidal freshwater invertebrate communities. Yozzo and Diaz (1999) assert that, while the diversity of vascular plants in tidal freshwater wetlands is the highest of any wetland type, invertebrate communities are species depauperate when compared to non-tidal freshwaters or downstream saline tidal areas— the unconsolidated sediments of tidal freshwaters may provide a less complex habitat type than those found in non-tidal river reaches or estuaries, which typically have larger average substrate particle sizes. The invertebrate communities of tidal freshwaters are

comprised mostly of freshwater taxa with a few brackish taxa that can persist under low salinity conditions (Yozzo and Diaz 1999).

Most data reviewed by Yozzo and Diaz (1999) came from two main river systems, the James River, VA and the Hudson River, NY and date from the 1970's and 1980's. Those investigations all took a similar approach to sampling communities, either using a benthic grab (e.g. Ponar sampler) from a boat in subtidal areas, or by coring intertidal sediments by hand. The apparent depauperate nature of benthic communities in tidal freshwaters may be due to sampling artefacts common to many previous studies. First, as tidal freshwaters are most likely found in areas that are heavily populated (Barendregt et al. 2009a), their benthic communities are likely constrained by waterbody impairment caused by human activities. This would be especially true for the James and Hudson Rivers which are in very densely populated areas and received heavy pollutant loads before the Clean Water Act of 1972 (Dauer 1993; Feng et al. 1998). Second, many previous studies have focused on the subtidal or intertidal mudflat areas of tidal freshwaters, where benthic habitat complexity is relatively low. These unvegetated areas are more likely to have loose, unconsolidated sediments that would exclude many invertebrate taxa. Vegetation complexity has been shown to have a positive relationship with invertebrate richness in non-tidal and tidal waters alike (Gilinsky 1984; Orth et al. 1984; Hornung and Foote 2006), by providing forage and refugia from predation. Third, the sampling devices used in previous studies could underrepresent larger-bodied, mobile taxa that may not be collected by benthic grabs or hand corers that sample a small area, or may perform poorly in vegetated or rockier intertidal habitats (Elliott and Drake 1981).

Alternatively, tidal freshwaters, in the absence of anthropogenic influence, may represent a distinct biotope because the tradeoffs that generated and structured the regional species pool (freshwater taxa from non-tidal rivers, ponds, lakes etc.) are arranged differently in tidal

freshwaters from the evolutionary history of the taxa that could potentially colonize and persist in them. The depauperate nature of tidal freshwaters could result from compounding pressures of abiotic stress (desiccation during low tide) and high predation during flood tide. For a member of the benthos, as one stressor is relaxed (desiccation), another is levied (fish predation) as the tide reinundates exposed sediment. Ultimately, benthic taxa in tidal freshwaters may experience limited opportunities for low risk-foraging. The benthos of tidal freshwaters may therefore be dominated by generalist taxa, as the tradeoffs that favor specialists in non-tidal freshwaters (Stoks and McPeek 2003b; Wissinger et al. 2006) are broken down.

This study utilized multiple sampling methods to characterize the benthic communities of vegetated tidal freshwater wetlands in a relatively unimpacted and rural river, and the communities of nearby non-tidal freshwater wetlands of varying hydrology. By controlling for the potential biases of previous studies, this work investigated how the benthos of tidal freshwater wetlands may be structured across a gradient of desiccation stress (tidal height) with varying (but high) levels of predation. The expectation was that the benthic communities of tidal freshwaters would be dominated by a subset of the regional fauna found in non-tidal freshwater habitats, and moreover, that the fauna of tidal freshwaters would be dominated by generalists, due to compounding selection filters. Additionally, it was expected that the benthos of tidal freshwater wetlands would exhibit some level of community zonation or differentiation, (cf. rocky intertidal: Lubchenco (1980); Menge et al. (1986)), reflecting the gradients of abiotic and biological conditions associated with changes in tidal height.

Methods

Field study site

Swan Island (44° 3'55" N, 69°47'41" W) is an island in the upper Kennebec estuary, in Sagadahoc County, Maine (Figure 2.2) and forms the majority of the 817 hectare Steve Powell Wildlife Management Area managed by the Maine Department of Inland Fisheries and Wildlife (MDIFW). The island is ~6 km long and 1.25 km wide, and is surrounded by ~200 hectares of freshwater tidal flats (Maine Department of Inland Fisheries and Wildlife 2015). These flats are vegetated seasonally, and are typically dominated by wild rice (*Zizania palustris*), three-square bulrush (*Schoenoplectus pungens*) and pickerelweed (*Pontederia cordata*). The island experiences lunar tidal fluctuations of between 1.5 m and 2.1 m in height, which vary seasonally with river discharge. The limit of saline intrusion during seasonal lowest riverine flows (September) is just downstream of the most southerly point on the island (Kistner and Pettigrew 2001) which means that the salinity of the tides experienced by the island never exceeds 0.5‰ and can thus be considered truly freshwater (McLusky 1993). There are eight man-made ponds on the island, some of which have been stocked with brown trout (*Salmo trutta*) (Kennedy et al. 2012), as well as numerous natural seasonal wetlands and vernal pools. The island has not been inhabited since 1936 (Kennedy et al. 2012), and receives around 2000 visitors per year, so with the exception of yearly management of the grasslands that surround the man-made ponds there are few ongoing human impacts (J. Pratte, *pers. comm.*).
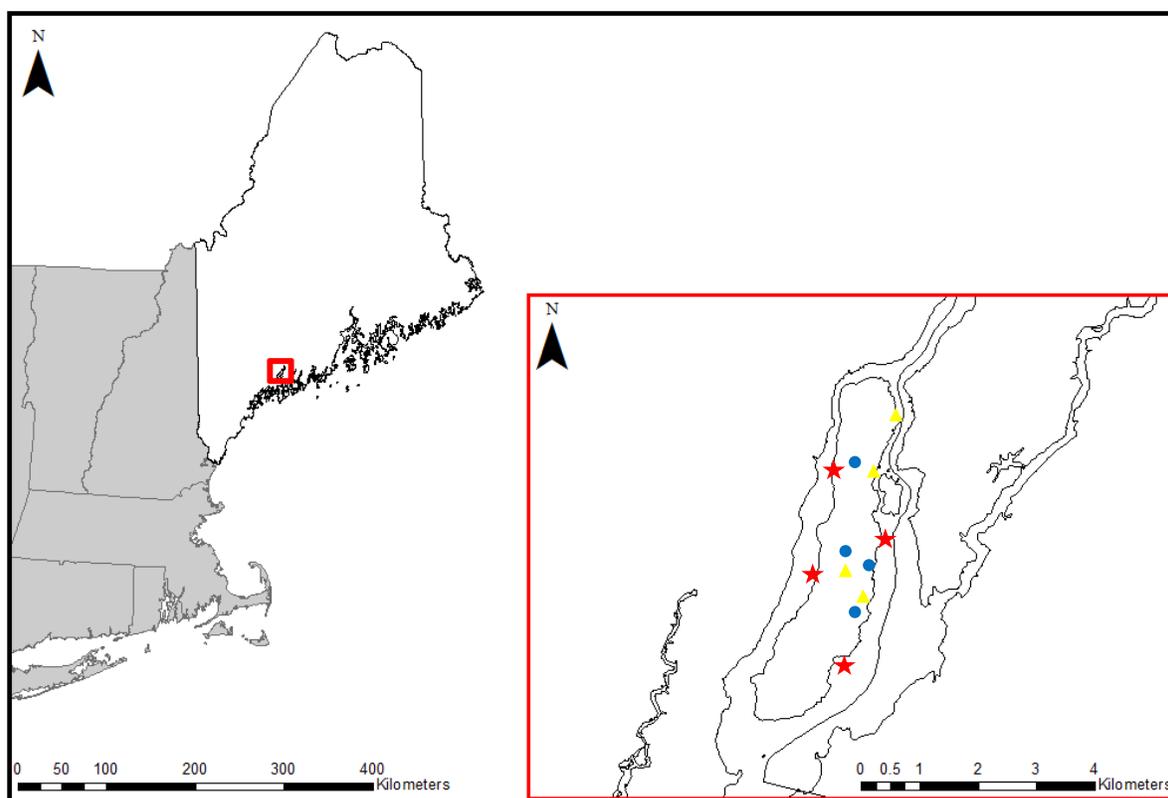
Figure 2.2. Location of Swan Island on the coast of Maine and sampling sites. Red stars denote freshwater tidal sampling locations, blue circles denote permanent ponds, and yellow triangles denote temporary wetlands.

Sampling design

Four tidal sites, four ponds deemed hydrologically stable ("permanent"), and four wetlands that experience significant seasonal dry-down ("temporary") were chosen for sampling sites. Inland sites were subjectively assigned to either group based on local knowledge (J. Pratte, MDIFW, pers. comm.) and by looking at historical aerial photography to see which sites varied greatly in their surface area seasonally (i.e. suggestive of significant dry-down). Sampling occurred at three points along a transect of tidal height with zones decreasing in their duration of inundation (low marsh, mid marsh, and high marsh) (see Plate 2.1), and in the littoral zones of the inland sites. Transect length differed at each tidal site (range: 82 – 217 m) due to differences in slope, and were measured as the distance between the mean high and low water lines (assessed visually). Tidal

areas with lower height gradients (slope) had longer transects to ensure that points sampled along the transects experienced similar hydrological conditions (i.e. were exposed/inundated for similar lengths of time). Sampling occurred within a one-week window at three time-points during the summer of 2015 (May, June, and August) to account for seasonal changes in the environment and benthic invertebrate communities.
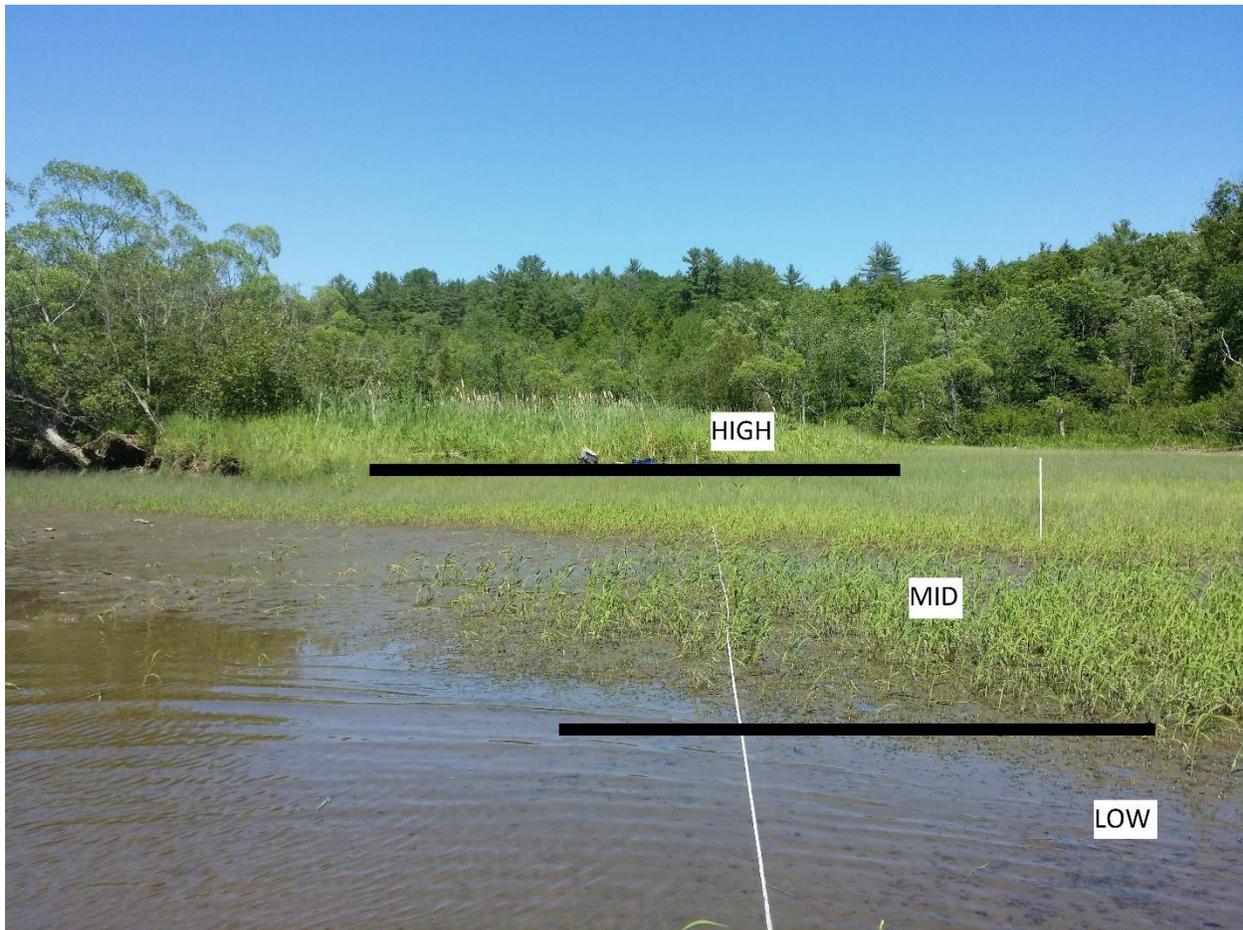
Plate 2.1. Photograph of typical sampling transect in a tidal freshwater wetland on Swan Island, Maine. Black bars highlight different tidal heights (note changes in vegetation).

Physicochemical sampling

The location of each sampling site was recorded to the nearest 5 m using an Etrex Waterproof Hiking GPS Unit (Garmin Ltd., Schaffhausen, Switzerland). Water pH, specific

conductance, and dissolved oxygen concentration were measured at each site in June and August using a Hach HQ40d portable multi-parameter Meter (Hach Company, Loveland, Colorado), which was calibrated before each sampling occasion. Temperature and light intensity data were recorded at 30 minute intervals during the season using HOBO pendant dataloggers (Onset Computer Corporation, Bourne, Massachusetts) attached to a staging post at the sediment-water interface. These dataloggers were deployed at both high and low tidal heights in tidal sites. Staging posts were also installed in inland sites to record water height changes between sampling occasions.

Biological sampling

Benthic communities of tidal and non-tidal habitats were characterized by sweeping four replicate 0.33 m^2 plots with a D-frame net (1 mm mesh-size) for 30 seconds to collect large-bodied macroinvertebrates. A modified stovepipe sampler (⌀ 0.01 m section of PVC pipe) was pushed into the substrate next to each area swept by the D-frame net and an aquarium net (0.35 mm mesh-size) was repeatedly swept inside the stovepipe for 30 seconds to collect smaller-bodied invertebrates. These complementary sampling methods enabled the detection of rare large-bodied macroinvertebrates (e.g. leptocerid caddisflies, gomphid dragonflies) and the quantification of small-bodied, highly numerous taxa (e.g. caenid mayflies, gammarid amphipods), respectively (method following Wissinger et al. (2009)). Samples were collected on the incoming tide and always at a water depth of 10 cm. Samples were stored in 95% ethyl alcohol for transport back to the lab.

Laboratory sample processing

Benthic macroinvertebrate samples were washed over a 500 µm Endecott sieve, transferred to a white picking tray, and all invertebrates were removed and identified to the lowest possible taxonomic level (typically genus) using Peckarsky et al. (1990), Merritt et al. (2008) and other taxon-specific keys, where appropriate. Invertebrates were placed in a petri dish with graph paper for scale and photographed using a tripod-mounted Canon EOS Rebel DSLR camera (Canon Inc., Tokyo, Japan). Adobe Acrobat X Pro (Adobe Systems, San Jose, California) was used to enumerate and measure the body-lengths of every individual using a method that followed Galatowitsch and McIntosh (2016a). Molluscs were not included in analyses due to difficulties associated with identification and determining accurate estimates of their abundances and biomass. For the remainder of this thesis, invertebrates will refer to the non-molluscan component of the benthos.

Data analysis

Invertebrate abundances for a given site and date were pooled across the four replicate samples (or three on the four occasions with a missing sample) and converted to densities (number of individuals per m^2) by dividing by the total area sampled. Invertebrate density data were log transformed before analysis.

A variety of diversity indices were calculated to characterize the invertebrate community. Taxonomic richness, simply the number of unique taxa found at each site, was the simplest measurement of diversity calculated, but is highly dependent on sampling effort and number of individuals collected (Magurran 2004). Margarlef's Index (Equation 2.1) was used *in lieu* of taxonomic richness to aid in site comparison of richness as invertebrate abundances often varied greatly between sites.

$$D_{MG} = \frac{S-1}{ln\ N} \qquad\qquad \textbf{(equation 2.1)}$$

where **S** = number of unique taxa; **N** = number of individuals in sample.

