Resilience of Pool Habitat in a Bay of Fundy Salt Marsh: A Comparative Study

by

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ABSTRACT

A combination of DGPS/GIS mapping, invertebrate surveys and environmental monitoring over one year (July 2004 – July 2005) were used to examine the recovery of permanent tidal pools on a salt marsh in the lower Bay of Fundy which underwent an unmanaged restoration after breach of the dyke over 50 years ago. The results are compared to those of a nearby relatively undisturbed reference marsh.

Pools were found to represent a substantial portion of the marsh habitat, comprising 13% of the total marsh area in the recovering marsh and 4.8% in the natural marsh. Observations indicate ice may be an important mechanism of pool formation and growth in these marshes. Water temperature in the pools ranged from freezing (-2°C) to a maximum of 36°C with ice covering pools for up to one month in the winter. Salinity of the pools ranged from near freshwater (4) to hypersaline (41). Environmental variability was mainly driven by climatic conditions with increased tidal flooding of pools at low elevations tending to make the conditions more stable.

A total of 42 macroinvertebrate taxa were identified in pools of the two marshes, with species richness (S) of individual pools ranging from 13 to 23. An estimated 50 years since dyke failure, the invertebrate fauna of pools in the recovering marsh is indistinguishable from that of the reference marsh. No significant differences in macroinvertebrate communities were detected between sampling dates, pool size or pool depth. Non metric multidimentional scaling and hierarchical cluster analysis supported separating the pool invertebrate communities of this study into those occurring in regularly flooded pools, and those occurring in irregularly flooded pools. Average production of pool macroinvertebrates ranged from 1.79 to 4.03 g dry wt m^{-2}, depending on the amount of vegetative cover in the pools. The pools are characterized by low equitability in species abundance and biomass. The numerically dominant organisms of the pools were mites (Acarina), the gastropod *Hydrobia tottentei*, Tubificidae oligochaetes, and *Chironomus* sp. larvae as well as copepods and ostracods.

RÉSUMÉ

Une combinaison de cartographie DGPS/GIS, des inventaires d'invertébrés et d'un suivi environnemental, s'échelonnant de juillet 2004 à juillet 2005, ont été utilisés afin d'examiner le recouvrement des cuvettes de marée permanentes dans un marais salé, situé dans la partie inférieure de la Baie de Fundy, Nouveau-Brunswick, Canada. Le marais est une ancienne zone endiguée qui fût restaurée lors de la brèche des digues il y a 50 ans. Les résultats ont été comparés à ceux d'un marais avoisinants qui semblaient relativement peu perturbés. Ceux-ci ont servi de références.

Les résultats ont montré que les cuvettes marines étudiées représentent une partie substantielle de la superficie totale de recouvrement des marais salés étudiés, soit 13% et aussi 4.8% dans le marais de référence. Les observations indiquent que la glace pourrait être un mécanisme important de formation et de croissance des cuvettes marines de ces habitats côtiers. La température de l'eau dans les cuvettes marines du point de congélation (-2°C) à un maximum de 36.°C avec des cuvettes marines de bâche de glace pendant un mois en hiver. La salinité des cuvettes de marée est passée près de celle de l'eau douce (4) à celle d'hypersalinité (41). La diversité environnementale des cuvettes est causée principalement par des conditions climatiques; la température et la salinité devenant plus stables avec l'accroissement des marées.

Un total de 42 taxa de macro invertébrés ont été identifiés dans les cuvettes de marée des deux marais, avec la richesse spécifique (S) de différentes cuvettes s'étendant de 13 à 23. Même après 50 années environ depuis l'échec de la digue, la faune invertébrée des cuvettes marines avec recouvrement n'est pas reconnaissable de celle du marais de référence. Aucune différence significative dans les communautés de macro invertébrés n'a été détectée entre les dates de prélèvement, la taille de cuvette de marée ou la profondeur de cuvette. La graduation non métrique multidimentionelle et l'analyse hiérarchique de cluster ont montré que les communautés d'invertébrés étudiées se retrouvent soit séparer dans les cuvettes régulièrement inondées ou bien irrégulièrement inondées. La production moyenne des macro invertébrées de cuvette de marée s'est étendue de 1.79 à 4.03 g de

poids secs / m^2, selon la quantité de couverture de végétation. Les cuvettes de marée sont caractérisées par bas l'équivalence en abondance et en biomasse d'espèces. Les organismes dominants étaient des acarides (Acarina), le gastéropode *Hydrobia tottentei*, les oligochaetes (Tubificidae), et des larves de *Chironomus* spp. aussi bien que des copépodes et des ostracodes.

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Finally, my thanks go to my friends and to my family. To my parents who always told me I could achieve anything I set my mind to and who nurtured any early love of nature. And of course, to Tracey Lavigne, who has been incredibly patient and supports me in every way.

This thesis is dedicated to my grandmother, Dorothy (Estey) Steen.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 2.

Chapter 1: Introduction

Salt marshes occur in temperate coastal areas around the world. Like all coastal habitats, salt marshes have suffered from human population pressure and exploitation (Mitsch and Gosselink 2000). Though not as densely populated as many coastal regions, marshes in the Bay of Fundy have been greatly altered or lost through drainage and conversion to other land uses, mainly agriculture. In parts of the Bay as much as 85% of the original area of salt marsh habitat has been lost since the arrival of European settlers (Ganong 1903, Hanson and Calkins 1996).

Historical loss of salt marsh in the U.S. led to many early studies on the ecology of salt marshes, particularly on the southern Atlantic coast. Early researchers described the high level of primary production in salt marshes and theorized this production was exported as detritus to the adjacent bay, supporting coastal fisheries (Teal 1962). Later work (Haines 1976, Nixon 1980, Odum 2000) partially refuted this outwelling hypothesis, but more recent research (Kneib 1997, Deegan et al. 2000) indicates that salt marshes are a major exporter of secondary production (rather than detritus) by harbouring large juvenile populations of estuarine species and by supporting a high rate of avian foraging. This correlates with another established biological value of salt marshes: their role as a nursery habitat for fish and invertebrates (Daiber 1982, Boesch and Turner 1984).

PHYSICAL STRUCTURE OF SALT MARSHES AND ASSOCIATED POOLS

Like all intertidal regions, distinct zones of dominant flora and fauna in salt marshes relate to the hydroperiod of flooding tides. The hydroperiod, and therefore vegetative zones, is determined by elevation. Vegetative zones of salt marshes on the North Atlantic coast of the United States have been described in detail by Miller and Egler (1950), Redfield (1972) and Niering and Warren (1980) and in the Bay of Fundy by Ganong (1903) and Chmura et al. (1997). Typically, *Spartina alterniflora* dominates the low marsh zone, which is flooded at every high tide, while *Spartina patens* dominates the high marsh zone and is flooded only on spring tides. Chmura et al. (1997) also described a middle marsh zone of *Plantago maritima* in Bay of Fundy marshes of southern New Brunswick. Growth of emergent vegetation is limited in areas where standing water keeps soils permanently saturated.

Permanent or semi-permanent areas of standing water of the marsh surface are alternately called pools, ponds or pannes in salt marsh literature. In this study the term "pool" is used to refer to shallow depressions in the marsh surface that typically remain flooded throughout a tidal cycle, after Chapman (1960); while "panne" refers to shallow depressions which tend to dry up between tidal cycles. There is no consensus on pool morphology, with some researchers defining pools as "steep-sided depressions" (Harshberger 1916; Adamowicz 2002), and other studies reporting a continuum of types ranging from steep to very gradually sloping sides (Clarke et al. 1984; Miller and Egler 1950). Shape has been reported as nearly circular (Nicols 1935) too highly variable (Adamowicz 2002).

Pools occur on the high and low marsh and can cover a substantial portion of the marsh surface (Erwin et al. 1991, Lathrop et al. 2004, Adamowicz and Roman 2005), and there is some indication they are a more abundant landscape feature on geologically "younger" portions of salt marshes (Redfield 1972). In some marshes, pools can be particularly abundant around the marsh/upland border, which may indicate a marsh that is actively transgressing overland (Dame et al. 1992). Recent studies in New England and Louisiana have proposed that increasing pool area, through the combined mechanisms of expansion and coalescence of existing pools, is indicative of a declining salt marsh which is failing to keep pace with sea level rise (Kearney et al. 1988, Delaune et al. 1994, Cavatorta et al. 2003). Through analysis of aerial photos and nautical charts, Kearney et al. (1988) estimated that the average rate of marsh loss in a Chesapeake Bay fluvial coastal marsh was 49.6 ha per year between 1938 and 1985, and that loss of marsh area was primarily due to increases in interior ponding. In a previous study on this marsh, Stevenson et al. (1985) noted that once the pools reached about 1 ha in size, they rapidly elongated along a NW–SE axis, consistent with the direction of the majority of storms through the area.

Miller and Egler (1950) and Redfield (1972) proposed different mechanisms by which salt marsh pools are developed and maintained in New England marshes such as inadequate drainage or deposition of tide drifted materials causing decay of the marsh surface, localized decay of underlying peat, relict depressions or uneven plant growth from the initial saltmarsh formation over intertidal sediments, and slumping of creeks resulting in pools cut off from the drainage system. Pools believed to form by these last two methods are called primary and secondary or channel pans respectively in British salt marsh literature (Little 2000). Ice has been reported as a mechanism of pool and panne formation in marshes of the St. Lawrence Estuary (Dionne 1968).

Functionally, salt marsh pools complement the nursery and foraging values of the marshes as they serve as important habitat for fish (Smith and Able 1994, Adamowicz 2002) and invertebrates (Nicols 1935, Bromley and Bleakney 1979, Clarke et al. 1984), and important feeding sites for birds (Clarke et al. 1984, Erwin 1996). Clarke et al. (1984) found a strong correlation between pool density and bird use in Massachusetts salt marshes, particularly for shorebirds, herons, and terns.

PREVIOUS STUDIES ON POOL ECOLOGY

Despite their apparent ecological importance in the salt marsh, only a handful of studies have focused specifically on the pools. The most complete studies I could find were from widely disparate times and locations. Nicols (1935) studied salt marsh pools extensively in a marsh in Scotland. Nixon and Oviatt (1973) examined pools as part of a larger energy flow study in a Rhode Island marsh. Two papers by Bromely and Bleakney (1979) and Bleakney and Meyer (1979), on environmental parameters and invertebrates of salt marsh pools in Minas Basin in the upper Bay of Fundy are probably the most comprehensive characterization of this habitat. Ward and Fitzgerald (1983) looked for patterns of benthic invertebrate diversity in a marsh in the Gulf of St. Lawrence. Clarke et al. (1984), in a study primarily examining bird use on ditched and unditched marshes in Massachusetts, sampled pool invertebrates over a two-week period in the summer. Ingolfsson (1994) looked at pools in a salt marsh in western Iceland in 1977–78 and returned for follow-up samples on one visit in 1991. A comparative study by Heck et al.

(1995) looked at diversity and production of macrofauna in estuarine nursery habitats, including marsh pools, in a Massachusetts marsh. Stocks and Grassle (2003) compared benthic macrofauna in partially impounded salt marshes to that of natural marshes including associated pools. All of these studies listed the invertebrate species found in the pools. Macrofaunal diversity from these studies is summarized in chapter 3 (table 7). Adamowicz and Roman (2005) described physical characteristics of pools and determined pool density on ditched and unditched marshes from Long Island Sound to southern Maine. Adamowicz (2002) also determined macrophyte cover of pools in 12 marshes and examined the response of nekton to the creation of new pools by ditch plugging in 3 marshes. Recent articles by Giberson (2001) and Mackenzie (2005) have focused specifically on insects of the pools and have demonstrated that the coarse level of taxonomic scale used in earlier studies have underestimated insect diversity in the pools, although the same could probably be said of diversity studies in most habitats.

The most thorough studies on salt marsh pools were those of Nicols (1935) and the two papers co-authored by Bleakney (1979). Nicols studied 13 pools on a Scottish salt marsh intermittently over three years. Bromley and Bleakney (1979) sampled benthic pool invertebrates every month randomly in one of their 10 study pools situated in five individual salt marshes in Minas Basin over a two-year period. Two of the pools in one marsh were studied intensively by students of Acadia University from 1965 to 1967. This information and additional data collected from 1967 to 1977 were summarized by Bleakney and Meyer (1979). Bromley and Bleakney reported 56 species of benthic macro- and meio-fauna (to species retained on a 0.233 mm mesh), including 18 new species records for the Bay of Fundy. Excluding meiofauna, 37 species of benthic macrofauna were reported from Minas Basin. The next highest diversity, 25 species, was reported by Nicols (1935). Other studies reported much lower diversity; for instance, Nixon and Oviatt (1973) sampled macrofauna weekly for most of a year and included a sample that examined meiofauna but only reported 14 species from their study pools. The difference in diversity may simply be related to sampling intensity, but there could be other factors influencing these results. Bromley and Bleakney (1979) and Nicols (1935) were the only researchers who specified that their sampling was designed to bracket extreme tide events or climatic events, such as heavy rains, and therefore may have included some transient fauna of the pools.

A few other published studies of salt marsh pools can be found in entomology and pest control journals, as this habitat was perhaps most frequently studied by researchers concerned with the salt marsh mosquitoes. Some of these studies have examined physical characteristics and conducted invertebrate censuses, but only included pools near the upland edge where infrequent flooding allows mosquitoes to develop (e.g., Campbell and Denno 1978).

There has not been enough research conducted in these pools to make any generalizations, but there is potential here to see how these biological communities respond to extreme environmental fluctuations. Tidal pools on rocky shores, which may be somewhat analogous to regularly flooded pools in the low marsh, have been extensively studied, and there is a good understanding of community organization in this habitat (Kneib 1984). However, intertidal soft substrates, including mudflats and salt marshes, which form a more extensive habitat than rocky shores, are less studied despite the fact that much of the preliminary research on community organization in this habitat conflicted with paradigms developed from rocky shore studies (Peterson 1979). Kneib (1984) noted the need for more investigation into community organization and distribution patterns in intertidal soft substrates.

RESTORATION / RECOVERY OF SALT MARSHES

In the U.S., much work is being done to actively "restore" salt marsh habitat or to "create" habitat as some state legislation allows marsh to be destroyed providing an equal or greater area of comparable habitat is created elsewhere (Warren et al. 2002). In Canada, where urban pressure in the coastal zone is not as great as in parts of the U.S., some salt marshes that were dyked in the past for agricultural use have been recovering for many years since dykes were breached by natural causes. This is the case for Saint's Rest marsh, the recovering marsh in this study. Trajectory, a recent term in restoration ecology, has been used to describe the hypothetical path and length of time a restored system might take to reach the level of function in healthy, natural systems (Morgan and Short 2002). Trajectory times have been empirically determined for some functional components of salt marshes in restored or created marshes in the United States. Vegetative succession to a typical salt marsh community occurs within 5 to 10 years (Burdick et. al. 1997, Boumans et. al. 2002, Morgan and Short 2002). Creek use by nekton (fish and decapod crustaceans) can return to a level similar to a pristine marsh in as little as one year (Roman et. al. 2002), although a gut content study of mummichogs by Allen et al. (1994) found that the forage value of a restored marsh had not fully recovered after 15 years. This is related to findings that invertebrate communities of the marsh surface may take over 20 years to recover (Fell et al. 1991, Warren et al. 2002).

Recovery of breeding bird populations of salt marsh specialists takes about 15 years; however, 3 to 5 years after restoration or creation of a salt marsh, generalist bird species populations may be significantly higher than in nearby reference marshes and this increased use has persisted in some marshes for more than 20 years (Brawley et al. 1998, Fell et. al. 2000, Warren et. al. 2002).

Recovery trajectories of some components of the salt marsh ecosystem, such as marsh pools and associated flora and fauna, have not yet been examined. I believe this is the first study to quantitatively compare pool habitat of an undisturbed and a recovering marsh. From Bleakney and Meyer's (1979) description of Canard marsh in Minas Basin (upper Bay of Fundy), one of their study sites, it appears this was a recovering marsh. They observed that it differs from nearby marshes in its geomorphology (more gradual slope) and in its number and variety of pools. Though they did not do any quantitative analysis, they noted that some of the abundant invertebrate species in the pools of Canard marsh were not found in other local marshes and suggested this marsh might be "an important reservoir for marsh species". These observations, in association with the established importance of shallow pools on the marsh to avian foraging (Burger 1982, Clarke et al. 1984, Master 1992, Erwin 1996) and the observed elevated use of recovering marshes by some bird species mentioned above, suggest that pool habitat and the species which depend on them may be enhanced in recovering marshes.