Shannon's Index (H') is one of the most commonly calculated diversity statistics for community data, but is often difficult to interpret and confounds two important aspects of diversity, taxonomic richness and evenness (Magurran 2004). However, Shannon evenness, or Pielou's J' was derived from Shannon's H' to compare community structure evenness (Equation 2.2).

$$J' = \frac{H'}{H_{max}} = \frac{H'}{ln\ S} \qquad\qquad \textbf{(equation 2.2)}$$

Where **H'** = observed Shannon diversity; **H_{max}** = Shannon diversity if all taxa had equal abundances; **S** = number of unique taxa.

These univariate responses of Log invertebrate density and untransformed values for the normally-distributed Margalef's index and evenness were analyzed with two-way analyses of variance (ANOVAs) in which habitat and month were treated as fixed effects and models included the interaction term (habitat x month). Tukey's Honest Significance Difference (HSD) test was performed post-hoc to determine significant differences among treatment levels. Data were analyzed using R (R Core Team 2016)

Beta diversity and community dissimilarity

Beta diversity, simply stated, describes the differences in diversity between two or more samples in time or space (Magurran 2004; Anderson et al. 2011). Jaccard's index (Equation 2.3), which assesses community similarity based on taxon presence-absence; and Bray-Curtis

dissimilarity index (Equation 2.3) which incorporates relative abundances of taxa (Magurran 2004) were used to characterize beta diversity between sites. A presence-absence transformation was applied to community data before calculating Jaccard's index. Invertebrate density data were square root transformed for Bray-Curtis calculations to dampen the effect of hyper-abundant taxa.

$$C_J = \frac{a}{a+b+c}$$ (equation 2.3)

Where a = number of taxa in common between site A and site B; b = number of unique taxa at site A; c = number of unique taxa at site B.

$$C_N = 1 - \frac{2jN}{(N_a - N_{b)}}$$ (equation 2.4)

Where N_a = total number of individuals at site A; N_b = total number of individuals at site B;

$2jN$ = sum of the lower two abundances for taxa found at both site A and site B.

The dissimilarity of communities based on these indices was visualized with non-metric multidimensional scaling plots (NMDS). To test whether communities at different habitats are significantly different from each other in multivariate space, a permutational multivariate analysis of variance (PERMANOVA) was performed using generated matrices of dissimilarity values. An assumption of PERMANOVA is that multivariate dispersion is somewhat homogeneous between groups, although PERMANOVA is generally robust to heterogeneity of dispersions (Anderson and Walsh 2013). Homogeneity of dispersions was tested using Marti Anderson's PERMDISP procedure to aid in interpretation of PERMANOVA results (Anderson et al. 2006).

Multivariate dispersion (the Euclidean distance to the centroid of a group of observations of communities in multivariate space) was also used as a measure of beta diversity; namely, how variable community structure was at a site (Anderson et al. 2006). The two dissimilarity measures

(Jaccard's and Bray-Curtis) used in this study produce negative eigenvalues in ordination space which prevents calculation of the true centroid, and so a correction (Cailliez method) was applied when testing for multivariate dispersion [*see* Legendre and Anderson (1999) for details]. Tukey's HSD was used post-hoc for pairwise comparisons of multivariate dispersion (Oksanen et al. 2016).

Diversity index calculation and multivariate analyses were performed in R using the package "vegan" (Oksanen et al. 2016).

Results

Sites were identified and selected for this study in April during the spring freshet. This meant that one site that was classified as a temporary inland site was in fact in the floodplain of the Kennebec River and was tidally influenced. Data from that site were not included in analyses. Additionally, one of the remaining temporary sites had dried completely by August and could not be sampled.

Physicochemical variables

The greatest variation in daily temperature was experienced by high tidal sites where temperatures often surpassed 42°C and could rapidly fall by as much as 32°C in a single day (Appendix A.), likely due to a combination of reinundation and time of day. Low tidal sites were less warm (infrequently reaching 35°C), but still experienced rapid fluctuations in temperature. Inland permanent and temporary sites experienced a similar range of daily temperatures as low tidal sites, but appeared to change more gradually. Ponds that experienced significant dry down experienced more rapid increases in temperature later in the season.

Freshwater habitats on and around Swan Island ranged in pH from 5.15 to 7.64 and conductivity values fell between 16.5 and 73.5 $\mu S.cm^{-1}$ (Appendix B.). Observed water chemistry

conditions were within the normal ranges reported in state biomonitoring data from nearby wetlands on and near the Kennebec River (Maine Department of Environmental Protection 2016).

Taxonomic composition

A total of 27,383 individual invertebrates were enumerated in this study, representing 107 taxa, 62 of which were identified to genus (Appendices C and D). Of these 107 taxa, almost a quarter (24.3%) were only found in tidal freshwaters, nine (8.41%) were restricted to permanent inland freshwaters, and eight (7.48%) were unique to temporary inland freshwaters. Of the 26 taxa found only in tidal freshwaters, ten were unique to high marsh sites, and five and three taxa were found only at mid and low marshes, respectively. Almost 60% of taxa were found at more than one habitat (Figure 2.3). A total of 70 taxa were found at permanent inland sites, 68 taxa were ound at temporary inland sites, and 65 taxa were found in tidal freshwaters (across all tidal heights).
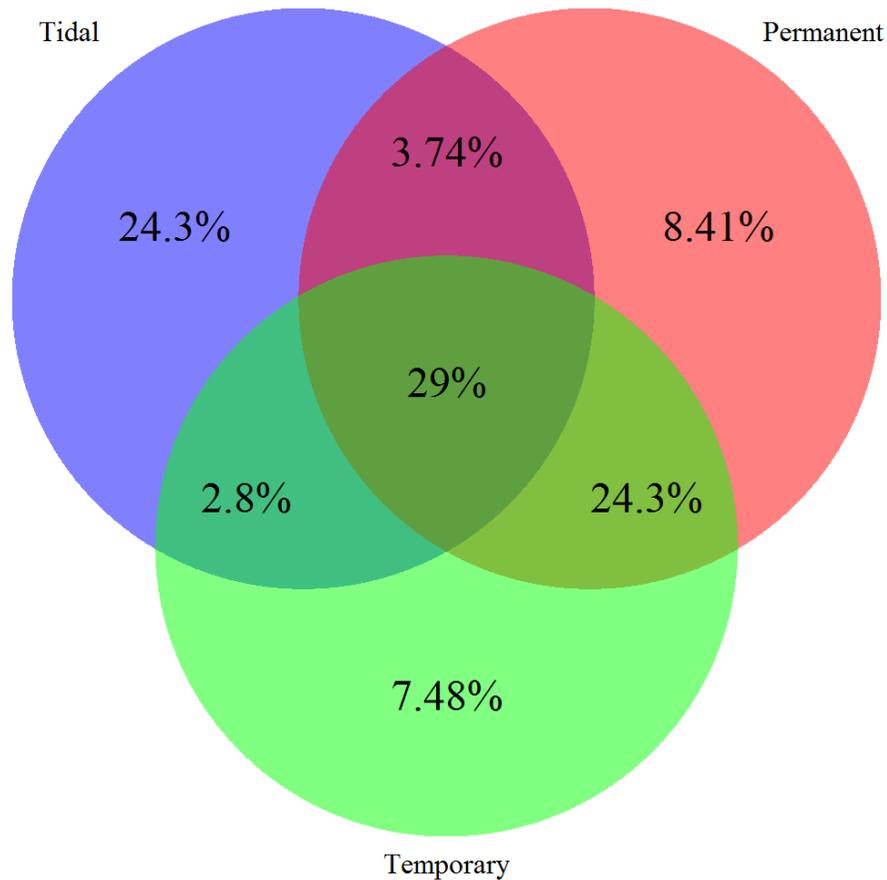
Figure 2.3. Taxonomic overlap of benthic communities of tidal, non-tidal permanent, and non-tidal temporary freshwater habitats on Swan Island, Maine. A total of 107 taxa were found in this study.

Low—Communities at low tidal sites were numerically dominated by chironomid midge larvae, oligochaetes, and dipteran pupae—most of which were chironomids. Additionally, chironomids were one of the top three most abundant taxa found in 66% and 83% of samples taken from high and mid tidal sites, respectively. Taxa that were found only at low tidal sites included taxa that are generally considered lotic, such as the hydropsychid caddisfly *Cheumatopsyche* sp. and the

gomphid dragonfly *Stylurus spiniceps*, the latter being a new species record for Sagadahoc County, Maine.

Mid—The amphipods *Gammarus* and *Hyalella*, corixid water boatmen, and the mayfly *Caenis* were all abundant at mid tidal sites. Nematodes and oligochaetes also ranked among the most abundant taxa.

High—High corixid density was also observed at high tidal sites, which may suggest that these mobile predators follow the incoming tide. Other numerically dominant taxa were ceratopogonid midges (in particular *Atrichopogon), Caenis*, and the beetles *Haliplus* and *Berosus.*

Tidal sites also supported a unique assemblage of beetles that was not seen in inland freshwaters. The beetle fauna of the tidal freshwater sites included lotic taxa, such as elmids (four genera) and many taxa that are considered "sub-aquatic" or littoral specialists, including the families Lampyridae (fireflies), Heteroceridae (variegated mud-loving beetles), Staphylinidae (rove beetles), and Tenebrionidae (darkling beetles), which were all found at high tidal heights.

Inland—Odonates from families Coenagrionidae, Lestidae, and Libellulidae were the most numerically common invertebrates found in inland sites, and these taxa were rare or absent from tidal sites. Like tidal sites, chironomids and *Caenis* were also among the most abundant taxa inland.

Univariate responses

Mean invertebrate density differed significantly between habitats but did not vary significantly over the season, nor was there any interaction between habitat and month (Table 2.1). Invertebrate density was generally lower in tidal sites than non-tidal sites, and within tidal sites, high marshes had fewer individuals per m^2 than sites at lower tidal heights (Figure 2.4).

Table 2.1. Statistical summary of effects of habitat type (low, mid, and high tidal, non-tidal permanent, non-tidal temporary) and month and their interaction on benthic invertebrate communities. Bold denotes significance at 0.05 level.

	Invertebrate Density[a]			Margalef Diversity[b]			Community Evenness[c]			Multivariate Dispersion			Community dissimilarity			
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F**	*P*	*df*	*F**	*P*	*R²*
Habitat	**4, 41**	**9.72**	**< 0.001**	**4, 41**	**17.13**	**< 0.001**	**4, 41**	**6.90**	**< 0.001**	**4, 51**	**8.55**	**0.002**	**4, 55**	**7.97**	**0.001**	**0.37**
Month	2, 41	1.18	0.31	2, 41	0.24	0.78	2, 41	0.46	0.63	2, 53	2.15	0.129	**1, 55**	**3.19**	**0.001**	**0.04**
H x M	8, 41	0.71	0.67	8, 41	0.19	0.99	8, 41	1.96	0.07	-	-	-	4, 55	1.16	0.21	0.05

a Model R² = 0.37
b Model R² = 0.51
c Model R² = 0.35
* Pseudo-F (999 permutations)

Even when differences in total invertebrate density were corrected for, taxon richness was significantly lower in tidal habitats than non-tidal (Table 2.1; Figure 2.4). Margalef diversity was lowest in low tidal sites and was significantly lower than at high tidal sites.
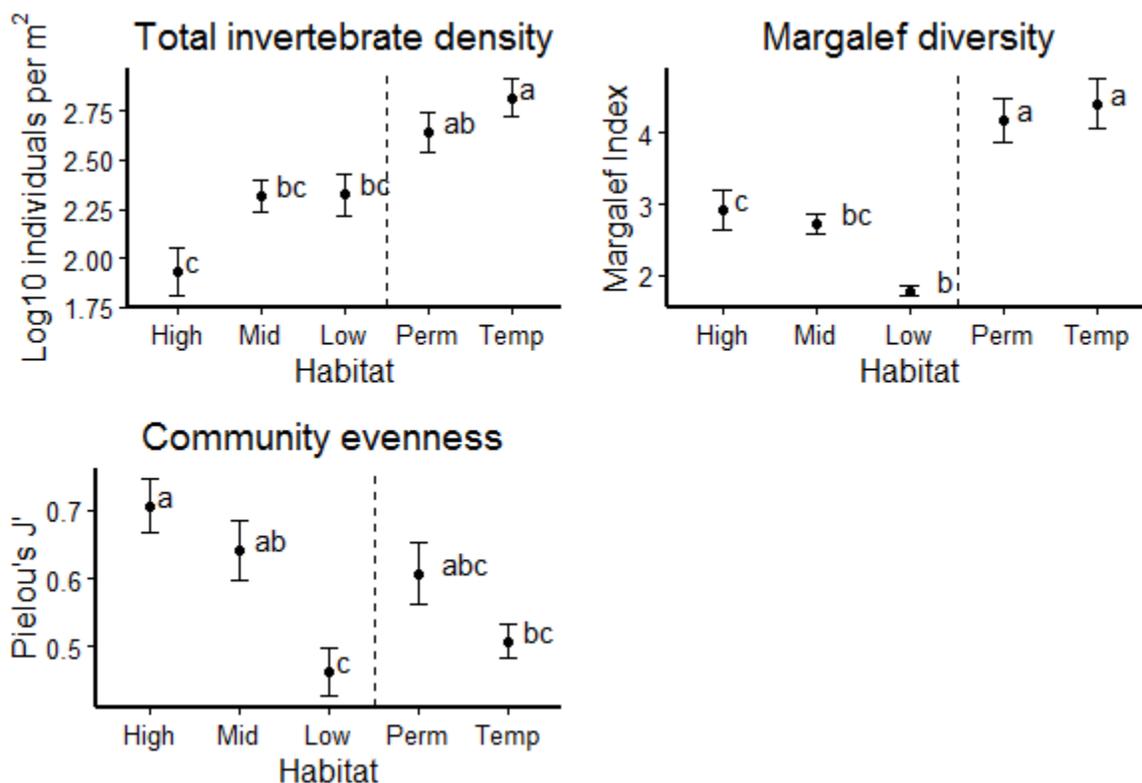
Figure 2.4. Invertebrate density, diversity, and community evenness of benthic invertebrates in tidal and non-tidal freshwater habitats on Swan Island, Maine. "High", "Mid", and "Low" refer to tidal height in tidal sites; "Perm" and "Temp" refer to permanent and temporary non-tidal freshwaters, respectively. Means are plotted with standard errors. Lowercase letters refer to significant post-hoc pairwise comparisons (Tukey's HSD method).

Additionally, community evenness was significantly lower at low tidal sites (driven by high chironomid densities) than sites at higher tidal heights (Figure 2.4). The greatest community evenness was observed at high tidal sites (Figure 2.4). While month was not found to have a significant influence on community evenness, the interaction term was marginally not significant (Table 2.1).

Multivariate responses

Near identical trends were observed when Jaccard's or Bray-Curtis indices were used in analyses, indicating patterns of taxa occupancy mirrored those of relative abundance. The following results are reported for Bray-Curtis dissimilarities. A two-way PERMANOVA found that invertebrate communities were significantly different between habitats and months, although the latter explained little of the variance (4%) and there was no significant interaction between habitat or month (Table 2.1). NMDS plots (Figure 2.5) suggest that tidal habitats became more differentiated from each other later in the summer, and that the two inland sites converged in their community structure.

Multivariate dispersion (within-height beta diversity) was significantly different across habitat types but not between months (Table 2.1). High tidal sites were significantly more spatially variable in community structure (larger polygons in Figure 2.5) than both lower tidal heights, as were inland sites (Figure 2.6). Although PERMDISP is unable to provide a rigorous test of two-way interactions, the NMDS plots suggest that there are some habitat-specific changes in dispersion between months (Figure 2.5). Communities at high and mid tidal heights trended towards higher variability in June than in May or August, whereas variability at low tidal sites appeared to stay relatively constant over the season.

Figure 2.5. Non-metric multidimensional scaling (NMDS) ordination plots of benthic macroinvertebrate communities based on Bray-Curtis distances in freshwater habitats of Swan Island, Maine. H = high tidal; M = mid tidal; L = low tidal; P = permanent non-tidal; T = temporary non-tidal. Stress values: May = 0.15; June = 0.17; August = 0.13.