Research Strategy and Thesis Structure

In order to examine the difference in the form and function of pools as a component of salt marsh habitat between a recovering and an undisturbed marsh, as well as contribute to the body of knowledge on pool environments and invertebrate communities, a combination of techniques: mapping, environmental monitoring and invertebrate sampling, were employed. Dipper Harbour Marsh, a relatively undisturbed marsh located in the lower Bay of Fundy serves as the reference site. Saints Rest Marsh, 28 km northeast of Dipper Harbour, has a long history of human alteration including dyking and ditching as well as construction of roads and a rifle range. Currently, the marsh is bounded on one side by a highway and a sewage treatment plant discharges into the head of the creek. Abandonment of the dykeland in the 1950's resulted in eventual breaching of the dyke. Saints Rest marsh is a natural laboratory in which to study the process of recovery in salt marshes after tidal restriction and other disturbances.

Chapter 2 of this thesis examines and compares the spatial coverage and distribution of pool habitat in the reference and recovering marshes. Results are also reported on intensive observation and monitoring over a one year period in order to determine the extent of and controls on environmental variability. In Chapter 3 the results of the invertebrate surveys are reported with analysis of community and species patterns. Both of these chapters will be submitted for publication to *Estuaries and Coasts* as separate journal articles, thus, there is some repetition in text. Chapters 2 and 3 have been formatted according to the journal's specifications.

Chapter 2: Spatial and Environmental Variability of Pools on a Natural and a Recovering Salt Marsh in the Bay of Fundy

ABSTRACT: Differential GPS was used to map salt marsh pools in a natural and a recovering salt marsh in the lower Bay of Fundy. Pools were found to represent a substantial portion of the marsh habitat, comprising 13% of the total marsh area in the recovering marsh and 4.8% in the natural marsh. Observations indicate ice may be an important mechanism of pool formation and growth in these marshes. Pools at different elevations were selected at each marsh to monitor variability in temperature and salinity over one year. Water temperature ranged from freezing (-1.97°C) to a maximum of 36.1°C with ice covering pools for up to one month in the winter. Salinity of the pools ranged from near freshwater (4) to hypersaline (41). Environmental variability was mainly driven by climatic conditions with increased tidal flooding of pools at low elevations tending to make the conditions more stable.

Introduction

A natural salt marsh on the Atlantic coast of North America is characterized by a network of meandering creeks and isolated pools and pannes distributed across an emergent vegetated platform (e.g., Miller and Egler 1950; Redfield 1972). Most of the salt marsh area of the Bay of Fundy has been altered; dyked and ditched to convert the land to agricultural use (Ganong 1903; Bleakney 2004). Abandonment of some dykes in the 1940's and 50's has resulted in unmanaged recovery of salt marshes. These sites can serve as natural laboratories to examine the long-term outcome of salt marsh restoration and help inform current restoration management. In this study, I examine the status of salt marsh pools on a recovering marsh in comparison to an undyked reference site.

Salt marsh pools are shallow depressions in the marsh surface that typically remain flooded throughout a tidal cycle (Chapman 1960). Some researchers define pools as "steep-sided depressions" (Harshberger 1916; Adamowicz 2002), while other studies report a continuum of types ranging from steep to very gradually sloping sides

(Clarke et al. 1984; Miller and Egler 1950). Shape has been reported as nearly circular (Nicols 1935) to highly variable (Adamowicz 2002). Miller and Egler (1950) and Redfield (1972) proposed mechanisms by which salt marsh pools are developed and maintained in New England marshes such as inadequate drainage or deposition of tide rafted materials causing decay of the marsh surface, localized decay of underlying peat, relict depressions, uneven plant growth from the initial salt marsh formation over intertidal sediments, and slumping of creeks resulting in pools cut off from the drainage system. Ice has been reported as a mechanism of pool / panne formation in marshes of the St. Lawrence Estuary (Dionne 1968). Functionally, salt marsh pools complement the nursery and foraging values of the marshes (Daiber 1982; Boesch and Turner 1984) as they serve as habitat for invertebrates (Nicols 1935; Bromely and Bleakney 1979; Clark et al. 1984), including important prey species of fish and birds (Ferringno 1961; Ward and Fitzgerald 1983; Clark et al. 1984; Smith and Able 1994; Erwin 1996).

Recent studies of some locations in New England and Louisiana have found that interior ponding (expansion and coalescence) increased at the expense of vegetated marsh (Kearney et al. 1988; Delaune et al. 1994; Cavatorta et al. 2003; Erwin et al. 2004). Through analysis of aerial photos and nautical charts, Kearney et al. (1988) estimated that the average rate of marsh loss in a Chesapeake Bay fluvial coastal marsh was 49.6 ha per year between 1938 and 1985, and that loss of marsh area was primarily due to increases in interior ponding. Also using aerial photos, Erwin et al. (2004) found interior ponding had resulted in a 6.9% decrease in marsh platform in one New Jersey marsh over a 63 year period and that the rate of loss was increasing.

Despite their ecological importance there is little baseline information on the spatial distribution and controls on the environment of salt marsh pools. This information would inform management recommendations for restoration projects, and research on the role of pools in marsh stability. The purpose of this study was twofold. The first goal was to examine and compare the spatial coverage and distribution of pool habitat in a "natural" salt marsh and a marsh which was formerly ditched and dyked, but has been recovering since an unmanaged dyke breach approximately 50 years ago. The objective of this comparison was to test the hypothesis that the recovering marsh reverts to a "young" stage of marsh development as described by Redfield (1972). Visual observation of the marshes suggested the recovering marsh would have more pool area than the reference site, and that pools were hydrologically connected to each other or to marsh channels and not isolated habitats. The second goal was to determine the extent of and controls on environmental variability. To this end, individual pools on each marsh were chosen for intensive observation and monitoring over a one year period. It was hypothesized that small changes in elevation would have a large effect on environmental variability and that there would be a positive correlation between pool elevation and environmental variability due to increased flooding frequency with decreasing elevation.

SITE DESCRIPTIONS

Both sites are located in the lower Bay of Fundy near Saint John, New Brunswick where the tidal range is approximately 6 m (fig. 1). Saints Rest marsh, the recovering site, is a broad, back barrier marsh in which the predominant vegetation is *Spartina alterniflora* except near the upland edge where it is replaced by *Spartina patens*, *Juncus* *gerardii* or *Carex palacea*. Dipper Harbour marsh, the control site, is a narrow river valley marsh with a mosaic of vegetation but generally with *S. alterniflora* dominant near the creek edge and *S. patens* at higher elevations' but with a middle marsh zone dominated by *Plantago maritima* (Chmura et al. 1997). The physiography of Dipper Harbour marsh was described in detail by Chmura et al. (1997). It would have been desirable to pair the recovering marsh with a control marsh of similar size and type, however there are few marshes in the region which have not been dyked and ditched in the past and those that exist tend to be small as they were probably considered not worth the effort required for dyking.

Saints Rest marsh has a complicated history of human use including dyking, ditching, and construction of barns and roads, as well as forestry and gravel extraction in the adjacent upland and beach. Sometime prior to WWII the marsh was greatly modified as a military shooting range. Subsequent abandonment in the 1950's resulted in the dyke and tidal gate falling into disrepair and eventually being breached. Aerial photos of the site around the time of the dyke breach show extensive ditching and no pools and sediment cores show an agricultural sediment horizon (Noel et al. 2004). Part of the remaining dyke was removed and a boardwalk constructed in 1991allowing increased water flow onto the marsh. Currently a sewage treatment plant discharges at the head of the marsh creek. Now the largest salt marsh in Saint John, Saints Rest marsh is a natural laboratory in which to study the process of recovery in salt marshes after tidal restriction and other disturbances.

Dipper Harbour marsh is located approximately 28 km southwest of Saints Rest marsh in the village of Dipper Harbour, New Brunswick. There has been no major alteration of this marsh and it is considered reasonably undisturbed. The main impact at this site is a bridge passing over the marsh creek outlet that allows relatively unrestricted flow.

Three pools on each of Saint's Rest marsh and Dipper Harbour marsh were chosen for regular (intensive) monitoring. Pools were chosen to represent three elevations on the marshes, high marsh, low marsh and one pool in the transition between high and low marsh (mid-marsh) as indicated by pool salinity and surrounding vegetation. Pools surrounded predominately by *S. patens* were considered high marsh pools while those predominately surrounded by *S. alterniflora* were considered low marsh pools. The 6 main study pools were highly variable in shape, dimensions and depth (figs. 2 and 3, table 1).

The three study pools at Saints Rest marsh are located along a transect from the upland to the main creek, about midway between the creek mouth and headwater (fig. 2). The high marsh pool (hereafter referred to as SRH) has steep well-defined banks and is surrounded by a mosaic of vegetation, mainly *S. patens* and *Pucinellia* sp., but also including *P. maritima, Atriplex sp.,* and *S. alterniflora*. *Spartina alterniflora* and *Schoenoplectus robustus* are dominant around the pool edges. The mid-marsh pool (SRM) has gradually sloping edges with *S. alterniflora*, the dominant surrounding vegetation, growing into the edges of the pool. There are also scattered stems of

Pucinellia sp. around this pool. The low marsh pool (SRL) is close to the mid-marsh pool, but located across the old road bed of the shooting range, and is connected to the main creek by a shallow drainage channel. This pool has gradually sloping edges around most of the pool. Surrounding vegetation is *S. alterniflora* with some *Salicornia europaea*.

At Dipper Harbour the high and low marsh study pools are located on opposite sides of the main creek, about 350 m up from the mouth of the creek (fig. 3). The mid-marsh pool is located about 400 m further up the marsh. The high marsh pool (DHH) is long and narrow. The side closest to the creek has well-defined banks while the upland side is a gradually sloping edge. *Spartina patens* is the dominant surrounding vegetation, along with *J. gerardii* and *Pucinellia* sp., except on the upland side where *S. robustus* is dominant and grows into the edge of the pool. The mid-marsh pool (DHM) is nearly circular with well-defined banks except on the upland edge where *S. robustus* grows into the pool. The rest of the pool is surrounded mainly by *S. patens* except for a section closest to the creek where *S. alterniflora* is dominant. The low marsh pool at Dipper Harbour (DHL) is ovoid with well-defined banks surrounded mainly by stunted *S. alterniflora*, along with *P. maritima* and *S. europaea*.

Methods

Pool mapping

Position and elevation data were collected for all pools and their suspected drainage patterns on the recovering marsh (inside the dyke) at Saint's Rest and at Dipper

Harbour marsh, using a Trimble 4700 differential Global Positioning System (DGPS). Data were collected using GPS standard datum (WGS84) and post-processed using GPSurvey with TS Office software (Trimble Navigation Limited). The rover data were differentially corrected with the base data using published coordinates for the Saints Rest monument (Survey New Brunswick (SNB) monument no. 20091, published vertical precision ±1 cm). Corrected coordinates were required for the Dipper Harbour monument (SNB monument no. 20704, published vertical precision ±10 m) because of the high distortion vectors in the published data. The coordinates for the Dipper Harbour monument were derived from a differential correction obtained through a GPS Static survey (1 hour point reading) between this monument and a monument about 10 km away at Chance Harbour, N.B. (Secondary infill monument of the New Brunswick High Precision Network no.28125). The corrected data have an estimated accuracy of ±1 cm in the horizontal and vertical. During post-processing a data transformation was performed to the NAD83 CSRS (Canadian Spatial Reference System) datum. The WGS84 ellipsoidal heights were adjusted to mean sea level with the HT v 2.0 geoid model using Natural Resources Canada GPSH software.

GPS points were taken around the edge of Saints Rest marsh to obtain a total marsh area measurement. The steep valley slopes surrounding Dipper Harbour marsh interfered with satellite signals and prevented the collection of GPS data at the marsh/upland border and so the marsh edge at Dipper Harbour, as well as the main creeks at both marshes, were digitized as polygon layers from the most recent air photos. Historic (1945) and recent (1994) air photos (Natural Resources Canada) were georeferenced to the NAD83 CSRS projection using topographic maps. The total mapped marsh areas (minus the main creek) at Saints Rest and Dipper Harbour marsh are 93.9 ha and 8.6 ha, respectively.

Features were considered 'pools' if they contained no emergent vascular plants, which would indicate a panne habitat, and contained water most of the time. A combination of hot, dry weather and neap tides can cause temporary drying in virtually all pools but this was only observed once over the 2 year study. Pools types included the "*Ruppia* pools" and "potholes" of Miller and Egler (1950). Data points were collected around pool edges and through apparent connecting channels (narrow strips with no, or very stunted, vegetation). The pool edge was indicated by an abrupt change in substrate or cessation of emergent vegetation growth, usually in combination. A sufficient number of measurements were made around each pool to determine the approximate size and shape using mapping software and to estimate the elevation of the pool edge within the tidal frame (3 – 80 points per pool). A total of 11,425 points were collected at Saints Rest, 4,934 at Dipper Harbour. Concentrated areas of small pools were encountered at Dipper Harbour marsh, near the upland edge. Since it was not possible to walk into these areas to map individual pool edges the whole area was mapped and coded as 'standing water'. To be coded as standing water a section of marsh surface had to consist of $\geq$ 50% pool area.

The corrected data were projected as points in ARCMAP 9.1 (ESRI 2005), in the Universal Transverse Mercator (UTM) coordinate system (zone 19N). The GPS points defining pools were connected as polygons with elevations from individual points spatially joined to polygon layers to determine average pool elevations. Spatial analyst tools in ARCMAP were used to determine pool and marsh area and for buffer analysis, to determine the total pool area occurring in 10 m buffers from the main creek. ARCMAP tools were also used to determine clustering of pools by Euclidean distance of average nearest neighbor.

SALINITY

Salinity was measured with a refractometer first at the water surface, then at the sediment surface by siphoning water from the pool bottom carefully, so not to mix the water column, to check for stratification in the water column. Measurements were made at approximately the same location within the pools on each sampling occasion. During some sampling events additional measurements were taken at other locations within the pools to determine spatial variability of salinity. A single factor ANOVA test was performed using SAS 9.1 software on the surface salinity and bottom salinity measurements for all pools. Salinity was monitored in each of the 6 pools at least once per month from late July 2004 to July 2005. To examine the effects of tidal flooding and precipitation on pool salinity, additional measurements of salinity were made from August 11 – 25th 2004 in Saints Rest marsh pools to bracket a period of increased precipitation and no tidal flooding. Also, salinity was measured in the pools of both marshes the last week of August, and again on September 2, 2004, to bracket a one week period of extreme high tides.

TEMPERATURE

Temperature variation was examined over one year in a high marsh pool and a low marsh pool on both marshes. Hobo™ dataloggers in waterproof containers were placed in each of these 4 pools on August 3, 2004 and maintained until August 2005. After installing the dataloggers it was noted that the pools considered to be located on the low marsh did not flood every day as had been expected, but only on higher spring tides. A pool at a lower elevation on Dipper Harbour marsh was located which appeared to be flooded on most high tides and an additional datalogger was placed in this pool ("lower-low marsh pool") in November 2005. Additional temperature data were collected using a digital thermometer to examine temperature variability and stratification within individual pools and within the sediment.

The dataloggers were weighted and placed about 2.5 m from pool edges. Although there was occasionally substantial drying in the pools, the datalogger containers were covered by water throughout the study. Dataloggers were also placed at the edge of each marsh on November 1, 2004 to monitor ambient air temperatures about 1 m above the marsh surface.

The dataloggers were set to record temperature at intervals of 5, 16, or 36 min, depending on the location of the datalogger and the time of year. Longer intervals were generally used in the winter to minimize the need to retrieve and reset the instrument when accessibility was limited. Occasional gaps in temperature data occurred because of equipment failure or loss, inability to retrieve dataloggers under ice, and movement of the dataloggers out of the pool during ice breakup. Due to a combination of these factors, there was no winter temperature data collected for the low marsh pool in Saints Rest marsh. The unexpected movement of two of the dataloggers during parts of the winter resulted in some measurement of the air temperature at the sediment surface, as well as the temperature of the seawater during submersion by flood tides. Tide water was considered to have flooded a pool if the rate of water temperature change exceeded $1^{\circ}C$ over 16 min and this increased rate of change coincided with the time of a high tide as recorded from the Saint John tide gauge.

Temperature data were examined by tidal cycle, with a tidal cycle being defined as the 14-day period between the first quarter and last quarter phases of the moon. Tide data for the Saint John tide gauge, maintained by the Canadian Hydrographic Service, was downloaded from the website of the Canadian Department of Fisheries and Oceans (www.lau.chs-shc.dfo-mpo.gc.ca). The Saint John gauge is located just outside of Saint John Harbour, approximately 5 km northeast of Saints Rest marsh (Station no. 65, $45.251^{\circ}N$ $66.063^{\circ}W$). Tide heights at Dipper Harbour were calculated from the Saint John tide gauge data using calculations from the Canadian Tide and Current Tables.

Results

Pool Mapping

At Saints Rest marsh the pools cover 13.1% of the total marsh surface, while at Dipper Harbour pools cover 4.8% of the marsh. If the areas mapped as standing water in

Dipper Harbour are considered to consist of approximately 50% pool habitat, then the total pool coverage at Dipper Harbour marsh increases to 6.7%. The pool coverage therefore, is 2 to 3 times greater on the recovering marsh.