May

June

August

Multivariate dispersion (Bray-Curtis)
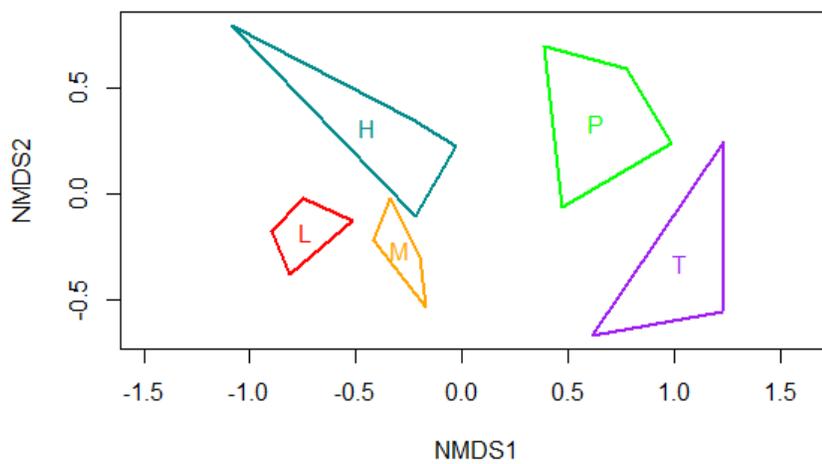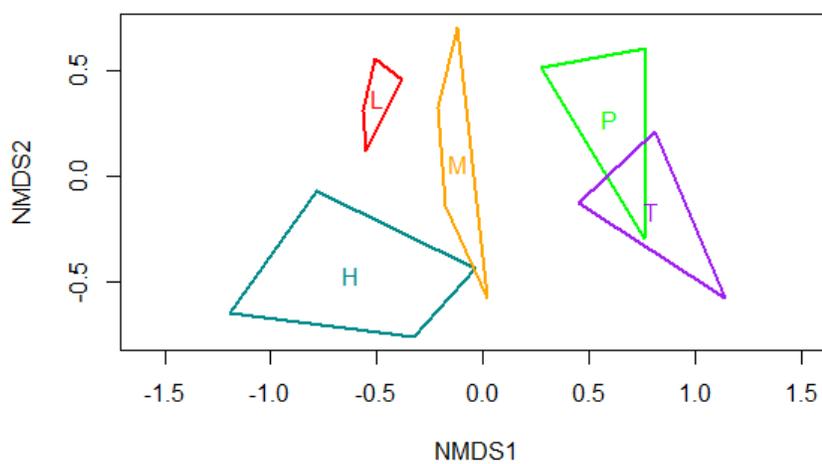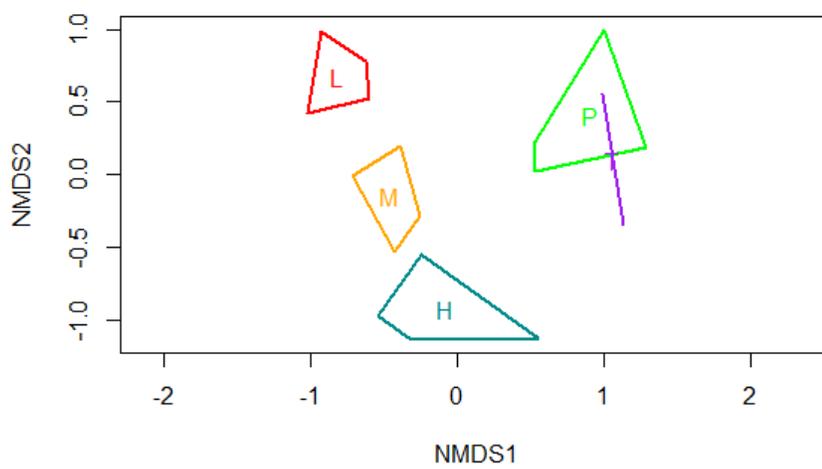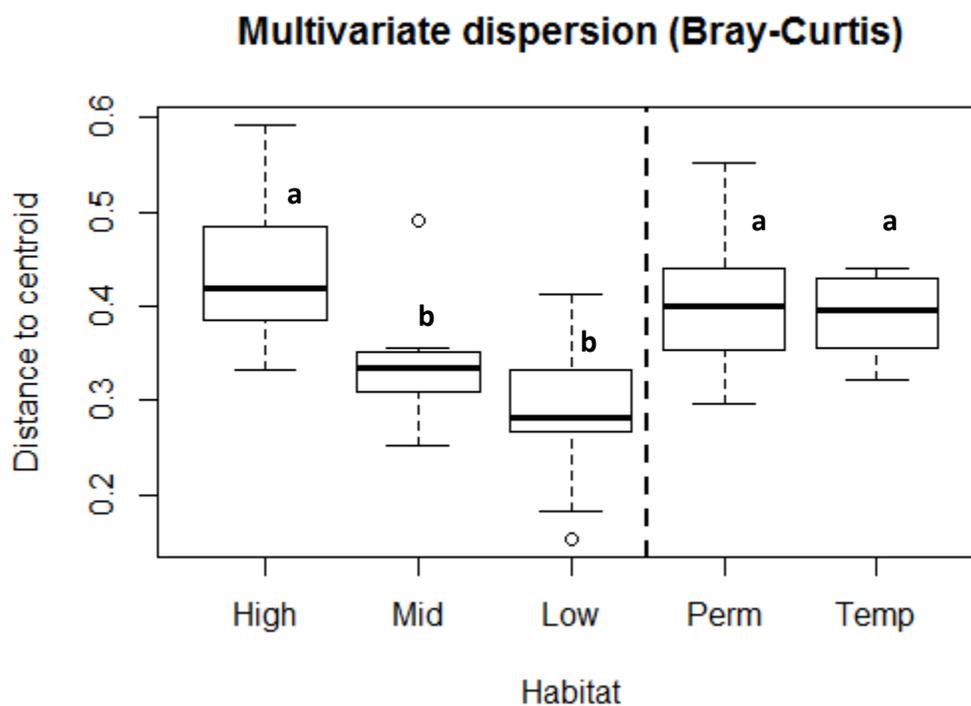
Figure 2.6. Boxplot of multivariate dispersion (distance to group centroid of multivariate space) for tidal and non-tidal freshwater habitats on Swan Island, Maine. "High", "Mid", and "Low" refer to tidal height in tidal sites; "Perm" and "Temp" refer to permanent and temporary non-tidal freshwaters, respectively. Means are plotted with standard errors. Lowercase letters refer to significant post-hoc pairwise comparisons (Tukey's HSD method).

Discussion

This study sought to investigate how benthic communities in tidal freshwater wetlands were structured across a gradient of tidal height and whether these communities were organized differently from nearby non-tidal freshwater wetlands. The expectation was that as tidal freshwater communities are mainly comprised of freshwater benthic taxa that the structure and diversity of these communities would be a less diverse subset of the fauna found at non-tidal freshwater wetlands. Additionally, as a tidal height gradient represents multiple gradients of abiotic and biological conditions regardless of salinity, I expected to observed community differentiation or zonation between different tidal heights in the tidal freshwater wetlands. While less diverse than

nearby non-tidal freshwater wetlands, the benthic communities of tidal freshwater wetlands appear to be structured differently and are not merely a subset of the regional fauna. These results are discussed below.

Community zonation in tidal freshwaters

The benthic communities of tidal freshwater wetlands are subjected to highly-predictable alternating abiotic and biological stressors. Temperatures at upper tidal heights at low tide can reach 42°C in the middle of the day and fall to around 15°C when reinundated at high tide in the night. Desiccation risk and heat stress are correlated with tidal height, much like in marine intertidal areas [e.g. Dayton (1975)]. When this physiological stressor is relaxed by reinundation during the flood tide, the benthos is then subjected to predation by foraging fishes which follow the wetting front of the incoming tide (personal observation). Predation risk is likely greater at lower tidal heights that are inundated for longer, as fish have more time available to forage (Kneib and Wagner 1994; Ellis and Bell 2008). Communities were differentiated along this gradient of tidal height. Community structure was significantly different at each tidal height sampled, and each tidal height zone supported taxa that were not found at other points on the transect (Appendix D.). Low tidal communities were less taxonomically rich, and were less even than at higher tidal heights. Chironomids and oligochaetes were numerically dominant in the low tidal areas, which is consistent with other studies into the benthos of tidal freshwaters (Ristich et al. 1977; Strayer and Smith 2001). Low tidal heights still experience daily drying for a few hours and are subjected to fish predation for the remainder of the day during the flood tide. Antón-Pardo and Armengol (2016) found that fish predation of the benthos in coastal ponds caused an increase in the dominance of a few small-bodied taxa, like chironomids. Similarly, fish predation has been shown to reduce species richness and evenness in non-tidal freshwaters (Gilinsky 1984; Chase et al.

2009). Given the importance of tidal freshwaters for migratory fishes, quantifying fish predation at different tidal heights (through fyking or seining) will be necessary to assess predation pressure.

While desiccation risk and predation risk may appear to be opposing gradients in tidal freshwaters [as they are in non-tidal freshwaters (Wellborn et al. 1996)], several of my results indicate that these stressors are compounding rather than orthogonal due to daily oscillation of wet and dry phases. Invertebrate density and richness was lower in tidal freshwaters than nearby non-tidal freshwaters. For tidal heights that are inundated for a short period of time, benthic invertebrates will have limited time available for foraging, a time period that also corresponds with the highest risk of predation. In non-tidal freshwaters, especially in hydrologically isolated water-bodies (ponds, lakes, etc.), vertebrate predators, especially fish, are subject to the same abiotic constraints as lower trophic levels [e.g. Werner and Anholt (1993); Wellborn et al. (1996); Walls et al. (2013)] and so their ability to depress invertebrate community structure is limited [but see (Greig et al. 2013)]. In tidal freshwaters, highly mobile fish predators are not subject to the same limitations as the invertebrate benthos; the connectedness of the intertidal area to the subtidal river stem means that there is always a refuge for fish to return to at low tide. Furthermore, the strength of predation effects in tidal freshwaters is likely far higher than in ponds or lakes, as fish are unlikely to experience bottom-up limitations as they have far greater areas to forage in (discussed in further detail in Chapter 3). As tidal freshwaters are connected to a much larger water body, a larger number of predators can be supported, as they can constantly move between patches. The benthos of tidal freshwater wetlands could be continually hit with wave after wave of abundant predators. In isolated non-tidal wetlands, the abundance of predators will be limited by the availability of prey that can be supported by the wetland (*sensu lato* Rosenzweig and MacArthur (1963))

Although I observed significant community differentiation among tidal habitat types, there were many taxa that were found across all tidal heights (Appendix D.). While it is possible that some patterns of species' zonation may be obscured by a coarse level of taxonomic resolution, especially in speciose groups like Chironomidae, Ceratopogonidae, Oligochaeta etc., several taxa appear to be 'hydrological generalists' that are tolerant of desiccation or predation risk associated with tidal height. Some winged taxa (like corixid water boatmen) can follow the ebb and flow of the tide whilst avoiding predation and were found at all heights. *Caenis* mayflies, *Gammarus* amphipods, and the larvae of *Haliplus* and *Dubiraphia* beetles, were also abundant at all tidal heights, but have low dispersal ability (Merritt et al. 2008) and are unlikely to move with the tide. The presence of these less-mobile taxa across the tidal gradient suggests that some generalist taxa may share some traits that allow persistence despite high abiotic and predation stress, like predator avoidance or refugium use. Invertebrate traits like these have been shown to be flexible within species along hydrological gradients in freshwaters (Galatowitsch and McIntosh 2016b), and apparently contrasting selection pressures (like desiccation risk and predation) can actually facilitate the development of specialized strategies that allow persistence of generalists across environmental gradients (Greig and Wissinger 2010). While these trait flexibilities have been observed for life-history strategies, the same idea could be true for feeding mode or other short-term adaptations. For instance, *Caenis* mayflies have operculate gills for ventilation in low oxygen environments and are benthic biofilm feeders. Here, their highly benthic nature may confer resistance to both abiotic stress and predation pressure, perhaps allowing them to persist and even forage in very shallow pools or wet areas when the tide is out. Further work is needed to discern the importance of traits that confer co-tolerance to opposing selection pressures.

While tidal freshwaters were less taxonomically diverse than non-tidal freshwaters, they did support unique species; almost a quarter of taxa observed in this study were only found in tidal freshwaters. While compounding abiotic and predation pressure may be limiting invertebrate community diversity in tidal freshwaters, taxonomic richness generally increased with increasing tidal height, and the greatest community evenness was observed at high tidal sites. High tidal freshwater wetlands may represent a 'peak' in ecotonal diversity which is commonly observed in aquatic-terrestrial transition zones (Décamps and Naiman 1990; MacKenzie et al. 2015; Tonkin et al. 2016) , as many taxa were found only at these sites. These taxa included many 'sub-aquatic' or 'littoral' specialists (*sensu* Merritt et al. (2008)) that may use these sites during the ebb tide and may experience inundation as a stressor. Few sub-aquatic or littoral taxa were collected at lower tidal heights, although it is likely that these taxa (which were mostly beetles) forage in these areas at low tide, but retreat to upland areas with the incoming tide (Barendregt 2005). Additionally, some aquatic taxa that are unable to respire atmospheric oxygen, and would therefore be susceptible to drying (for instance mayflies and caddisflies), were rare or not observed at upper tidal heights (Appendix D.). Vegetation diversity was generally much higher at these upper tidal heights (personal observation), and could reflect a greater resource base or structural habitat complexity than lower tidal heights. Perhaps given that littoral or sub-aquatic specialists were mostly found at high tidal heights, and some obligate aquatic taxa were excluded, high tidal freshwater areas should be considered as terrestrial habitats that are rarely inundated, rather than aquatic habitats that are frequently exposed (*cf.* Dell et al. (2014)).

Tidal freshwater wetland vegetation is highly dynamic, undergoing striking phenological changes over the growing season driven by high production by annual plants (Leck et al. 2009). I observed marked differences in vegetation height and density between sampling events along the

tidal height gradient (personal observation; Plate 2.2) but curiously, the invertebrate communities did not reflect these changes to any great degree. Invertebrate density, richness, nor evenness were influenced by month, nor did month interact with tidal height to influence these univariate measures of the benthos. Some signal of seasonality was detected in PERMANOVA and PERMDISP models, but explained little of the variance. Thorp et al. (1997) reported large seasonal differences in the invertebrate communities of submerged aquatic vegetation (SAV) in tidal freshwater wetlands related to phenology. David Strayer and colleagues investigated the importance of aquatic vegetation for invertebrate communities in the tidal freshwater Hudson reporting that invertebrate densities were much higher on SAV than unvegetated areas (Strayer and Malcom 2007), but that seasonal patterns of invertebrate community structure were hard to discern due to the influence of fish predation and other environmental effects (Strayer et al. 2003). While benthic communities in freshwaters can be highly seasonal, which can affect data collection and interpretation (Hawkins and Sedell 1981; Miller et al. 2008), it is likely that the strong and persistent environmental filtering of tidal hydrology and fish predation overwhelms any seasonal patterns driven by invertebrate colonization or emergence. Interestingly, Beauchard et al. (2013), in one of the few comparable studies to this thesis, found no difference in benthic community structure between unvegetated mudflats and reedbeds in tidal freshwaters over several years, and yet found that tidal freshwater communities were differentiated along a gradient of tidal height. While vegetation complexity may be correlated with tidal height, arguably it is the gradient of hydrology and associated biological conditions that is the "master variable" driving community structure in tidal freshwater wetlands.

Plate 2.2. Photo sequence of marsh phenology in tidal freshwater wetlands of Swan Island, Maine. From top: May 2015, June 2015, November 2015.

An interesting result of testing for homogeneity of dispersions (PERMDISP) was that this measure of beta-diversity was greater in high tidal communities, i.e. high tidal sites were more dissimilar to each other than sites within lower tidal heights. While the mechanisms are difficult to disentangle, this result could suggest that high freshwater tidal zones represent a highly-disturbed environment (*sensu* Myers et al. (2015)) that exerts a strong environmental filter on potential colonists that are unable to persist under highly-variable temperatures and prolonged daily drying. Chase (2007) found that drying disturbance in freshwater communities reduced beta diversity—a result potentially counter to the findings of this study. He found that a smaller subset of the regional fauna was able to persist in habitats that experience severe drying, a disturbance strong enough to override the influence of stochastic processes like colonization. By contrast, in this study, low tidal heights, which should be least affected by drying consistently had the lowest beta diversity (Figure. 2.5; Figure 2.6). However, if fish predation is considered a disturbance (*sensu* Sousa (1984)), then the low dispersion observed at low tidal sites could be explained by the findings of Chase (2007), whereby a strong environmental filter (in this case predation) homogenizes community composition by selecting for taxa that are predation-resistant and by removing rare taxa (Spiller and Schoener 1998; Shurin 2001; Chase et al. 2009; Anton-Pardo and Armengol 2014). The relative importance of deterministic and stochastic drivers of beta diversity are still relatively poorly understood (Chase and Myers 2011; Myers et al. 2015), but the results of this study suggest that fish predation may a stronger filter on the benthos than drying.

Comparison of tidal vs. non-tidal freshwater communities

Tidal freshwaters were comparatively less diverse than nearby non-tidal freshwaters, but contributed unique taxa to the regional taxa pool (Figure 2.3) and had distinct community structures (Figure 2.5). Previous studies that attest to the depauperate nature of tidal freshwater

benthic communities have made comparisons with the non-tidal river upstream (Yozzo and Diaz 1999) but few studies have compared the benthic communities of tidal freshwater wetlands and nearby inland wetlands or lentic habitats. Hansen and Castelle (1999) found that tidal freshwater wetlands, whether forested or marshy, had lower soil insect diversity than a nearby levee non-tidal marsh. The authors suggested that a combination of hydrological stress and low vegetation structure was the driver of the observed low diversity in tidal wetlands.

In this study, inland sites had higher taxonomic richness than any point on the tidal gradient. Few taxa were only found in either inland habitat type and there was considerable overlap in their invertebrate faunae. This suggests that the selection pressures, whether abiotic or biological were not that different between sites that were categorized as either "temporary" or "permanent", and these environmental gradients were not as strong as those along the transects in tidal freshwaters. This is surprising given inland sites were discrete and isolated habitat patches whereas tidal transects were along a contiguous block of habitat. Greater differentiation between inland habitat types may have been observed if more ephemeral habitat types were considered (ditches, rain-puddles etc.) or if better information on their vertebrate predators were available.

The tradeoffs that structure benthic communities in freshwaters (habitat permanence, predation, resource supply etc.) are likely arranged differently in tidal and non-tidal freshwaters. First, as mentioned previously, the potential predation pressure in tidal freshwaters is likely much higher in tidal freshwaters as fish can move with the tides and are not limited by drying or the smaller available forage space in isolated inland habitats and the associated negative feedbacks between resource depression and predator populations. Greater fish abundances, especially during the movements of migratory stages of anadromous species (Veiga et al. 2006; Sheaves et al. 2014), could mean that predation risk could be exceptionally high for a member of the benthos of tidal

freshwaters compared to a non-tidal pond or lake. Second, the risk of desiccation or thermal stress in tidal freshwaters is on a daily scale, which for non-tidal freshwaters would only similarly occur in the most ephemeral or variable of systems like rain-pools (Vanschoenwinkel et al. 2010), freshwater shore zones [reviewed in Strayer and Findlay (2010)], or in the artificial "intertidal" zones created by hydropeaking dams (Kennedy et al. 2016). In seasonally drying habitats— "temporary" in this study— hydroperiod will select for organisms that can avoid or tolerate drying, either by having high powers of mobility or expedited or periodically dormant life-history strategies (Williams 1996, 1998; Galatowitsch and McIntosh 2016a).

Interestingly, most taxa that were not observed in tidal freshwaters were adult beetles and hemipterans, which have high tolerances for desiccation (Pallarés et al. 2016) and are highly mobile, but their larger body size may make them more sensitive to fish predation (Blumenshine et al. 2000; Zimmer et al. 2001; Antón-Pardo and Armengol 2016). While speculative, adult dytiscid beetles were only found, and corixid water boatmen were found in greatest numbers, in the shallower waters of upper freshwater tidal heights where they may be less susceptible to fish predation [*see* Galatowisch and McIntosh (2016a)], while tolerating high temperatures and desiccation. Furthermore, odonate nymphs, which would be especially vulnerable to fish predation given their large body size and inability to fly, were rarely observed in tidal sites but were numerically dominant in inland sites.

Conclusions

Hydrology, as a function of tidal height, appears to drive community structure and taxon distribution in tidal freshwater wetlands, probably due to interactive effects of desiccation and predation risk. In contrast to many freshwater systems, hydrological changes occur on a daily scale, and the mobility of predators in tidal freshwaters means they are not subjected to the same

environmental and resource constraints as lower trophic levels. Thus, habitat conditions in tidal freshwaters are offset from the aforementioned evolutionary tradeoffs that structure communities along the permanence-predation gradients in non-tidal freshwaters. Understanding the tradeoffs associated with freshwater hydroperiod faced by benthic communities (*reviewed in* Wellborn et al. (1996)) is challenging in non-tidal freshwaters as the presence of vertebrate predators like fish is strongly collinear with habitat permanence (drying habitats are physiologically stressful, ergo they don't have fish). Replication along the habitat permanence gradient is also problematic in non-tidal freshwaters without introducing distance effects, as in many cases geographically close habitats are more likely to experience similar hydroperiods. By contrast, tidal freshwaters are physiologically-challenging environments that are also subject to intense predation, and their invertebrate faunas likely reflect that. The tradeoffs that structure communities will also vary along the tidal height gradient, which represents a broad range of abiotic and biological conditions on a condensed spatial scale.

Tidal freshwater habitats are a geologically transient habitat type and do not appear to have levied a sufficiently consistent evolutionary selection pressure to generate obligate aquatic invertebrate taxa. Understanding how benthic invertebrate communities are structured in tidal freshwaters will allow valuable insight into how taxa can persist in environments that they have not been specifically adapted to. Future studies should include in-situ manipulations of hydroperiod and fish predators in tidal freshwaters to elucidate the relative importance of these important drivers of benthic community structure and will be key for understanding how communities might respond to novel environmental conditions or species interactions driven by climate change (Alexander et al. 2016).

As aquatic-terrestrial ecotones, tidal freshwaters contribute taxa to the regional species pool that are not found in nearby inland non-tidal freshwaters. Tidal freshwaters have historically been poorly understood and undervalued. The importance of ecotones in a landscape is well known, and future land and water management and conservation efforts should arguably prioritize tidal freshwaters because they represent an important area for taxa with limited distribution.

CHAPTER 3:

TROPHIC STRUCTURE OF INVERTEBRATE COMMUNITIES ACROSS A

FRESHWATER TIDAL HEIGHT GRADIENT

<u>Introduction</u>

Advances in the field of ecology have largely been driven by the desire to understand trophic interactions between individuals within communities (Layman et al. 2015). The development of the Eltonian niche and the idea of size-structured interactions (Elton 1927) created a general framework that has been used to characterize the structure and stability of food webs on the basis of body-size (Woodward et al. 2005; Brose et al. 2006; Gravel et al. 2013). Understanding the trophic structure of communities can provide insight into pathways of energy flow from a suite of basal resources to top predators, and can give additional information on the biotic constraints that determine community membership and patterns of diversity.

While discerning patterns of community structure in terms of taxon identities (richness) and abundances is relatively straightforward even with dozens of taxa (Chapter 2), understanding the trophic connections between every taxon and what that means for community function and stability presents a challenge that is often insurmountable given the complexity of natural food webs (Yodzis and Winemiller 1999; Thompson et al. 2012; Morales-Castilla et al. 2015). Community traits such as body size distributions, functional feeding group or diet (trophic guild), and predator-prey body size and abundance ratios are all informative proxies than can be used to assess food web structure and stability (Lindeman 1942; Yodzis and Winemiller 1999; Woodward et al. 2005; Wolkovich et al. 2014) and the niche constraints posed to organisms by biotic interactions (Menge et al. 1986; Menge and Farrell 1989; Urban 2007). For example, individual body size is easily measured and is strongly correlated with metabolism, consumption rate, and

diet breadth (Woodward and Hildrew 2002; Emmerson et al. 2005; Woodward et al. 2005). Because predators will need to consume more smaller prey than larger prey items to satisfy energy demands, the relationship between the body sizes of predators and their prey is an effective proxy for determining the magnitude and distribution of trophic interaction strengths that underlie food web stability (Jonsson and Ebenman 1998; Emmerson and Raffaelli 2004; Woodward et al. 2005).

Additionally, the distribution of trophic guilds and relative importance of "brown" detritus and "green" primary producer pathways (sensu Odum 1956 and Hairston et al. 1960) can have ramifications for community membership, energy flow and food web stability (Moore et al. 2004; Blanchard et al. 2010; Wolkovich et al. 2014). Freshwater systems receive more allochthonous detrital inputs than any other habitat type (Shurin et al. 2006; Leroux and Loreau 2008), and in tidal freshwaters, secondary production is thought to be mainly driven by detritivory (Findlay et al. 1996). Moore et al. (2004) suggest that food web stability in most ecosystems requires a strong "brown" energy base (detritus), detritivores to utilize this resource, and mobile predators to couple the allochthonous detrital energy source to autochthonous primary production ("green pathway") by freeing up matter and energy bound-up in detritivores. In aquatic systems, these predator-mediated links between energy pathways (known as benthic-pelagic coupling) have been strongly implicated in food web and community stability (Rooney et al. 2006; Blanchard et al. 2010; Wolkovich et al. 2014); thus information about trophic guilds and predator-prey interactions can aid in predicting community responses to disturbances (Brose et al. 2012).

This chapter will further explore the patterns of community structure observed in Chapter Two to better understand the biotic constraints and functioning of the benthic communities of tidal freshwater wetlands. Using patterns of body size, predator-prey size and abundance ratios, and biomass distributions of trophic guilds, this study investigated whether aspects of trophic structure

that contribute to the stability of the benthic communities of tidal freshwaters differs over a gradient of tidal height. Some expectations were that a) mean body size would decrease at lower tidal heights due to increased predation pressure by fishes; b) by extension, invertebrate predators (which are generally larger-bodied than invertebrate consumers) would be less abundant and comprise less of the total invertebrate biomass at lower tidal heights where fish predation is higher; and c) detritivory would predominate at lower trophic levels across all tidal heights given the high levels of detrital inputs and high turbidity associated with the position of tidal freshwaters in an estuary. If trophic structure and community functioning of the benthos of tidal freshwater wetlands varies across the tidal height gradient, then this could provide clues to the biotic niche constraints that underlie species distributions (Chapter 2) and guide predictions about the response of intertidal wetlands to future sea-level rise and land use—topics that are discussed herein.

Methods

Analyses and comparisons in this chapter focus on tidal transects only. Transects (n = 4) provided the grain of replication for three tidal heights (low, mid, and high) and each site was sampled in three months to encompass seasonal variation in taxon occupancy and body size. Data were collected and processed as described in Chapter 2. Estimates for invertebrate biomasses were obtained by converting body lengths to dry masses using published taxon-specific length-dry mass regression equations (Appendix E.). If no taxon-specific equation could be found in the literature, an equation for a taxon of similar body form, or for a higher taxonomic level was used for biomass calculation.

The most common format for regression equations was a power law relationship (Equation 3.1).

$$M = aL^b$$ **(equation 3.1)**

Where M and L are the dry mass and length of the individual in milligrams and millimeters respectively, and *a* and *b* are constants. If the measured body length value was outwith the range of body lengths used to develop the regression equation, then the maximum or minimum value from the published regression was used for biomass estimation instead. This avoided gross (several orders of magnitude) over- or underestimations of dry mass for very large or very small individuals.

Trait information

Information regarding the habitat, trophic level, and functional feeding group for each taxon found in this study was taken from comprehensive trait summaries in Merritt et al. (2008) and U.S. Environmental Protection Agency (2011).Non-predators were classified as feeding in "brown" energy pathways if they were consumers of detritus and their microbial biofilms (detritivores, filterers etc.) or "green" if they relied on living autotrophic production (herbivores, scrapers etc.) (Odum 1956; Hairston et al. 1960; Mattson et al. 2014). Non-feeding individuals, i.e. pupae, were excluded from "brown-green" analyses. Predatory invertebrates are typically generalists (Cummins 1973) and cannot reliably be assigned to predators of detritivores or herbivores. Biomass was not estimated for molluscs for the reasons stated in Chapter Two. Biomass was also not estimated for sponges (Porifera) due to their colonial nature and sporadic detection. Two single occurrences of *Stylurus* dragonflies were removed from predator-prey biomass ratio analyses as their large body size and rarity made them significant outliers in the

distribution of body sizes, and their presence/absence likely reflected sampling effects rather than ecologically significant patterns.

Data analysis

Data were appropriately transformed prior to analyses to normalize residuals and/or correct skewness. Invertebrate body mass data were $\log_{10}$ transformed. A logit transformation was applied to predator-prey body mass and density ratio data. Predator density data were square root transformed. A fourth root transformation was applied to density and biomass data of "green" and "brown" consumers and to predator biomass data. Response variables were analyzed with two-way ANOVAs in which tidal height (High, Mid, Low) and Month (May, June, August) were treated as fixed effects. Tukey's Honest Significance Difference (HSD) test was performed post-hoc to determine where significant differences in the dependent variable occurred. All analyses were performed in R (R Core Team 2016).

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Results

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A total of 10,108 individuals were collected across all three tidal heights. Of these, 8,717 individuals (~86%) were classified as non-predators and 1,391 (~14%) individuals were classified as predators. Non-predators were distributed unevenly between "brown" (~89% of non-predators) and "green" (4%) pathways. The remainder were non-feeding individuals, which were mostly dipteran pupae.

Body mass[1]

      Individuals were on average significantly smaller at low tidal heights (Figure 3.1a), but mean body mass did not vary significantly between months, nor was there any interaction between tidal height and month (Table 3.1). The ratio of predator to non-predator body mass (PPMR) scaled inversely with tidal height (Figure 3.1b), but was not influenced by month (Table 3.1). The trend in PPMR across the tidal gradient was driven by an overall increase in the abundance of smaller non-predators at lower tidal heights rather than by a systematic increase in predator body size.

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[1] *Between tidal and inland sites, I measured 140,571 mm / 460 ft / 300 cubits of invertebrates or about the supposed length of Noah's ark, or 0.57 Hindenburgs, or 1/6 of the height of the Burj Khalifa- the tallest building on earth, or two weeks' worth of tendonitis in my wrist.*

Table 3.1. Statistical summary of effects of tidal height (High, Mid, Low) and month and their interaction on selected parameters of benthic invertebrates. Bold denotes significance at 0.05 level.

	Mean body size[a]			Predator/non-predator body size ratio[b]			Predator/non-predator density ratio[c]		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Height	**2, 27**	**17.46**	**< 0.001**	**2, 27**	**5.22**	**0.01**	**2, 27**	**28.14**	**< 0.001**
Month	2, 27	1.82	0.18	2, 27	0.67	0.42	**2, 27**	**14.16**	**< 0.001**
H x M	4, 27	0.69	0.60	4, 27	1.60	0.22	4, 27	0.46	0.76
	Predator density[d]			"Brown" consumer density[e]			"Green" consumer density[f]		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Height	**2, 27**	**10.34**	**< 0.001**	**2, 27**	**11.12**	**< 0.001**	**2, 27**	**4.55**	**0.02**
Month	**2, 27**	**15.15**	**< 0.001**	2, 27	3.25	0.054	2, 27	3.11	0.06
H x M	4, 27	0.75	0.63	4, 27	0.31	0.87	4, 27	0.57	0.67
	Total invertebrate biomass[g]			Predator biomass[h]			"Brown" consumer biomass[i]		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Height	**2, 27**	**12.04**	**< 0.001**	**2, 27**	**5.57**	**0.009**	**2, 27**	**13.73**	**< 0.001**
Month	**2, 27**	**7.38**	**0.003**	**2, 27**	**10.52**	**< 0.001**	**2, 27**	**4.14**	**0.02**
H x M	4, 27	0.29	0.88	4, 27	0.54	0.71	4, 27	0.60	0.67
	"Green" consumer biomass[j]								
	df	*F*	*P*						
Height	2, 27	3.04	0.07						
Month	2, 27	0.30	0.74						
H x M	4, 27	1.64	0.19						

a Model R^2 = 0.49
b Model R^2 = 0.21
c Model R^2 = 0.69
d Model R^2 = 0.57
e Model R^2 = 0.39
f Model R^2 = 0.21
g Model R^2 = 0.48
h Model R^2 = 0.43
i Model R^2 = 0.46
j Model R^2 = 0.14

Predator-prey densities

The ratio of predator to non-predator density increased significantly with increasing tidal height (Figure 3.1d) and was influenced by month (Table 3.1). Post-hoc comparisons determined that the ratio of predator to non-predator density was significantly higher in August than in prior months, but the patterns between tidal heights remained consistent across months (no month x height interaction).

Invertebrate predators

There were significantly fewer invertebrate predators per m^2 at low tidal heights (Figure 3.1e) and while predator density differed significantly between months (Table 3.1), no differences were detected between months during post-hoc comparisons, and the influence of tidal height on predator density was not seasonally dependent (no interaction between month and height; Table 3.1). Invertebrate predator biomass per m^2 was significantly higher at mid tidal heights (Figure 3.1c) and was significantly higher in May than in later months (Table 3.1; post-hoc comparisons) but there was no significant interaction between height and month.