Saints Rest had 6 times as many pools as Dipper Harbour (table 2). The average pool size at Saints Rest marsh is 144 m^2, but this average is highly skewed by a few very large pools, while the majority of the pools on this marsh are < 100 m^2. The largest pool (12,384 m^2) at Saints Rest is more than twice the size of the next largest pool (5,439 m^2). The overall average pool size at Dipper Harbour marsh is 31 m^2, again, skewed by large pools with pools < 100 m^2 averaging 8 m^2 (table 2). Pools at Dipper Harbour marsh ranged from < 1 m^2 to 522 m^2.

Elevations of channels 'connecting' pools were at slightly higher elevation than pool edges indicating that the pools are mostly isolated between flood tides. Field observations suggest that some of these "channels" between pools may be wildlife paths, formed particularly by waterfowl as they move between pools to feed. Although these paths do not increase the flooding frequency in pools they most likely facilitate the movement of fish and some invertebrates between pools when the marsh surface is flooded.

Flooding frequency of the pools was predicted from the lowest mapped elevation between each pool edge and the nearest creek, and the tide heights from the Saint John tide gauge record (fig. 4). The pools mapped at Saints Rest are predicted to flood on 6 to

65% of high tides over one year (fig. 4). At DH, 2 to 68% of high tides were predicted to flood mapped pools (fig. 4). Actual observed flooding frequency, determined for the intensively studied high and low marsh pools by examining the rate of change in water temperature, was similar to the predicted rate (table 1). Frequency distribution diagrams for the pools based on elevation show a near normal distribution of pools across the range of elevation of the marsh platform, slightly skewed towards more pools at higher elevation (fig. 5). This pattern is not as clear at Dipper Harbour due to the much lower number of pools (fig. 5B).

Buffer analysis was performed to examine spatial distribution of pool area on the two marshes. Saints Rest is a much wider marsh than Dipper Harbour so for comparison the buffers were converted to percent distance from creek, with 100% distance being the farthest pool from the creek. There was greater pool area with proximity to creek at both marshes (fig. 6). Pool area at Saints Rest increased rapidly with distance from creek to a maximum of over 10 km^2 at the 50 m buffer or about 20% of the distance from the creek to the upland. There was a steady decline in pool area from 50 m to the marsh edge, except for a slight increase at the 200 m buffer, 75% distance from the creek. Pool area at Dipper Harbour peaked at about 3 km^2 at the 30 m buffer (fig. 6). The pools were clustered at both marshes, more strongly at Saints Rest. (Saints Rest: Z score = -35 SD, p=0.01; Dipper Harbour: Z score = -16.4 SD, p=0.01)

SALINITY

An ANOVA of salinity measurements showed that the differences in both surface and bottom salinity were strongly significant ($p>0.01$). When the high marsh pool was removed, the surface salinity of mid and low marsh pools was still significantly different, but the difference was not as significant ($p<0.05$). When the salinity measurements of mid and low marsh pool bottoms were compared, there was no significant difference. The lowest salinity recorded in the study pools was 4 at the surface in the high marsh pool at Dipper Harbour on September 16, 2004; the highest was 41 at the sediment surface in the mid-marsh pool at Saint's Rest on April 20, 2005.

Initial measurements of salinity (in June 2004) showed that high marsh pools had lower salinity then low marsh pools. The high marsh pool at Saint's Rest marsh had consistently lower salinity than the other two study pools on this site, for both surface and bottom measurements throughout the study (fig. 7) with one exception; on March 30, 2005 the bottom salinity in the high marsh pool at Saints Rest exceeded that of the low and mid marsh pools. The high marsh pool at Dipper Harbour also had the lowest average surface and bottom salinity of the Dipper Harbour marsh pools, but at times exceeded the salinity of the mid or low marsh pools at Dipper Harbour.

In all pools, except the lower-low pool, salinity was highly variable. The average salinities of mid and low marsh pools within and between marshes were similar (figs. 7, 8). The lower-low pool at Dipper Harbour that was added to the study in November 2004 had an average salinity of 34 and showed virtually no stratification or variability in salinity. Weather extremes (heavy rains, stretches of hot dry weather) and pool depth seemed to have more influence over pool salinity than flooding frequency. The most rapid change in salinity observed was at the sediment surface of the mid-marsh pool at Saint's Rest, which decreased from 38 on August 11th to 18 by August 25th (fig 12).

The high marsh pool and mid marsh pools in Dipper Harbour were the most stratified with average difference between the surface and bottom salinity measurements 13 and 8, respectively (fig. 7). The difference in the Saints Rest high marsh pool was 5; all other pools differed an average of 2 from the surface to the bottom salinity. Stratification increased in all pools after November. This coincided with the formation of ice in the pools. As the freshwater was incorporated into the ice, the denser salt water became concentrated at the bottom. The last recorded observation of ice or slush in the pools was on March 14, 2005, when tides were flooding the pools and the stratification of the water in terms of salinity had returned to pre-winter conditions.

The low marsh pool at Dipper Harbour and all Saints Rest pools had relatively uniform salinity throughout individual pools. Additional measurements at various locations within the high and mid marsh pools at Dipper Harbour showed spatial variability within the pools with lower salinities (surface and bottom) consistently recorded on the side closest to the upland edge (table 3).

Temperature

Water temperature in the pools ranged from freezing (-1.97°C) to a maximum of 36.1°C. There was little difference between the average temperatures in the four study pools on a yearly or seasonal basis. The air temperature at Saints Rest was generally slightly cooler (table 4), likely because Dipper Harbour is a more sheltered site. The Hobos were weighted to sit on the bottom of the pools and, as was expected, the rate of temperature change was lower in deeper pools. The water temperature in the high marsh pool at Saints Rest (SRH), the deepest pool in the study, was the least variable as evidenced in the generally lower standard deviations in temperature over the five seasons included in this study (table 4).

A single factor ANOVA was performed to test for differences in the mean temperature of each of the high and low marsh pools by tidal cycle. Although the average mean temperatures of the low marsh pools were lower that that of the high marsh pools when compared by tidal cycle the differences were not significant ($p=0.26$). Inclusion of the lower-low marsh pool at Dipper Harbour marsh in the analysis revealed no overall significant difference between mean temperature of pools by tidal cycle ($p = 0.28$), however multiple comparisons of the means showed that the lower-low marsh pool was significantly different from the high marsh pool at Dipper Harbour.

Air temperature was very similar at the two marshes, as was expected given their proximity. The maximum air temperature was 31.5°C on August 5, 2005 at 2:30 PM (recorded at Dipper Harbour marsh). The minimum air temperature was recorded on January 22, 2005, between 7:30 to 7:50 AM; -26.1°C at Dipper Harbour, -27.2°C at

Saints Rest. Greater extremes of temperatures at Saints Rest marsh are due to differences in topography of surrounding uplands. Dipper Harbour marsh is a narrow, river valley marsh with steep banks on either side, protected from cooling winds and is likely more resistant to rapid temperature change than Saints Rest marsh, which is at a flat, open site behind a barrier beach. The air temperature at both marshes changed rapidly, with rates of increase or decrease sometimes exceeding 5°C over 15 to 25 min. The rate of temperature change was generally highest in the winter months at both marshes.

In the high marsh pools the warmest temperatures were observed in June 2005, with both the highest monthly average temperature and the maximum overall temperature. The low marsh pools in Saints Rest and Dipper Harbour had maximum temperatures occur in July and June 2005, respectively, yet in both pools the warmest monthly average temperature occurred in August 2004. Ice formed in all of the pools over the winter. The lowest monthly average temperature in all pools occurred in January. The high marsh pool in Saints Rest had an average temperature below zero over three tidal cycles; from January 17th to February 15th, and from March 3-16th. Examination of the continuous temperature data over this period shows some warming in the pool in February when peaks in temperature coincided with extremely high spring tides despite falling air temperature (fig. 9). The highest tide of the study was 4.44 m above mean sea level on February 11, 2005 (fig. 9). Lower ambient temperature and lower spring tides resulted in the pool re-freezing over the next tide cycle. Thawing coincided with the next spring tide and the water temperature rose quickly after this (March 17 onward), surpassing the rate of increase of the air temperature.

EFFECT OF TIDES

Temperature in the pools fluctuated continuously with changing ambient conditions, but the rate of change was low, generally < 1°C over 16 min. However, the effect of tide waters reaching the pools was to rapidly drive the temperature of the water in the pool towards the temperature of the incoming seawater (fig. 10). This resulted in a drop in pool water temperature in summer or an increase in the winter. The effect in the spring and fall varied according to whether the pool temperature was above or below the temperature of the incoming seawater. For example, in November of 2004 flooding tides caused the water temperature in the high marsh pool at Saints Rest marsh to drop, while the temperature in the low marsh pool increased. In both pools the effect of the flooding was to drive the water temperature towards about 5°C (fig. 11). Observed flooding frequency for the high and low marsh pools is reported in table 2.