Figure 3.1. Selected traits and trophic parameters of invertebrate communities across a tidal height gradient in tidal freshwater wetlands of Swan Island, Maine. (a) Mean body size; (b) predator-prey body size ratio; (c) total invertebrate biomass; (d) predator-prey density ratio; (e) predator density; (f) predator biomass; (g) "brown" consumer density; (h) "green" consumer density; and (i) "brown" consumer biomass. Means are plotted with standard errors. Lower case letters refer to significant post-hoc pairwise comparisons (Tukey's HSD method).
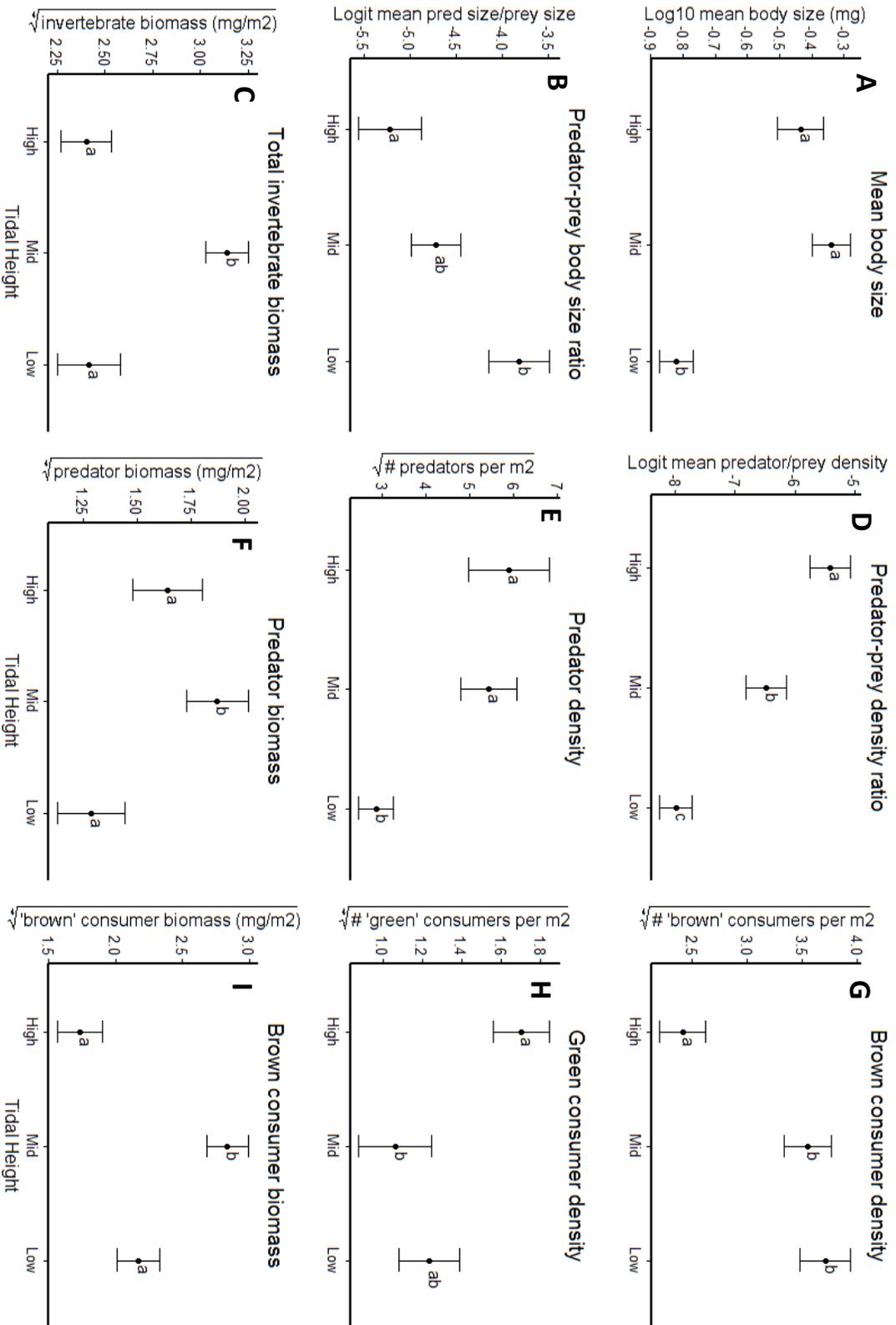
Invertebrate consumers

Total invertebrate biomass and the biomass of "brown" invertebrate consumers exhibited the same trend as invertebrate predator biomass (Table 3.1; Figure 3.1c). A marginally non-significant relationship was found between tidal height and "green" consumer biomass (Table 3.1). Low and mid tidal heights had significantly more "brown" consumers per m^2 than high tidal heights (Figure 3.1g), but the relationship for "green" consumers was less clear (Figure 3.1h). High sites had significantly more "green" consumers per m^2 than mid tidal heights, but neither high nor mid sites differed significantly from low sites. Densities of "brown" and "green" consumers both had marginally statistically non-significant relationships with month (Table 3.1). In summary, detritivores were more abundant at lower tidal heights (mid, low) but had highest biomass at mid tidal heights. Overall, green consumers were less abundant than "brown" consumers at all tidal heights.

<div align="center">

Discussion

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The composition of benthic communities in tidal freshwater wetlands are structured differently along a gradient of tidal height (Chapter Two). The results from this chapter provide strong evidence that zonation of communities along this gradient also generates marked differences in the trophic structure and distribution of invertebrate body sizes and biomass. Mean invertebrate body sizes were not constant across the gradient, nor was the ratio of invertebrate predators to non-predators. As predicted, detritivores were the dominant consumer guild, but the trends for "brown" consumer density and secondary biomass were not the same. While consumers were more prevalent at low tidal heights, the greatest biomasses of all trophic guilds were highest in mid tidal heights. These results have broad implications for both how energy flows from basal resources in these unique systems, and for how invertebrate and fish predation might influence

benthic community structure. Understanding that tidal freshwater benthic habitats are not homogenous in terms of their community structure and food web dynamics will be important for predicting outcomes in the face of sea-level rise and land use changes, especially coastal squeeze.

Invertebrate body size distribution

Benthic invertebrates at the low end of the freshwater tidal height gradient had significantly smaller body masses than those at higher tidal heights. Heavier predation pressure by fishes at these lower tidal heights may be filtering larger individuals from the benthos, which has been observed in other systems, both tidal and non-tidal (Blumenshine et al. 2000; Zimmer et al. 2001; Antón-Pardo and Armengol 2016). Fish are strongly positively size-selective predators (Brooks and Dodson 1965; Ware 1972) and Antón-Pardo and Armengol (2016) found that increased predation pressure in coastal ponds lead to a loss of size diversity and higher densities of small taxa. Although fish predation was not measured in this study, fish predation pressure in marine intertidal systems is likely greatest at lower tidal heights, where fish have the longest available time to forage (Halpin 2000; Ellis and Bell 2008), and this mechanism could explain the observed reduction in mean invertebrate body size at low freshwater tidal heights.

Alternatively, it has recently been demonstrated that mean benthic macroinvertebrate size in soft-substrate intertidal systems decreases with decreasing hydrodynamic (shear) stress (Donadi et al. 2015). This is in keeping with the "habitat harshness hypothesis" (Defeo et al. 2003) commonly used to predict communities' parameters in soft-bottomed intertidal systems. To what extent this concept applies to intertidal freshwaters, which arguably experience limited tidal wave shear stress (Verney et al. 2006), but may experience variable shear stress from directional changes in riverine flow (Barendregt et al. 2009b), remains to be seen. Elucidating these alternative abiotic and biotic drivers of body size structure across tidal gradients will require direct experimentation

using manipulations that contrast the presence/absence of fish predators with physical stress. Regardless of the mechanisms, the reduction in body size in lower tidal zones will have important implications for interactions among invertebrates.

Predator-prey body size relationships

Body size distributions and body size ratios between predators and prey (commonly: predator-prey mass ratio, hence PPMR) can be used as an effective proxy for the trophic interaction strengths that underlie food web stability (Jonsson and Ebenman 1998; Emmerson and Raffaelli 2004; Emmerson et al. 2005; Woodward et al. 2005), especially in aquatic ecosystems, where communities tend to be highly size-structured and follow Elton's (1927) principle that predators are larger than their prey (Woodward and Hildrew 2002; Cohen et al. 2003; Trebilco et al. 2013), but see (Layman et al. 2005; Shurin et al. 2006). Although guilds of fishes form the upper trophic levels of tidal freshwaters (Rozas and Odum 1987; Odum et al. 1988), the observed pattern of invertebrate PPMRs across the tidal height gradient in this study is informative. The higher values for PPMR observed at lower tidal heights suggests that interaction strengths between predatory and non-predatory invertebrate taxa is stronger on average there than higher up the shore. Moreover, given that mean invertebrate body size was lower at low tidal heights, values for PPMR would be much greater if predatory fish were included in analyses. Thus the strength of trophic interactions could, on average, be greater at lower tidal heights, and these strong interactions could imply reduced food web stability (Emmerson and Raffaelli 2004), especially if these strong interactions are not balanced by numerous weak interactions (between invertebrate predators and prey), or those in slower energy pathways such as those fed by benthic detritus (McCann et al. 1998; Blanchard et al. 2010)

However, there are other traits of predators and prey that may influence the strength of these interactions, including whether prey have adaptations to resist/avoid predation (Wootton et al. 1996), or the density of prey relative to predators (Warburton 2015). Additionally, intraguild predation is thought to play an important role in structuring communities and their trophic interactions (Polis and Holt 1992; Arim and Marquet 2004) and has been observed in invertebrates in tidal freshwater wetlands (Witt et al. 2013). Future studies should investigate the importance of defended taxa (see Warburton (2015)) and intraguild predation, neither of which was part of this study, to fully understand the mechanisms driving PPMRs and interaction strength in tidal freshwaters.

Invertebrate community trophic structure

While invertebrate densities were generally greater at lower tidal heights (Chapter Two), the distribution of different trophic levels (predators, detritivores, herbivores) exhibited varying trends. The density of invertebrate predators decreased with decreasing tidal height, which is perhaps unsurprising given the observed reduction in mean invertebrate body size, mentioned previously; predatory aquatic invertebrates are often larger-bodied than their non-predatory counterparts and so would be penalized under greater size-selective predation by fish.

Within lower invertebrate trophic levels (consumers), detritivory was far more common than herbivory at all tidal heights. The relative densities of detritivores and herbivores exhibited contrasting patterns, whereby high marshes had significantly fewer detritivores than lower tidal heights and significantly more herbivores. Secondary production in tidal freshwater wetlands is generally thought to be mainly driven by detritivory (Odum et al. 1984; Odum 1988; Findlay et al. 1996). Their position in the river catchment means they receive large volumes of fine particulate organic matter (sensu Vannote et al. (1980)) and above-ground production by vascular plants and

thus autochthonous detritus generation in tidal freshwater wetlands is among the highest of any system (Whigham 2009). As terrestrial ecosystems are thought to receive fewer allochthonous resources than aquatic systems (Shurin et al. 2006; Leroux and Loreau 2008), this could explain the lower densities of "brown" pathway consumers at higher tidal heights, as the upper tidal heights in tidal freshwaters may function more like a terrestrial system that is periodically flooded than an aquatic system that is periodically dry (Beauchard et al. 2013; Dell et al. 2014).

In contrast to some patterns seen with invertebrate densities, biomasses of invertebrate predators and brown pathway consumers were significantly higher at mid tidal heights than both low or high tidal heights. Detritivore biomass and density were lowest at high tidal heights, suggesting that lack of detrital resources at this "more-terrestrial" tidal height could be limiting invertebrates that depend on allochthonous energy sources. Alternatively, the density of invertebrate predators was greatest at high tidal heights, which could be imparting some top-down control on lower invertebrate trophic levels. The increased abiotic stress (drying, temperature) and shorter inundation times that exclude fish predators for most of the tidal cycle in the high marsh could release invertebrate predators from predation pressure and strengthen their top-down control of consumers (Greig et al. 2013). While invertebrate predator biomass did not exhibit the same trend as density, there is likely further top-down control of aquatic invertebrate prey by terrestrial invertebrate predators that forage opportunistically at low tide (especially carabid beetles (Barendregt 2005) and spiders (Swarth and Kiviat 2009)), which may contribute invertebrate predator biomass that was unaccounted for and undetected in this study. The influence of predators in tidal freshwaters, where gradients of ecological conditions (like hydrology) are contiguous, is likely much higher than in the patchy mosaic of conditions created by inland freshwaters, which are more hydrologically isolated. Whether the predators are schools of predatory fish during high

tide, or opportunistic terrestrial invertebrate predators that forage at low tide, there are mobile upper trophic levels ("allochthonous predators" sensu Leroux and Loreau (2008)) in tidal freshwater food webs that are not subject to the same limitations as the lower levels they predate.

Entrainment and production of detritus by tidal freshwater wetlands is greater in the intertidal than at lower subtidal heights (Findlay et al. 1990). Standing stock of coarse detritus appeared significantly greater at mid tidal heights, often forming thick mats of dead tidal marsh vegetation (personal observation). This additional quantity of autochthonous detritus (i.e. detritus form wetland plant production) could account for the higher biomass of invertebrates observed at mid tidal heights in several ways. Most simply, there are greater basal resources for a greater diversity of detritivores (shredders, gatherers) at intermediate heights than at lower tidal heights, where proximity to the main-stem river flow prevents settlement of all but the finest organic matter, favoring collector-gatherer and collector-filterer modes of feeding. Coarser particulate organic matter also provides greater vertical habitat complexity (Reice 1991; Jabiol et al. 2014) which could provide refugia from fish predation for larger-bodied invertebrates and promote greater trophic complexity of the invertebrate guild. No significant relationship between tidal height and the biomass of green pathway consumers was observed, and these taxa were less abundant in general. However, this study did not include the high abundances of snails that were observed in samples (personal observation). Snail production is often very high in freshwater tidal systems and represent an important food source for anadromous fishes, especially sturgeon (Nellis et al. 2007; Sulak et al. 2012). Thus, it is likely that I underestimated the contribution of herbivorous taxa to the invertebrate community and thus the potential importance of "green" energy pathways in tidal freshwater wetlands.

Placing tidal freshwaters in conceptual frameworks

The trophic structure and standing biomass of benthic invertebrate communities in tidal freshwater wetlands was strongly differentiated along a tidal height gradient. At low tidal heights results were consistent with fish predation limiting the biomass of larger-bodied, predatory invertebrates and increasing the density of smaller-bodied non-predatory invertebrates; this pattern is commonly seen in non-tidal freshwater and saline tidal systems alike (Lubchenco and Menge 1978; Wellborn et al. 1996; Blumenshine et al. 2000; Quintana et al. 2014; Antón-Pardo and Armengol 2016).

At high tidal heights, fish predation is likely lower and may have less top-down impact on benthic invertebrates. The high marsh represents an abiotically stressful habitat (see Appendix A) and so predation by fishes could be relatively unimportant in driving trophic complexity and community composition, much like in ephemeral non-tidal freshwaters (Wellborn et al. 1996; Greig et al. 2013). However, the density of predatory invertebrates was greatest at high tidal heights. If fish, as top predators in the system, have limited access to high tidal heights, invertebrate mesopredators could be released from predation pressure, who, in turn, could have strong impacts on invertebrate consumers (Litvaitis and Villafuerte 1996; Prugh et al. 2009; Ritchie and Johnson 2009). Alternatively, this could reflect the importance of upper tidal freshwater wetlands for *semi-aquatic* invertebrate taxa that may experience flooding as a stressor (cf. truly aquatic taxa) as many of the predatory taxa found at these heights were semi-aquatic (Chapter 2).

In some respects, tidal freshwaters appear to fit in the conceptual predator-permanence model applied to non-tidal hydrodynamic freshwaters (Chapter 2 Figure 2.1; Wellborn et al. 1996). At lower tidal heights that experience infrequent, non-prolonged drying (c. 2 hours per day), invertebrates are smaller bodied, more numerous and feed at lower trophic levels, much like

permanent ponds that contain fish predators. At intermediate tidal heights (mid), invertebrates were large, and the biomasses of invertebrate predators and detritivores was higher than at lower tidal heights. While these tidal heights still experience predation by fishes, limited inundation periods imply that predation intensity is likely less than at lower tidal heights, and increased habitat complexity and potential refugia may help to further mitigate the influence of fish (Urban 2004; Antón-Pardo and Armengol 2016). The mid intertidal zone experiences near equal durations of flooding and drying and so the relative importance of predation to desiccation risk may be similar. This is congruent with the model for non-tidal freshwaters where the largest bodied invertebrates are found in systems that experience enough environmental variability that fish are excluded (Schneider and Frost 1996; Kiflawi et al. 2003) and thus predation pressure is somewhat relaxed.

The highest tidal heights in tidal freshwaters do not fit the predator-permanence model quite as well. While invertebrate predator and detritivore biomass was lower at upper (high) tidal heights than at intermediate (mid) tidal heights, the density of predatory invertebrates was greatest at the highest tidal heights. Abiotic stress may limit the production of the benthos in the high marsh, like in ephemeral ponds that dry frequently and unpredictably, but abundant terrestrial and semi-aquatic predators may be exerting top-down influence on the aquatic benthic community and depressing their biomass independent of abiotic constraints (Brendonck et al. 2002). Likewise, fish predators in tidal freshwaters are only limited in their foraging time and not their presence by the fluctuating hydrology and so have fewer abiotic constraints than the invertebrate benthos they predate.

<u>Conclusions</u>

While I do not have the data to ascribe specific mechanisms underlying these patterns, what is clear is that the trophic structure and secondary biomass of invertebrates in tidal freshwater wetlands is not consistent across the tidal height gradient and is more complex than previously thought. The current paradigm for tidal freshwaters paints their invertebrate communities as simple and uneven, dominated by oligochaetes and chironomids like in eutrophic lakes (Yozzo and Diaz 1999), and does not distinguish between different tidal heights. This study has demonstrated that not only are communities distinct between different tidal heights, but their trophic structure and function is also not constant along the tidal height gradient.