Discussion

EXTENT AND SPATIAL DISTRIBUTION OF POOLS

The 13.3% pool coverage at Saints Rest, the recovering marsh in this study, falls within the high range of published values. Dipper Harbour is on the low end of the range with 4.8% coverage. Few studies have reported the extent of pool habitat on a salt marsh. Erwin et al. (1991) gave details of pool area and total marsh area in 7 control sites in the mid-Atlantic region of the U.S. in their study of open marsh water management effects on birds and found pools covered 1 to 32% (average 10%) of the marsh area. Adamowicz and Roman (2005) digitized pools from aerial photos to determine pool density in selected areas of 24 ditched and 8 unditched salt marshes from southern Maine to Connecticut and reported 4 to 14% pool coverage in the unditched sites, and 0 to 5% in the ditched sites. Lathrop et al. (2004) digitized different spatial features of one natural (unditched) marsh in New Jersey and found that pools comprised 8% of the area of the marsh. They mention the minimum size of pools digitized was 8 m^2. This was the average size of the majority of pools at Dipper Harbour (table 2), thus many small pools would be missed using this technique. Adamowicz and Roman (2005) note that the wide range of values for pool density in the marshes they examined may be due in part to combining different marsh types (e.g., river valley and back barrier marshes) which may be the case in this study. Further examination of pool density in restored or recovering marshes are needed to see if this valuable habitat type is enhanced in these marshes.

A few authors have proposed methods by which pools form on the marsh surface (Harshberger 1916, Miller and Egler 1950, Redfield 1972, Pethick 1974), but there has been little observational evidence. Redfield (1972) postulated that geologically younger ("immature") marshes would have more pools. The pool coverage on the recovering marsh in this study is nearly 3 times that of the control site. It may be that as a part of the recovery process the marsh reverts to a "younger" stage, due to the subsidence that would have occurred while the marsh was cut off from tidal flow (Anisfeld et al. 1999). Ice is likely an important formative agent of pools in Bay of Fundy marshes, as it is in salt marshes on the St. Lawrence (Dionne 1968). Cores taken in the pools at both marshes often revealed shallow depths to partly decayed rhizomes, suggesting relatively recent formation of these pools over the vegetated marsh, although most of the current pools on the reference marsh do appear to be present in aerial photos of the site from the

1940's. The observed spatial distribution patterns of the pools, with the greatest amount of pool area at both marshes occurring within 40 to 50 m from the creek edge (fig. 6), could be related to greater ice scour with proximity to creek. Winter observations from this study suggest that ice is also an important mechanism for maintaining and deepening pools. During some visits to the sites the ice cover was too thick to break through, and likely reached the bottom of the more shallow pools. As temperatures rose a sheet of ice remained over the sediment surface while the water above was ice-free in several pools. On subsequent visits, chunks of ice with imbedded mud and rhizomes were observed around pools while at the same time pool bottoms had holes with numerous broken rhizomes intruding. This indicates that ice forming on the pool bottom can actually deepen the pools as the frozen portions of sediment and rhizomes can be lifted and rafted out of the pool during by flood tides. This same process may also maintain pools by removing sediment deposited by flooding tides when ice is not present.

Connection to Tidal Flow

The GIS analysis showed that these pools are isolated habitats, connected to the wider estuarine system only through irregular flooding by tides. Flooding influences the pool environment and is responsible for the most dramatic shifts in temperature, salinity and likely other physical parameters. For example a summer flood tide caused the temperature in the Dipper Harbour high marsh pool to drop by more than 15 °C in 30 min. These extreme changes limit the number of species able to survive in the pools but flooding allows for movement of species into and between pools.

ENVIRONMENTAL VARIABILITY

The wide variability in environmental conditions of the pools found in this study is consistent with other reports (Nicols 1935, Bleakney and Meyer 1979, Ingolffson 1994). This variability is considered responsible for relatively low biodiversity in marsh pools (Nixon and Oviatt 1973, Ward and Fitzgerald 1983).

Many factors play a role in influencing the salinity of these pools: precipitation, flood tides, and temperature. High precipitation caused the most dramatic change in salinity over the study. The immediate effect of a precipitation event is to lower salinity through the addition of freshwater to the pools. This can be seen in the salinity data collected on the Saints Rest marsh pools from August 11 to 25, 2005 (fig. 12), a period of neap tides and very little precipitation. The salinity of the mid and low marsh pools at Saints Rest was at or above that of seawater (ranging from 32 – 38). The salinity of the high marsh pool was 23 at the surface and 27 at the bottom. After heavy rains from August 13 to 21, the salinity of all three pools decreased to 15 to 18. Over the 2-week period, rain had caused a reduction in surface salinity of 8 to 15 and a reduction in bottom salinity of 10 to 20. There was little to no stratification, even in the high marsh pool, which indicates the rain also mixed the water column. From August 27 to September 1 at least 4 tides flooded the high marsh pool at Saints Rest. Measurements made on September 2 showed the salinity of the low and mid marsh pools had returned to that of the incoming tidal water (31 – 32) and the salinity of the high marsh pool had returned to levels following the previous spring tides (24 at the surface and 27 at the bottom).

Periods of high ambient temperatures with no tidal flooding caused increases in salinity and stratification. The *S. robustus* at the upland edge of the high and mid marsh pools at Dipper Harbour indicated freshwater seepage into these pools, which explains the greater stratification and spatial variability of salinity in these pools (fig. 7, table 3). The slightly higher level of stratification in the high marsh pool at Saints Rest marsh is likely related to the greater depth and lower surface area to volume ratio of this pool.

Water temperature in the high and low marsh pools followed the pattern of the air temperature with a slight lag (fig. 13), but rates of changes were more moderate than that of the air temperature. Water temperature in the pools was generally higher then the air temperature by as much as 10°C (fig. 13), likely due to a combination of the higher air temperature at the sediment / water interface and the resistance of the water in the pools to rapid temperature change. The exception to the generally slow rates of change in the temperature of the pools is the effect of flood tides, caused rapid temperature decreases (summer) or increases (winter) in the water of the pools (figs. 10 and 11). The lower-low marsh pool at Dipper Harbour had the most stable temperature with the lowest average standard deviation over all tidal cycles and the lowest standard deviation of the mean tidal cycle temperatures over the entire study. This stability is likely due to the increased flooding frequency of this pool, which was flooded on all but the lowest neap tides.

With the exception of the high marsh pool at Saints Rest (SRH), climate (temperature and precipitation) had the greater effect on the pool environment with tidal flooding tending to make the conditions more stable. The lower variability of the high marsh pool at Saint's Rest, is likely due to the fact this was the deepest pool in the study and had the smallest surface area to volume ratio (table 1), which mitigated rapid fluctuations in temperature and salinity. Increased variability in temperature and salinity with decreasing flooding frequency has also been reported by Barnby et al. (1985) in a study of potholes in a California salt marsh. This increased stability in the pools at lower elevations may improve their habitat value for fish and invertebrates, resulting in greater diversity and productivity of pools with decreasing elevation on the marsh platform.

The recovering marsh in this study had higher pool density than the control site. Given the importance of pool habitat to wildlife (Burger 1982, Erwin 2004) an increase in pool area on the recovering marshes may make it more valuable to wildlife than the undisturbed site. Over the course of this study, birds (waterfowl, shorebirds and herons) were observed much more frequently and in greater numbers at the recovering marsh. However, this observation could also be due to the greater size of the recovering marsh making it more attractive to birds. If recovering marshes tend to have more pool habitat then, when other factors are equal, this could partially explain the increased use by some bird species of restored marshes compared to reference sites reported by Brawley et al. (1998) and Fell et al. (2000).