Invertebrates act as the link for energy flow between the high levels of primary production (Whigham 2009) and the diverse array of anadromous fishes (Swarth and Kiviat 2009) observed in tidal freshwater wetlands. Sea levels are rising at a rate much faster than previously thought (Hay et al. 2015) which will have ramifications for prior predictions [e.g. Nicholls et al. (1999)] about intertidal wetland losses due to sea level rise. Given that communities and food webs are differentiated along a gradient of tidal height, any reduction in intertidal wetland area (through coastal squeeze or otherwise) could significantly impact on the ecosystem functions provided by tidal freshwaters and their communities. Ultimately, predicting the response of invertebrate communities and their associated ecosystem functions to altered hydrologies will be the key to conserving and maintaining tidal freshwater wetlands as nurseries and forage areas for fishes and waterfowl.

CHAPTER 4:

SYNTHESIS AND TIDAL FRESHWATERS AS MODEL STUDY SYSTEMS

Introduction

This study has highlighted the unique ecology of tidal freshwater wetlands and the consequences for their benthic communities. Tidal freshwaters have largely been overlooked by freshwater and marine ecologists alike, which is unfortunate given their potential to help answer key questions in community ecology. In this concluding chapter I will discuss some of the key results of the preceding chapters, highlight future potential lines of investigation for understanding tidal freshwater benthic ecology, and argue that the unique ecology of tidal freshwaters makes them ideal study systems to investigate some key questions in community ecology.

Key results

Current wisdom suggests that the benthic communities of tidal freshwaters are species depauperate (Yozzo and Diaz 1999; Swarth and Kiviat 2009; Barendregt 2016), made up of a few, highly dominant taxa, especially chironomids and oligochaetes—taxa commonly associated with low habitat complexity, pollution stress, or eutrophication. Furthermore, tidal freshwaters are commonly considered to be less diverse than their non-tidal counterparts, thought mainly to driven by low habitat heterogeneity found in tidal freshwater areas. Results from Chapter Two suggest that benthic communities in tidal freshwater wetlands are more complex than previously thought and that communities show strong zonation even over a relatively short longitudinal distance (<250 m). While inland habitats were more diverse than any one point on the tidal height transect, tidal freshwater wetlands contributed a large proportion of unique taxa to the regional species pool that were not found in inland habitats. Strikingly, there was greater community differentiation along the transect of tidal height in the contiguous tidal freshwater habitats than between the more

hydrologically isolated inland freshwater habitats. This observation suggests that the tradeoffs that structure communities (e.g. Wellborn et al (1996)) must vary strongly along the tidal height gradient, which encompasses a broad range of abiotic and biological stressors on a highly condensed longitudinal scale.

Biotic interactions provide a key niche constraint on members of a community and can vary across gradients of abiotic stress (e.g. Menge and Sutherland (1987)). Understanding how the trophic structure of tidal freshwater benthic communities varied by tidal height provided additional information about the mechanisms that drove patterns of community zonation. Chapter Three expanded on the findings of Chapter Two that suggest there are multiple and potentially compounding bottom-up and top-down forces that shape the structure and function of these communities. At low tidal heights fish predators likely excluded large-bodied invertebrates and generated an invertebrate fauna that was dominated by abundant small invertebrates. In contrast, invertebrates were less abundant at high tidal sites, which probably reflects a combination of harsh physiological conditions and top-down control by opportunistic semi-aquatic or terrestrial predators. Between these two heights, in the mid marsh, invertebrate biomass and body size were higher—perhaps, driven by more abundant detrital resources that provide an energy source and refugia space, coupled with a balance of intermediate predation pressure and physiological stress.

To fully understand the relative roles of abiotic and biological forces in structuring tidal freshwater communities and food webs, manipulations of hydroperiod, predation, basal resources, and habitat complexity are required. Tidal freshwater wetlands are one of the few true contiguous ecotones that span the entire gradient from permanently aquatic to upland terrestrial habitats; moreover, they experience daily and seasonal fluctuations in areal extent, predator identity and occupancy, and physical conditions including temperature and water availability. Tidal

freshwaters represent an underappreciated, dynamic ecosystem that is subject to multiple and complex selection pressures, but may be ideal for testing key questions in ecology.

Natural position of tidal freshwaters

Just as Bob Paine called experimental manipulation in the marine intertidal the gold standard for answering key questions on the relative importance of intrinsic and extrinsic forces in community ecology (Paine 1994), I argue that tidal freshwaters have many attributes that make them the ideal study systems for community ecology (perhaps even having broader utility than rocky shores). As tidal freshwaters lie at the interface between non-tidal freshwaters (studied by limnologists) and marine-influenced waters (studied by estuarine and marine scientists), there is potential for tidal freshwater ecology to reconcile the two major divisions of aquatic science, which have often worked in isolation from one another. A prime example of this is the development of two distinct models that explain patterns of diversity in aquatic habitats that are in reality on a continuum [freshwater: Statzner and Higler (1986); marine: Remane and Schlieper (1971), comparison discussed in Rundle et al. (1998)] (and see also Vannote et al. (1980)).

Non-tidal freshwater approach to community ecology

A great many advances in understanding the relative importance of drivers of community structure and assembly have been made using hydrodynamic non-tidal freshwaters (i.e. Stoks and McPeek (2003b); Urban (2004); Chase (2007); Urban (2007); Greig (2008); Chase et al. (2009); Vanschoenwinkel et al. (2009); Verberk et al. (2010); Brendonck et al. (2015); Kneitel (2016)), which represent a gradient of habitat permanence and predation pressure (Wellborn et al. 1996; Wissinger 1999). Although ponds and other inland freshwaters have long been touted as ideal systems for testing ecological and evolutionary hypotheses (Elton 1927; de Meester et al. 2005), there are some challenges in using inland freshwaters for these questions are that are often difficult

to overcome. First, with a few exceptions, it is often difficult to find a broad range of abiotic conditions and biological parameters in an area small enough so as not to introduce isolation effects that might influence propagule availability, dispersal, subsidies etc. (following Tobler's (1970) first law of geography). Second, habitat permanence in inland freshwaters is strongly collinear with both basin size and predation pressure (Wissinger et al. 1999). Smaller basin freshwater wetlands are more likely to be physiologically stressful because they dry more frequently, and are less likely to support a vertebrate top predator guild. This makes disentangling the effects of abiotic environmental filtering and top-down predation pressure problematic. Predators in hydrologically isolated freshwaters can also be limited by the availability of prey in that patch as invertebrate diversity and production is often dependent on basin size (Wissinger et al. 1999; Kneitel 2016). Many vertebrate predators (fish) are often unable to move between patches, so our ability to discern their impact on lower trophic levels cannot be separated from bottom-up effects without direct experimentation. Third, like marine intertidal areas, the communities of inland freshwaters have experienced sustained and predictable evolutionary tradeoffs (sensu Stearns (1976)) that have promoted adaptation and speciation along the predator-permanence gradient (Connell 1961; Stoks and McPeek 2003b, a; Wissinger et al. 2006). The fauna of hydrodynamic inland freshwaters have specific life-histories or physiologies like programmed dormancy, expedited growth, or high powers of dispersal that allow them to persist in temporary or ephemeral habitats (Wiggins et al. 1980), and so their community assembly and structure is likely strongly influenced by historical contingencies like priority effects and a limited potential species pool (Fukami 2015)—the latter is also especially true for marine intertidal systems due to salinity effects.

<u>Potential uses of tidal freshwaters in community ecology</u>

By contrast, this thesis has highlighted how tidal freshwaters could overcome these three challenges of using inland freshwaters for experimental community ecology. First, a broad range of environmental conditions occur in tidal freshwaters in a small geographic area. Temperature can change as much as 32°C in a single day and the temperature difference between the lowest and highest tidal heights is often 15°C or more. There is also a continuous gradient of other abiotic and biological conditions associated with tidal height (inundation period, desiccation risk, fish predation, terrestrial invertebrate predation, detrital resources, vertical habitat complexity etc.) that are all easily manipulated within a contiguous block of habitat. Tidal freshwater areas are often extensive in unimpacted estuaries, which means within-site replication can be much easier than in small inland pools or ponds. The role of abiotic and biological stressors in structuring communities and their food webs may also differ between patchy and continuous environmental gradients— especially if the gradients span a broad ecotone between two very different systems, as found in tidal freshwater wetlands.

Second, predators can come and go with the tides in tidal freshwaters and can move easily between patches. This means they are less constrained by the same abiotic conditions faced by lower trophic levels and can constantly apply strong selection pressure on any one patch, as their numbers are less dependent on the availability of prey in one patch. The ecotonal nature of tidal freshwaters means that they support both aquatic and terrestrial predators, neither of which face the same abiotic limitations as they prey. Cage experiments that exclude either or both of these predator guilds across a tidal height gradient would be illuminating on the importance and context dependency of top-down control in communities and what influence mobile predators that can forage across ecosystem boundaries have on lower trophic levels.

Third, tidal freshwater areas, like estuaries in general, are geologically ephemeral phenomena (Pasternack 2009). The tenuous balance between river discharge and incoming tides that maintains salinities below 0.5 ‰ and still permits tidal movements of water is unlikely to have exerted a sustained evolutionary selection pressure. Sea levels and precipitation regimes have fluctuated rapidly and often, and some gradient of brackish tidal conditions has likely been a persistent feature of the landscape. Likewise, while individual temporary inland freshwater habitats are transient, wetlands that dry seasonally have likely been a feature of landscapes for millions of years (Williams 2006). Given that tidal freshwaters are unlikely to have been a persistent feature of a landscape, there appear to be no taxa that are obligate tidal freshwater specialists like those seen in brackish or marine intertidal zones or non-tidal freshwaters. Almost all taxa found in tidal freshwaters can be found in a non-tidal freshwater (Yozzo and Diaz 1999), but this study also highlighted the potential importance of tidal freshwater wetlands for littoral or sub-aquatic edge taxa. Ultimately, the persistence of a taxon in tidal freshwater habitats means that it has some adaptations that confer tolerance to abiotic or biological conditions that was outwith its specific evolutionary history. Environmental selection pressures (e.g. desiccation risk and predation risk) can be easily manipulated and placed in novel configurations in tidal freshwaters using weirs and cages (for an example, see Cherry et al. (2015)). Tracking community structure in these manipulated plots will allow us to discern when tradeoffs faced by potential colonists are actually tradeoffs and not co-adaptation or co-tolerances. This information that can be used to predict community responses to novel environments following climate change or species introductions, and will be useful for prediction in invasion ecology.

And finally, the relative importance and context dependency of drivers of beta diversity are still not well known (Myers et al. 2015) and ex-situ mesocosm studies have often provided

contrasting results (Chase 2007; Chase et al. 2009). Preliminary findings of this study suggest that predation may be a stronger filter on beta diversity than drying, and this hypothesis could be tested with a well-designed in-situ experiment in tidal freshwaters, that allows multiple drivers to be extricated from one another.

<u>Conclusion</u>

The overarching aim of this thesis was to investigate how invertebrate communities, in an understudied habitat type, are influenced by an unusual suite of ecological conditions. By thoroughly understanding how tidal freshwater communities are structured we may gain valuable insight into how all communities are structured. Tidal freshwater ecology is currently, without doubt, a niche field, but it has the potential to generate consilience in community ecology.

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APPENDIX A:

DAILY TEMPERATURE DATA FOR FRESHWATER HABITATS

ON SWAN ISLAND, MAINE

Figure A.1. Daily temperature data for freshwater habitats on Swan Island, Maine between 28th June and 20th August 2015. Big Farm Pond is a permanently inundated man-made pond. Campsite Pool is a temporary pool that experiences significant dry-down. Maxwell Cove is a tidal freshwater wetland on the south-east shore of Swan Island where one temperature logger was installed at the mean high and low water lines.

Temperature (°C)

Big Farm Pond, Swan Island

Date (day intervals)

June 28

August 20

Figure A.1. (continued)

Campsite Pool, Swan Island

Temperature (°C)

Date (day intervals)

June 28

August 20

Figure A.1. (continued)

Temperature (°C)

Maxwell Cove (MLWL)

Date (day intervals)

June 28

August 20

Figure A.1. (continued)

Temperature (°C)

Maxwell Cove (MHWL)

Date (day intervals)

June 28

August 20
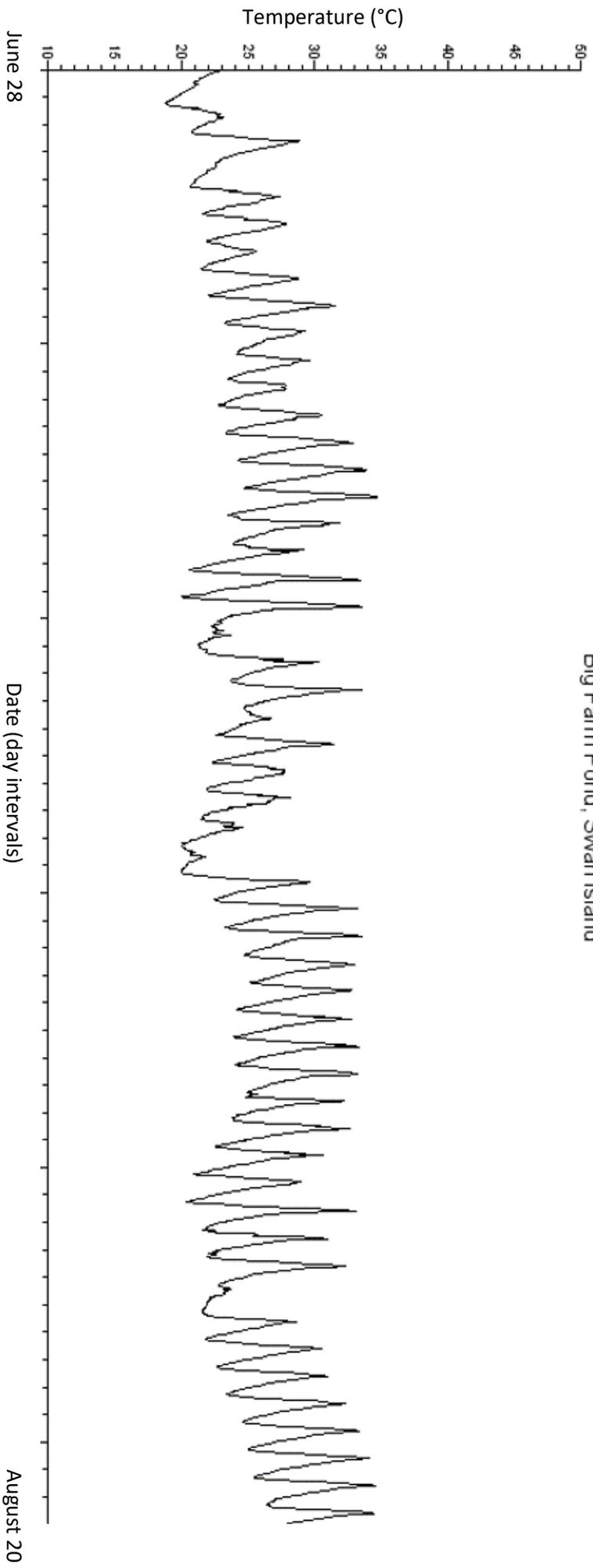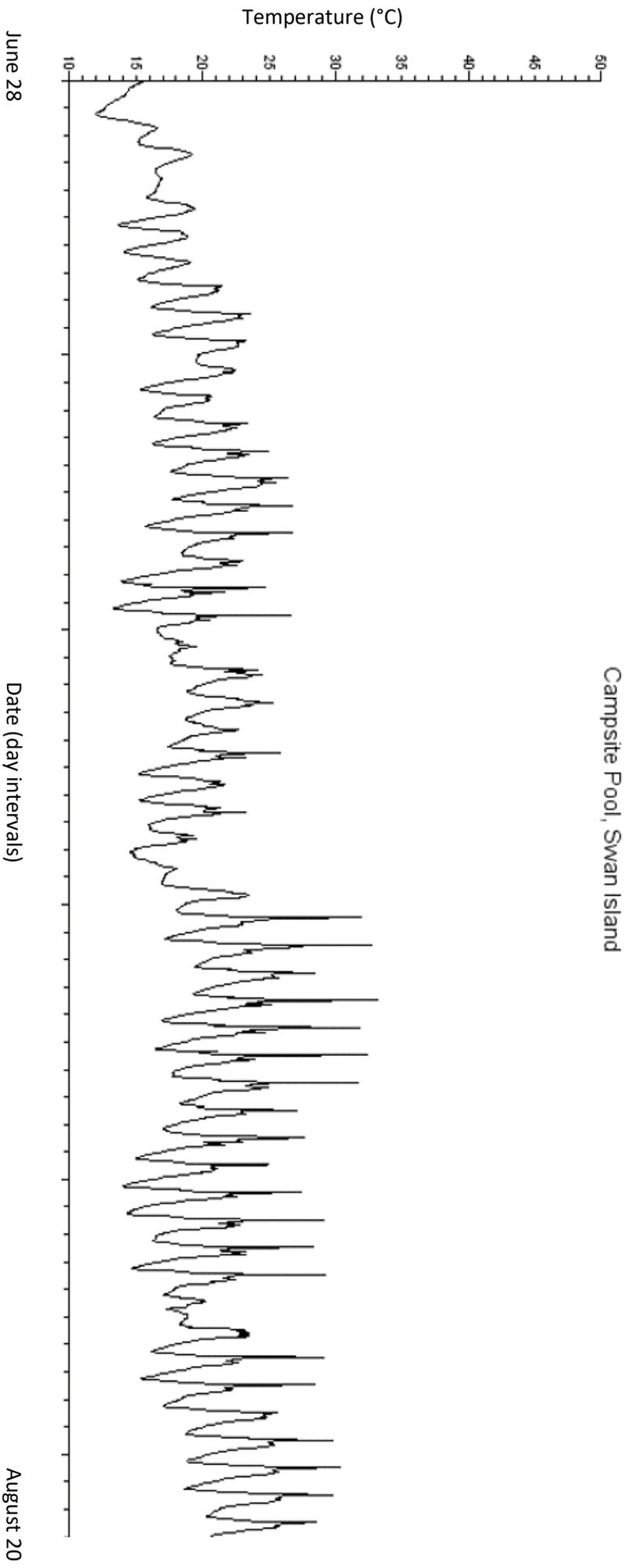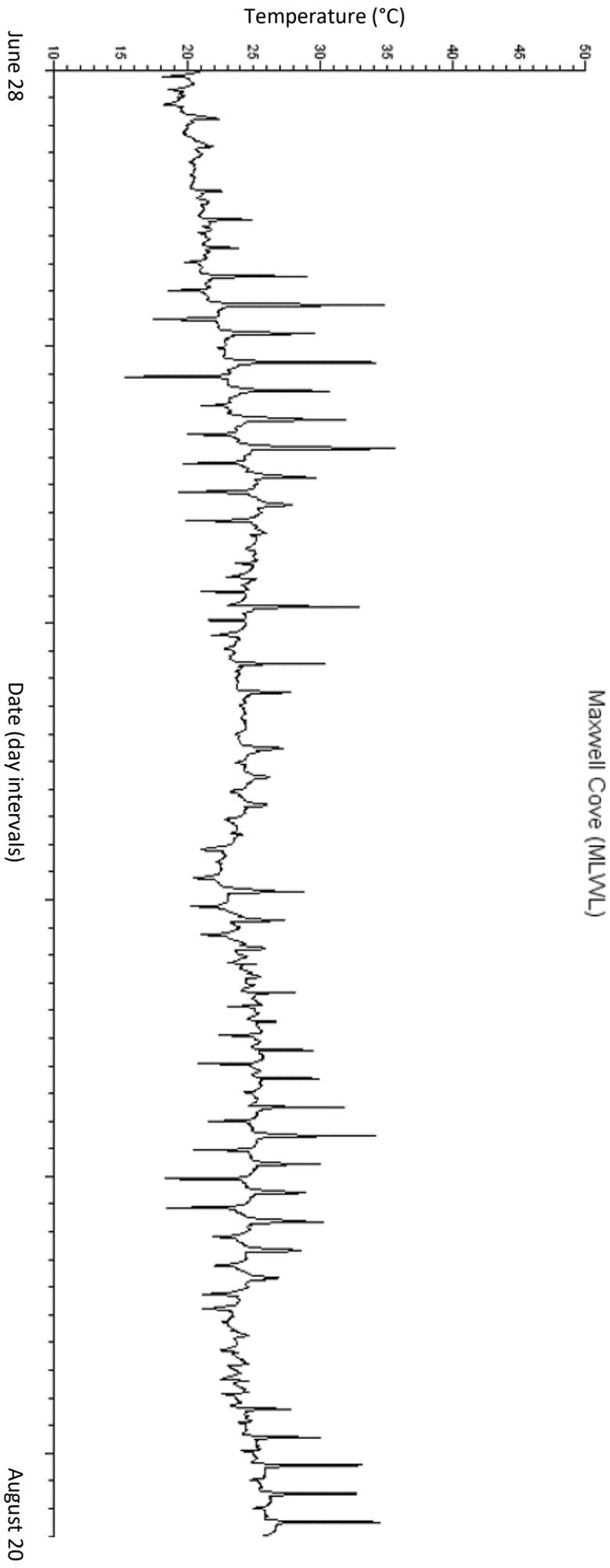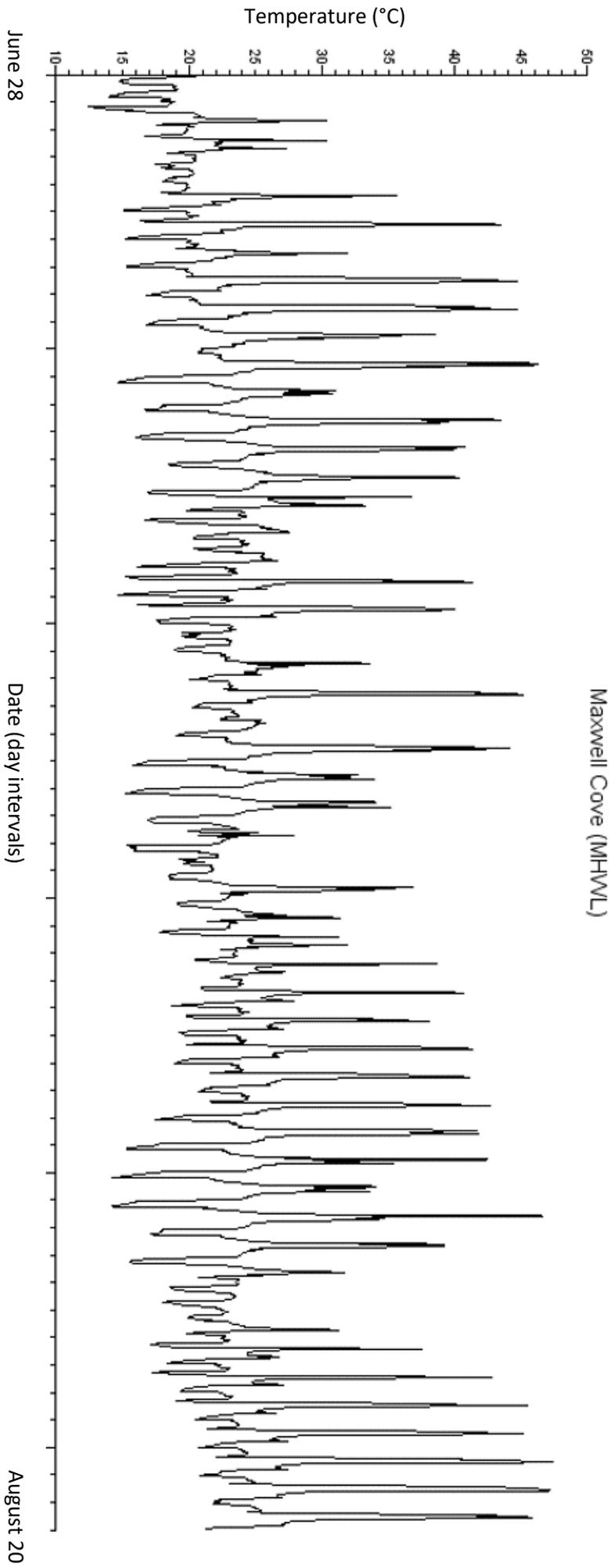
APPENDIX B:

WATER CHEMISTRY DATA FOR FRESHWATER HABITATS

ON SWAN ISLAND, MAINE

Table B.1. Water chemistry data for tidal and non-tidal freshwater wetlands on Swan Island, Maine. Asterisks denote that reading was taken in situ, all others collected in Nalgene bottle and tested within 6 hours. No data for site "VP" as site had dried up by August.

Habitat Type	Site	pH (June)[*]	pH (August)	Conductivity (μS.cm^{-1}) (June)[*]	Conductivity (μS.cm^{-1}) (August)
Permanent	BF	6.75	7.18	21.9	31.3
	CF	5.82	6.18	42.3	45.3
	DT	5.82	6.12[*]	22.9	22.5[*]
	WP	5.33	5.53	16.5	17.7
	Mean	**5.93 (0.30)**	**6.25 (0.34)**	**25.9 (5.6)**	**29.2 (6.1)**
Temporary					
	CS	5.33	5.93[*]	21.5	25.7[*]
	SF	5.75	5.95	38	49.3
	VP	5.15	dried	22.5	dried
	Mean	**5.41 (0.18)**	**5.94 (0.01)**	**27.3 (5.3)**	**37.5 (9.6)**
Tidal Low					
	LS	6.8	6.95	58.5	63.5
	MG	--	7.49	--	73.5
	WT	6.64	7.19	54.9	64.0
	XX	7.34	7.25	56	62.8
	Mean	**6.93 (0.21)**	**7.22 (0.11)**	**56.5 (1.1)**	**66.0 (2.5)**
Tidal Mid					
	LS	6.97	7.00	58.2	63.3
	MG	6.81	7.64	59.5	62.5
	WT	7.02	7.16	57.5	61.8
	XX	6.94	6.86	58.4	62.3
	Mean	**6.94 (0.04)**	**7.17 (0.17)**	**58.4 (0.4)**	**62.5 (0.3)**
Tidal High					
	LS	7.04	6.22	59.4	59.5
	MG	6.75	7.40	59.4	66.1
	WT	6.8	6.78	--	62.5
	XX	6.84	6.94	62.4	67.3
	Mean	**6.86 (0.06)**	**6.84 (0.24)**	**60.4 (1.0)**	**63.9 (1.8)**
Tidal Mean		**6.90 (0.06)**	**7.07 (0.11)**	**58.4 (0.7)**	**64.1 (1.0)**

APPENDIX C:

MACROINVERTEBRATE TAXONOMIC COMPOSITION OF FRESHWATER

HABITATS ON SWAN ISLAND, MAINE

Table C.1. Macroinvertebrate taxonomic composition of freshwater wetlands (four permanent, three temporary, and four tidal) on Swan Island, Maine in summer 2015 (May-August). Shaded boxes indicate that taxon was present in at least one sample taken from a site with that hydrological regime. A total of 70 taxa were found at permanent site, 68 taxa were found at temporary sites, and 65 taxa were found in tidal freshwaters.

Taxon	Permanent	Temporary	Tidal	Group
Hirudinea	■	■	■	Annelida
Oligochaeta	■	■	■	Annelida
Berosus	■	■	■	Coleoptera
Chrysomelidae	■	■	■	Coleoptera
Desmopachria	■	■	■	Coleoptera
Donacia	■	■	■	Coleoptera
Dytiscidae (larvae)	■	■	■	Coleoptera
Enochrus	■	■	■	Coleoptera
Haliplus	■	■	■	Coleoptera
Hydraena	■	■	■	Coleoptera
Liodessus	■	■	■	Coleoptera
Scirtidae	■	■	■	Coleoptera
Collembola	■	■	■	Collembola
Caecidotea	■	■	■	Crustacea
Ceratopogonidae	■	■	■	Diptera
Chaoborus	■	■	■	Diptera
Chironomidae	■	■	■	Diptera
Diptera (pupae)	■	■	■	Diptera
Sciomyzidae	■	■	■	Diptera
Tabanidae	■	■	■	Diptera
Tipulidae	■	■	■	Diptera
Caenis	■	■	■	Ephemeroptera
Corixidae	■	■	■	Hemiptera
Gerridae	■	■	■	Hemiptera
Mesovelia	■	■	■	Hemiptera
Veliidae	■	■	■	Hemiptera
Lepidoptera	■	■	■	Lepidoptera
Coenagrionidae	■	■	■	Odonata
Libellulidae	■	■	■	Odonata

Table C.1. (continued)

Taxon	Permanent	Temporary	Tidal	Group
Oecetis	■	■	■	Trichoptera
Trichoptera (pupae)	■	■	■	Trichoptera
Trombidiformes	■	■	■	Trombidiformes
Atrichopogon		■	■	Diptera
Hydrometra		■	■	Hemiptera
Nematoda		■	■	Nematoda
Peltodytes	■		■	Coleoptera
Staphylinidae	■		■	Coleoptera
Hyalella	■		■	Crustacea
Gomphidae sp.	■		■	Odonata
Acilius	■	■		Coleoptera
Agabus	■	■		Coleoptera
Gyrinus	■	■		Coleoptera
Hydrobius	■	■		Coleoptera
Hydrophilidae (larvae)	■	■		Coleoptera
Hydroporus	■	■		Coleoptera
Hydrovatus	■	■		Coleoptera
Hygrotus	■	■		Coleoptera
Laccophilus	■	■		Coleoptera
Matus	■	■		Coleoptera
Paracymus	■	■		Coleoptera
Tropisternus	■	■		Coleoptera
Uvarus	■	■		Coleoptera
Crangonyx	■	■		Crustacea
Daphnia	■	■		Crustacea
Culicidae	■	■		Diptera
Belostoma	■	■		Hemiptera
Hebridae	■	■		Hemiptera
Notonectidae	■	■		Hemiptera
Pleidae	■	■		Hemiptera
Ranatra	■	■		Hemiptera
Chauliodes	■	■		Megaloptera
Aeshnidae	■	■		Odonata
Lestidae	■	■		Odonata
Banksiola	■	■		Trichoptera
Cercyon	■			Coleoptera
Coptotomus	■			Coleoptera
Dytiscus	■			Coleoptera

Table C.1. (continued)

Taxon	Permanent	Temporary	Tidal	Group
Georissus	■			Coleoptera
Graphoderus	■			Coleoptera
Baetidae	■			Ephemeroptera
Naucoridae	■			Hemiptera
Cernotina	■			Trichoptera
Oxyethira	■			Trichoptera
Anacaena		■		Coleoptera
Helophorus		■		Coleoptera
Histeridae		■		Coleoptera
Hydrochus		■		Coleoptera
Ostracoda		■		Crustacea
Odontomyia		■		Diptera
Lethocerus		■		Hemiptera
Limnephilus		■		Trichoptera
Dubiraphia			■	Coleoptera
Ectopria			■	Coleoptera
Heteroceridae			■	Coleoptera
Hydraenidae sp.			■	Coleoptera
Lampyridae			■	Coleoptera
Latridiidae			■	Coleoptera
Macronychus			■	Coleoptera
Promoresia			■	Coleoptera
Stenelmis			■	Coleoptera
Tenebrionidae			■	Coleoptera
Gammarus			■	Crustacea
Dolichopodidae			■	Diptera
Empididae			■	Diptera
Forcipomyia			■	Diptera
Siphlonuridae			■	Ephemeroptera
Sparbarus			■	Ephemeroptera
Stylurus			■	Odonata
Porifera			■	Porifera
Ceraclea			■	Trichoptera
Cheumatopsyche			■	Trichoptera
Eurylophella			■	Trichoptera

Table C.1. (continued)

Taxon	Permanent	Temporary	Tidal	Group
Leptoceridae sp.				Trichoptera
Nectopsyche				Trichoptera
Philopotamidae				Trichoptera
Phryganeidae sp.				Trichoptera
Phylocentropus				Trichoptera

APPENDIX D:

MACROINVERTEBRATE TAXONOMIC COMPOSITION ACROSS A TIDAL HEIGHT GRADIENT IN TIDAL FRESHWATER WETLANDS ON SWAN ISLAND, MAINE

Table D.1. Macroinvertebrate taxonomic composition across a tidal height gradient in tidal freshwater wetlands on Swan Island, Maine in summer 2015 (May-August). Shaded boxes indicate that taxon was present in at least one sample taken from a site at that tidal height.