Table 1: Summary of descriptive measurements of 6 study pools from high (H), mid (M) and low marsh (L) on Saints Rest (SR) and Dipper Harbour (DH) marsh. (Observed % tides flooding the pools derived from temperature data.)

pool	area (m^2)	volume (m^3)	elevation (m >MSL)	% flooding		depth (cm)[a]		
				predicted	observed	average	max	min
SRH	33	13	3.94	10	6	38	50	26
SRM	312	24	3.71	18	—[b]	8	15	1
SRL	1648	169	3.72	18	18	10	16	4
DHH	104	12	3.36	19	16	12	19	4
DHM	153	19	3.32	20	—	13	19	3
DHL	61	11	3.20	26	21	18	27	10

[a] Depth from pool edge to pool bottom, water depth is variable.
[b] Dataloggers not placed in mid marsh pools

Table 2: Summary of pool size and coverage by marsh

	Saints Rest	Dipper Harbour
Total number of pools	854	134
Coverage as % marsh area	13.1	4.8
% pools <100 m^2	83.4	91
Average area <100 m^2 *	15 ±21	8 ±12
% pools 100-1000 m2	13.3	9
Average area 100-1000 m^2 *	342 ±221	216 ±133
% pools >1000 m^2	3.3	0
Average area <1000 m^2 *	2635 ±2327	-

*Average pool area: m^2 ±1SD.

Table 3: Spatial variability of salinity at the water surface (surface) and sediment surface (bottom) of Dipper Harbour high marsh pool. 'Near upland' is about 3.5 m from the upland edge, 'near creek' is about 14 m from the main creek, 'far creek' is farthest from both the upland and creek, about 21 m from the creek.

		near upland	near creek	far creek
3-Aug-04	surface	24	27	26
	bottom	31	33	32
1-Nov-04	surface	4	8	10
	bottom	31	33	32
9-Feb-05	surface	12	24	18
	bottom	30	34	32
6-Apr-05	surface	5	5	8
	bottom	29	31	30

Table 4: Average seasonal water (high, low and lower low pools) and air temperature, ^{o}C ± 1 standard deviation from fall 2004 through summer 2005.

	Saints Rest			Dipper Harbour			
	High	Low	Air	High	Low	Lower low	Air
Aug. 3-Sep. 20	19.9 ±2.2	18 ±3.8		22.1 ±4.6	19.3 ±4.6		
Sep. 21-Dec. 21	11.6 ±4.1	8.5 ±5.1	0.9 ±6.6	9.8 ±5.0	8.4 ±4.5	4.8 ±2.7	1.5 ±4.8
Dec. 22-Mar. 20	0.3 ±2.2		-5.3 ±7.9	2.7 ±3.8	1.9 ±3.4	-1.2 ±4.0	-5.1 ±7.6
Mar. 21-Jun. 20	13.0 ±4.0	11.9 ±4.9	5.4 ±5.6	15.0 ±6.8	11.8 ±6.0	7.53 ±4.4	6.4 ±5.8
Jun. 21-Aug 16	20.9 ±4.2	18.8 ±4.4		20.9 ±5.4	20.2 ±5.3	14.9 ±3.7	16.2 ±5.5

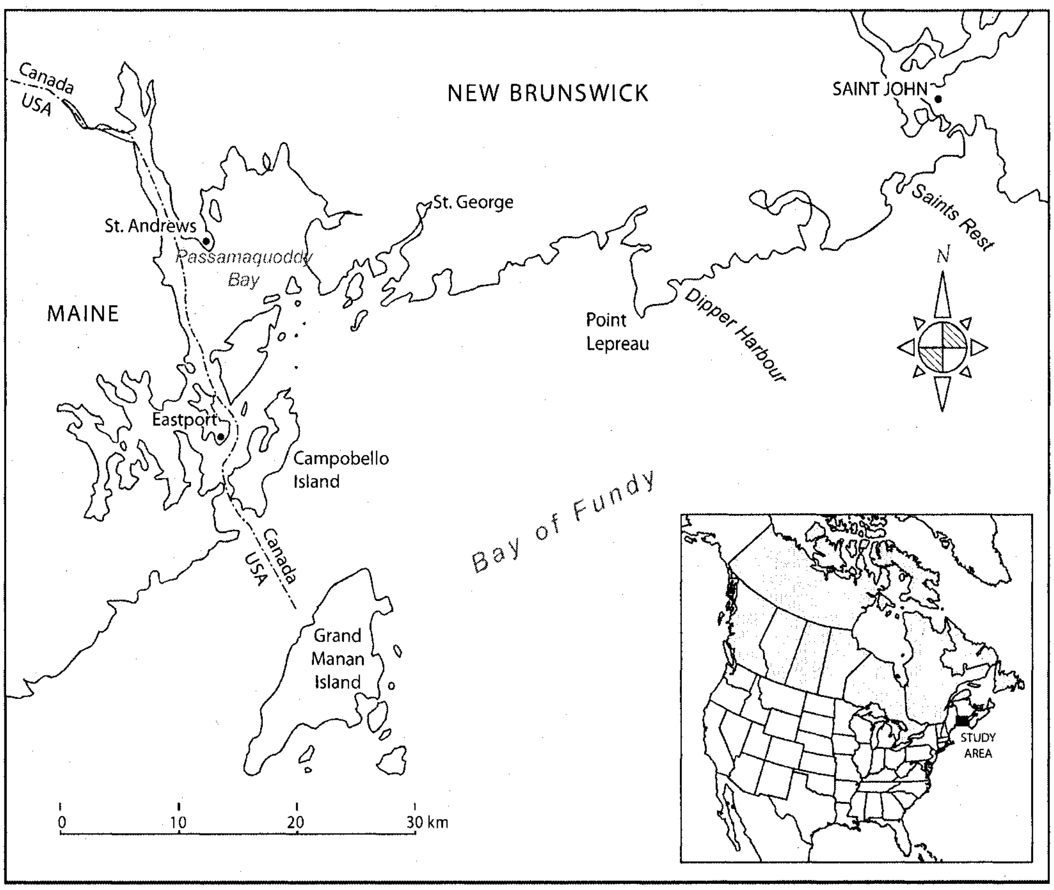

Figure 1: Location of the recovering (Saints Rest) and reference (Dipper Harbour) salt marshes in southern New Brunswick.

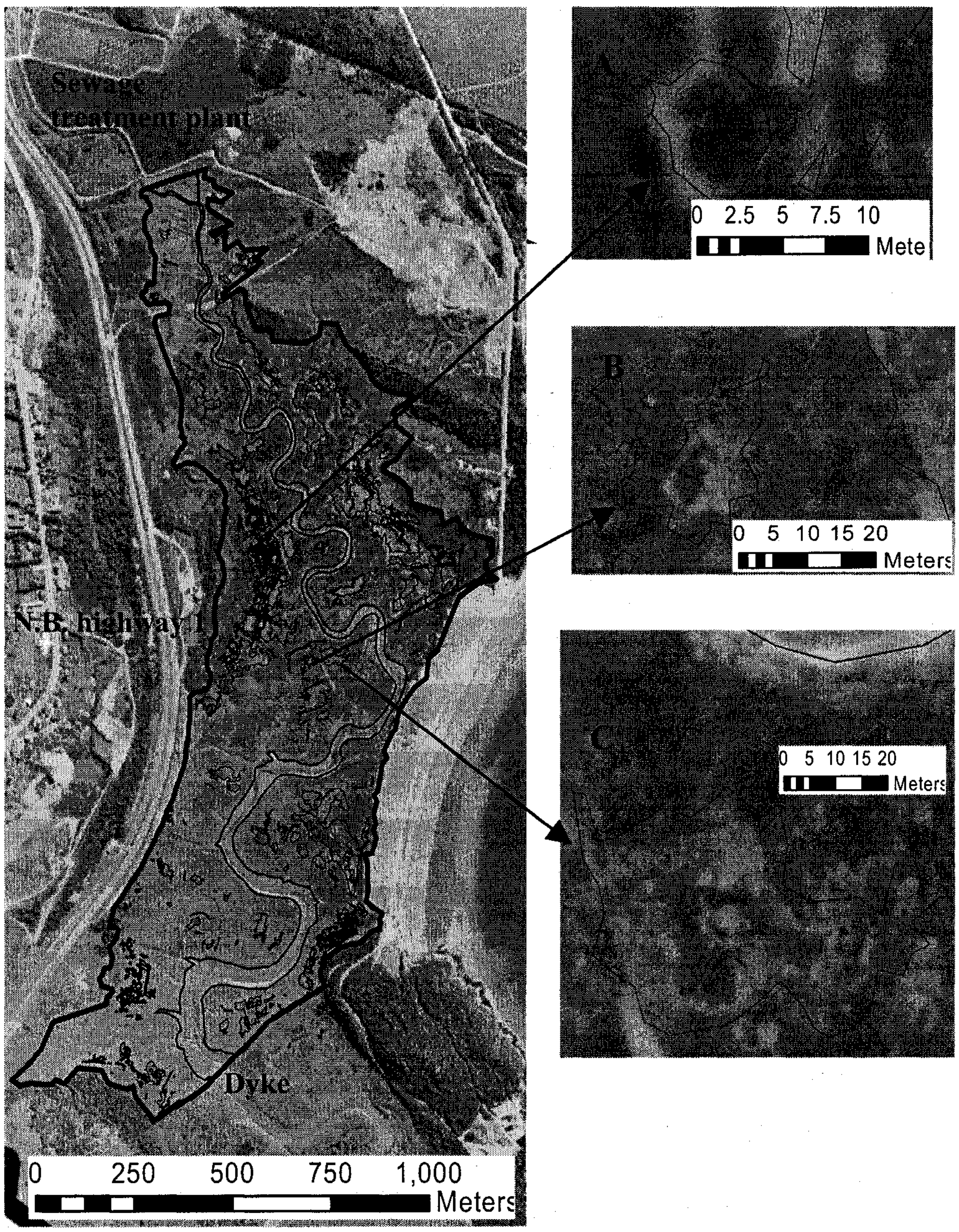

Figure 2: Saints Rest marsh showing area mapped and all pools. Inset are main study pools; A, high marsh pool, B - mid marsh pool, C - low marsh pool. Note different scales for study pools.