Taxon	High	Mid	Low	Group
Trombidiformes	■	■	■	Acari
Hirudinea	■	■	■	Annelida
Oligochaeta	■	■	■	Annelida
Chrysomelidae	■	■	■	Coleoptera
Dubiraphia	■	■	■	Coleoptera
Haliplus	■	■	■	Coleoptera
Staphylinidae	■	■	■	Coleoptera
Caecidotea	■	■	■	Crustacea
Gammarus	■	■	■	Crustacea
Ceratopogonidae	■	■	■	Diptera
Chironomidae	■	■	■	Diptera
Diptera (pupae)	■	■	■	Diptera
Caenis	■	■	■	Ephemeroptera
Corixidae	■	■	■	Hemiptera
Gerridae	■	■	■	Hemiptera
Lepidoptera	■	■	■	Lepidoptera
Nematoda	■	■	■	Nematoda
Coenagrionidae	■	■	■	Odonata
Nectopsyche	■	■	■	Trichoptera
Oecetis	■	■	■	Trichoptera
Berosus		■	■	Coleoptera
Eurylophella		■	■	Ephemeroptera
Sparbarus		■	■	Ephemeroptera
Gomphidae sp.		■	■	Odonata
Libellulidae		■	■	Odonata
Philopotamidae		■	■	Trichoptera
Phylocentropus		■	■	Trichoptera
Trichoptera (pupae)		■	■	Trichoptera
Scirtidae			■	Coleoptera

Table D.1. (continued)

Taxon	High	Mid	Low	Group
Chaoborus			■	Diptera
Siphlonuridae			■	Ephemeroptera
Stylurus			■	Odonata
Cheumatopsyche			■	Trichoptera
Collembola	■	■		Collembola
Hyalella	■	■		Crustacea
Atrichopogon	■	■		Diptera
Forcipomyia	■	■		Diptera
Sciomyzidae	■	■		Diptera
Tabanidae	■	■		Diptera
Mesovelia	■	■		Hemiptera
Veliidae	■	■		Hemiptera
Donacia		■		Coleoptera
Latridiidae		■		Coleoptera
Stenelmis		■		Coleoptera
Porifera		■		Porifera
Ceraclea		■		Trichoptera
Phryganeidae sp.		■		Trichoptera
Desmopachria	■			Coleoptera
Dytiscidae (larvae)	■			Coleoptera
Ectopria	■			Coleoptera
Enochrus	■			Coleoptera
Heteroceridae	■			Coleoptera
Hydraena	■			Coleoptera
Hydraenidae sp.	■			Coleoptera
Lampyridae	■			Coleoptera
Liodessus	■			Coleoptera
Macronychus	■			Coleoptera
Peltodytes	■			Coleoptera
Promoresia	■			Coleoptera
Tenebrionidae	■			Coleoptera
Dolichopodidae	■			Diptera
Empididae	■			Diptera
Tipulidae	■			Diptera
Hydrometra	■			Hemiptera
Leptoceridae sp.	■			Trichoptera

APPENDIX E:

LENGTH-MASS REGRESSION DATA FOR INVERTEBRATE TAXA COLLECTED

AT SWAN ISLAND, MAINE

Table E.1. Length-mass regression data for invertebrate taxa collected at Swan Island, Maine. Equations are for larvae unless otherwise stated. Equation formats are as follows. (1) $M = aL^b$ (2) $M = aL + b$ (3) $M = (aL^b)/1000$ (4) $M = (aL)^3$ (5) $M = a$, where M is mass in mg, L is body length in mm and a and b are constants. Ranges refer to the body lengths of individuals used to create published equations. Reference key: BAU – Baumgärtner and Rothhaupt (2003); BEN – Benke et al. (1999); BUR – Burgherr and Meyer (1997); CUL – Culver et al. (1985); DOR – Dorn et al. (2011); EAT – Eaton (1983); EDW – Edwards (1967) *in* Caballero et al. (2004); GRE – Greig (2008); GREU – Greig, unpublished data; HEY – Heydarnejad (2010); KES – Kesling and Crafts (1962); MAR – Marchant and Hynes (1981); PAV – Pavlov and Zubina (1990); ROS – Rosati et al. (2012); RUN – Runck and Blinn (1990); SAB – Sabo et al. (2002); SAM – Sample et al. (1993); SMO – Smock (1980); Stoffels et al. (2003). Asterisks denote that equation estimates ash-free dry mass (AFDM) rather than dry mass. N/As denote that data was not available.

Taxon	Format	a	b	R²	Range (mm)	Ref	Equation Taxon
Annelida							
Hirudinea	1	0.025	2.78	0.98	4.14-27.69	ROS	*Erpobdella**
Oligochaeta	1	0.0024	1.875	0.72	1.7-22	STO	Oligochaeta
Nematoda	1	0.0024	1.875	0.72	1.7-22	STO	Oligochaeta
Crustacea							
Crangonyx	1	0.002	3.211	0.90	2.0-13.0	BEN	*C. richmondensis*
Gammarus	1	0.0049	3.001	0.99	N/A	MAR	*Gammarus. pseudolimnaeus*
Hyalella	1	0.0049	3.001	0.99	N/A	MAR	*G. pseudolimnaeus*
Daphnia	3	16.1499	1.6626	N/A	N/A	CUL	*Daphnia galeata* ♀
Ostracoda	5	0.4328			N/A	KES	*Chlamydotheca unispinosa*
Caecidotea	1	0.0036	3.111	0.86	1.8-10.4	BEN	*C. racovitzai*
Trombidiformes	1	0.1327	1.66	0.48	0.55-2.53	BAU	Hydracarina
Collembola	4	3.06	3	N/A	N/A	EDW	Isotomidae
Ephemeroptera							
Baetidae	1	0.0053	2.875	N/A	0.6-8.5	BEN	Baetidae
Siphlonuridae	1	0.0001	4.14	0.96	5.4-18	BEN	*Siphlonurus*
Eurylophella	1	0.008	2.663	0.94	1.7-6.1	BEN	*E. temporalis*

Table E.1. (continued)

Taxon	Format	a	b	R^2	Range (mm)	Ref	Equation Taxon
Ephemeroptera (cont.)							
Caenis	1	0.0054	2.842	0.94	1.7-6.4	BEN	*C. diminuta*
Sparbarus	1	0.0054	2.842	0.94	1.7-6.4	BEN	*Caenis diminuta*
Odonata							
Aeshnidae	1	0.0082	2.183	0.97	3.3-35.4	SMO	*Boyeria vinosa*
Coenagrionidae	1	0.0051	2.785	N/A	2.9-15.2	BEN	Coenagrionidae
Gomphidae sp.	1	0.0088	2.787	N/A	0.9-37.1	BEN	Gomphidae
Stylurus	1	0.0088	2.787	N/A	0.9-37.1	BEN	Gomphidae
Lestidae	1	0.00745	2.97	N/A	4.9-21.0	PAV	*Lestes sponsa*
Libellulidae	1	0.0076	2.809	N/A	2.1-23.8	BEN	Libellulidae
Hemiptera							
Belostoma	2	2.254	-1.37	0.81	4-38.1	DOR	Belostomatidae
Corixidae	1	0.0031	2.904	0.81	3.4-6.8	BEN	*Sigara*
Gerridae	1	0.015	2.596	0.79	9-17.5	BEN	*Gerris remigis*
Hebridae	1	0.00836	3.075	0.93	3.2-40.23	SAM	Hemiptera
Hydrometra	1	0.0145	2.11	N/A	6-28.1	RUN	*Ranatra montezuma*
Mesovelia	1	0.015	2.596	0.79	9-17.5	BEN	*Gerris remigis*
Naucoridae	1	0.00836	3.075	0.93	3.2-40.23	SAM	Hemiptera
Ranatra	1	0.0145	2.11	N/A	6-28.1	RUN	*Ranatra montezuma*
Notonectidae	1	0.0037	3.709	N/A	N/A	GREU	Notonecta
Pleidae	1	0.0037	3.709	N/A	N/A	GREU	Notonecta
Veliidae	1	0.0126	2.719	N/A	2.8-5.5	BEN	Veliidae
Megaloptera							
Chauliodes	1	0.0037	2.873	N/A	2.4-69.2	BEN	Corydalidae

Table E.1. (continued)

Taxon	Format	a	b	R^2	Range (mm)	Ref	Equation Taxon
Trichoptera							
Phylocentropus	1	0.0056	2.839	N/A	0.7-28.2	BEN	Trichoptera
Cheumatopsyche	1	0.0045	2.721	0.83	1.1-11.8	BEN	*Cheumatopsyche*
Oxyethira	1	0.0122	2.57	0.36	1.8-4.17	BAU	*Hydroptila*
Ceraclea	1	0.00128	4.63	0.95	2.23-4.56	BAU	*Ceraclea*
Leptoceridae sp.	1	0.0034	3.212	0.71	1.2-8	BEN	*Oecetis*
Nectopsyche	1	0.0034	3.212	0.71	1.2-8	BEN	*Oecetis*
Oecetis	1	0.0034	3.212	0.71	1.2-8	BEN	*Oecetis*
Limnephilus	1	0.0015	3.115	0.87	5.6-19.2	BEN	*Limnephilus**
Philopotamidae	1	0.005	2.511	N/A	0.8-11.2	BEN	Philopotamidae
Banksiola	1	0.0054	2.811	0.74	3.8-28.2	BEN	*Ptilostomis*
Phryganeidae sp.	1	0.0054	2.811	0.74	3.8-28.2	BEN	*Ptilostomis*
Cernotina	1	0.0071	2.531	0.62	3.1-14.2	BEN	*Polycentropus*
Trichoptera	1	0.0056	2.839	N/A	0.7-28.2	BEN	Trichoptera
Trichoptera (pupa)	1	0.0056	2.839	N/A	0.7-28.2	BEN	Trichoptera
Lepidoptera	1	0.0065	2.959	0.93	6.26-44.62	SAM	Lepidoptera
Coleoptera							
Chrysomelidae (Ad)	1	0.0883	2.171	0.86	3.34-7.84	SAM	Chrysomelidae
Donacia	1	0.0392	3.111	0.96	0.9-4.1	BEN	Chrysomelidae
Acilius (Ad)	1	0.062	2.53	0.76	N/A	GRE	*Rhantus suturalis*
Agabus (Ad)	1	0.062	2.53	0.76	N/A	GRE	*Rhantus suturalis*
Coptotomus (Ad)	1	0.0620	2.53	0.76	N/A	GRE	*Rhantus suturalis*
Desmopachria (Ad)	1	0.0618	2.502	0.84	3.1-6.5	SMO	*Hydroporus*
Dytiscidae (Ad)	1	0.0618	2.502	0.84	3.1-6.5	SMO	*Hydroporus*
Dytiscidae	1	0.0012	3.164	0.95	N/A	GRE	*Rhantus suturalis*
Graphoderus (Ad)	1	0.0620	2.53	0.76	N/A	GRE	*Rhantus suturalis*
Hydroporus (Ad)	1	0.0618	2.502	0.84	3.1-6.5	SMO	*Hydroporus*

Table E.1. (continued)

Taxon	Format	a	b	R^2	Range (mm)	Ref	Equation Taxon
Coleoptera (cont.)							
Hydrovatus (Ad)	1	0.0618	2.502	0.84	3.1-6.5	SMO	*Hydroporus*
Hygrotus (Ad)	1	0.0618	2.502	0.84	3.1-6.5	SMO	*Hydroporus*
Liodessus (Ad)	5	0.69			N/A	GRE	*L. plicatus*
Matus (Ad)	1	0.062	2.53	0.76	N/A	GRE	*Rhantus suturalis*
Uvarus (Ad)	5	0.69			N/A	GRE	*Liodessus plicatus*
Laccophilus (Ad)	1	0.0118	3.117	0.91	2.9-5.8	HEY	*Laccophilus minutus* ♀
Dubiraphia (Ad)	1	0.0389	2.492	0.86	3.34-34.82	SAM	Coleoptera
Dubiraphia	1	0.0025	3.521	0.9	1.2-3.9	BEN	*Promoresia*
Macronychus	1	0.0181	2.311	0.91	1.6-3.7	SMO	*M. glabratus*
Promoresia (Ad)	1	0.0389	2.492	0.86	3.34-34.82	SAM	Coleoptera
Promoresia	1	0.0025	3.521	0.9	1.2-3.9	BEN	*Promoresia*
Stenelmis (Ad)	1	0.0389	2.492	0.86	3.34-34.82	SAM	Coleoptera
Georissus	1	0.0026	2.76	0.42	1.5-7.1	BUR	Coleoptera larvae
Gyrinus	1	0.0026	2.76	0.42	1.5-7.1	BUR	Coleoptera larvae
Haliplus (Ad)	1	0.0271	2.744	0.87	4.4-6	SMO	*Peltodytes sexmaculatus*
Haliplus	1	0.0025	3.521	0.9	1.2-3.9	BEN	*Promoresia*
Peltodytes (Ad)	1	0.0271	2.744	0.76	4.4-6	BEN	*Peltodytes*
Peltodytes	1	0.0025	3.521	0.9	1.2-3.9	BEN	*Promoresia*
Helophorus (Ad)	1	0.0389	2.492	0.86	3.34-34.82	SAM	Coleoptera
Heteroceridae	1	0.0026	2.76	0.42	1.5-7.1	BUR	Coleoptera larvae
Histeridae (Ad)	1	0.0389	2.492	0.86	3.34-34.82	SAM	Coleoptera
Hydraena (Ad)	1	0.0389	2.492	0.86	3.34-34.82	SAM	Coleoptera
Hydraenidae sp. (Ad)	1	0.0389	2.492	0.86	3.34-34.82	SAM	Coleoptera
Hydrochus (Ad)	1	0.0389	2.492	0.86	3.34-34.82	SAM	Coleoptera
Berosus (Ad)	1	0.015	3.012	0.89	3.3-5.9	HEY	*Enochrus bicolor* ♀

Table E.1. (continued)

Taxon	Format	a	b	R²	Range (mm)	Ref	Equation Taxon
Coleoptera (cont.)							
Berosus	1	0.0016	3.26	0.93	N/A	GRE	Hydrophilidae
Enochrus (Ad)	1	0.015	3.012	0.89	3.3-5.9	HEY	*E. bicolor* ♀
Hydrobius (Ad)	1	0.0101	2.952	0.95	17-35	HEY	*Hydrochara dichroma* ♂
Tropisternus (Ad)	1	0.0101	2.952	0.95	17-35	HEY	*Hydrochara dichroma* ♂
Anacaena (Ad)	1	0.0079	2.998	0.99	1.9-3.7	HEY	Laccobius syriacus ♀
Cercyon (Ad)	1	0.0079	2.998	0.99	1.9-3.7	HEY	Laccobius syriacus ♀
Paracymus (Ad)	1	0.0079	2.998	0.99	1.9-3.7	HEY	Laccobius syriacus ♀
Hydrophilidae	1	0.0016	3.26	0.93	N/A	GRE	Hydrophilidae
Lampyridae	1	0.0026	2.76	0.42	1.5-7.1	BUR	Coleoptera larvae
Latridiidae (Ad)	1	0.0389	2.492	0.86	3.34-37.82	SAM	Coleoptera
Ectopria	1	0.0164	2.929	0.99	0.6-5.2	BEN	*Ectopria*
Cyphon	1	0.0026	2.76	0.42	1.5-7.1	BUR	Coleoptera larvae
Scirtidae	1	0.0026	2.76	0.42	1.5-7.1	BUR	Coleoptera larvae
Staphylinidae (Ad)	1	0.001	4.026	0.99	N/A	SAB	Staphylinidae
Tenebrionidae	1	0.0026	2.76	0.42	1.5-7.1	BUR	Coleoptera larvae
Diptera							
Atrichopogon	1	0.00022	2.871	0.91	2.2-10.8	BEN	Ceratopogonidae
Forcipomyia	1	0.00022	2.871	0.91	2.2-10.8	BEN	Ceratopogonidae
Ceratopogoninae	1	0.00022	2.871	0.91	2.2-10.8	BEN	Ceratopogonidae
Chaoborus	1	0.000453	2.43	0.89	N/A	EAT	*Chaoborus punctipennis*
Chironomidae	1	0.0018	2.617	N/A	0.8-13.7	BEN	Chironomidae
Culicidae	1	0.0025	2.692	N/A	0.7-38.1	BEN	Diptera
Dolichopodidae	1	0.0066	2.436	0.69	1.6-8	BEN	Empididae
Empididae	1	0.0066	2.436	0.69	1.6-8	BEN	Empididae

Table E.1. (continued)

Taxon	Format	a	b	R^2	Range (mm)	Ref	Equation Taxon
Diptera (cont.)							
Sciomyzidae	1	0.0025	2.692	N/A	0.7-38.1	BEN	Diptera
Odontomyia	1	0.0032	2.61	0.65	2.43-7.93	ROS	Stratiomyidae*
Tabanidae	1	0.005	2.591	0.81	1.9-16.4	BEN	*Tabanus*
Tipulidae	1	0.0029	2.681	N/A	1-38.1	BEN	Tipulidae
Diptera (pupa)	1	0.0052	2.24	0.6	1.4-4.6	BUR	Diptera pupae
Unidentfied Diptera	1	0.0025	2.692	N/A	0.7-38.1	BEN	Diptera

BIOGRAPHY OF THE AUTHOR

Jack Robert McLachlan was born in Perth, Scotland on March 15, 1991. He was raised in Fort Augustus, in the Highlands of Scotland and graduated from Kilchuimen Academy in 2008. He attended the University of St Andrews and graduated in 2012 with a Bachelor of Science (Honours) degree in Ecology and Conservation. He came to Maine and entered the Ecology and Environmental Sciences graduate program at the University of Maine in the fall of 2014. After receiving his degree, Jack will enroll in the Ecology and Environmental Sciences Ph.D. program at the University of Maine. Jack is a candidate for the Master of Science degree in Ecology and Environmental Sciences from the University of Maine in December 2016.