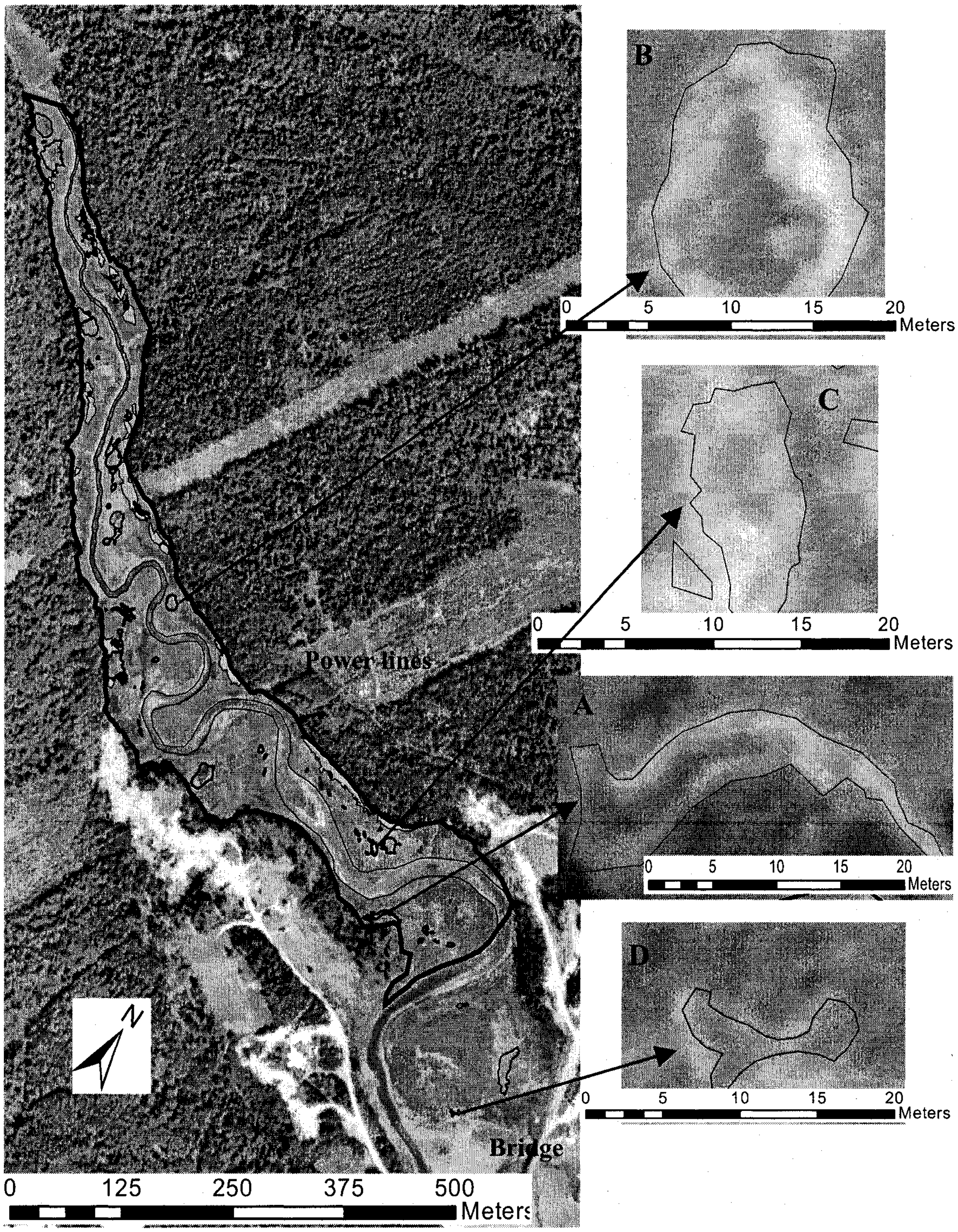

Figure 3: Dipper Harbour marsh showing area mapped and all pools. Sections coded as "standing water" are shaded. Inset are main study pools; A, high marsh pool, B - mid marsh pool, C - low marsh pool, D - lower low marsh pool (digitized). Study pools are shown on the same scale. Note scale for entire marsh is half that for Saints Rest marsh

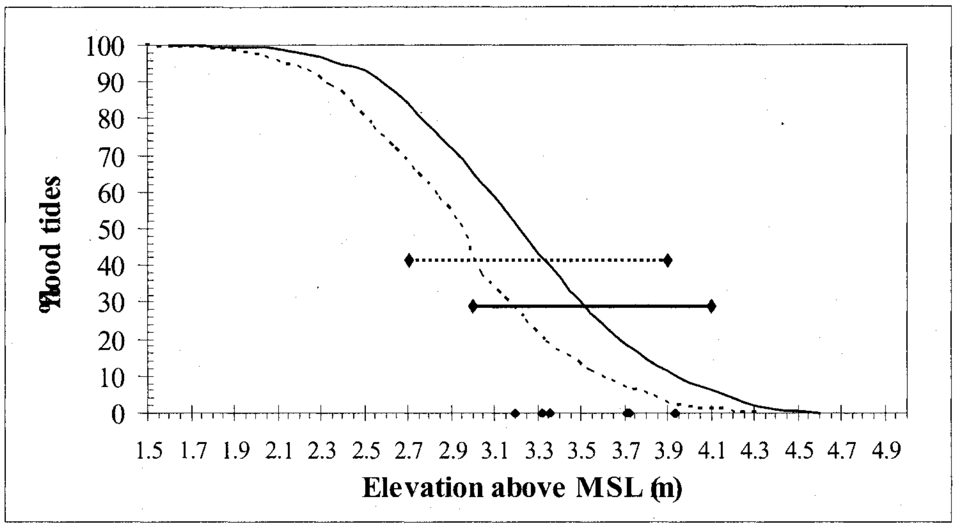

Figure 4: Percentage of high tides reaching or exceeding given elevation above mean sea level at Saints Rest (solid curve) and Dipper Harbour (dashed curve) based on published data from Saint John tide gauge (www.lau.chs-shc.dfo-mpo.gc.ca). Pools occur between 2.7 m to 3.9 m above MSL at Dipper Harbour (dashed line) and between 3.0 m to 4.1 m above MSL at Saints Rest (solid line).

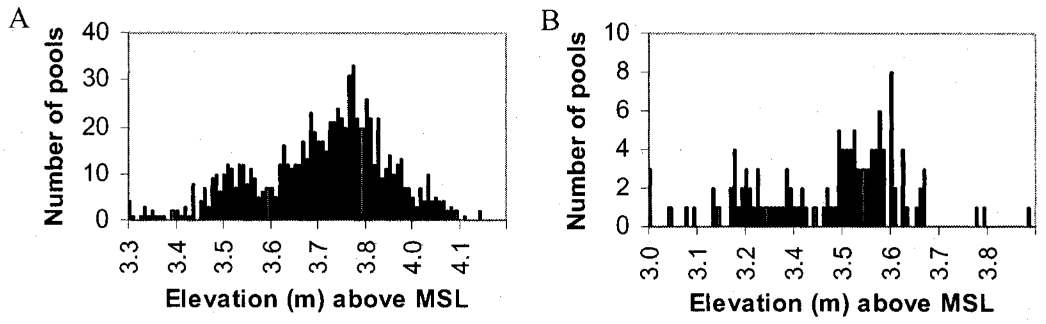

Figure 5A: Frequency distribution diagram for pools at Saints Rest marsh by elevation. B: Frequency distribution diagram for Dipper Harbour marsh pools.

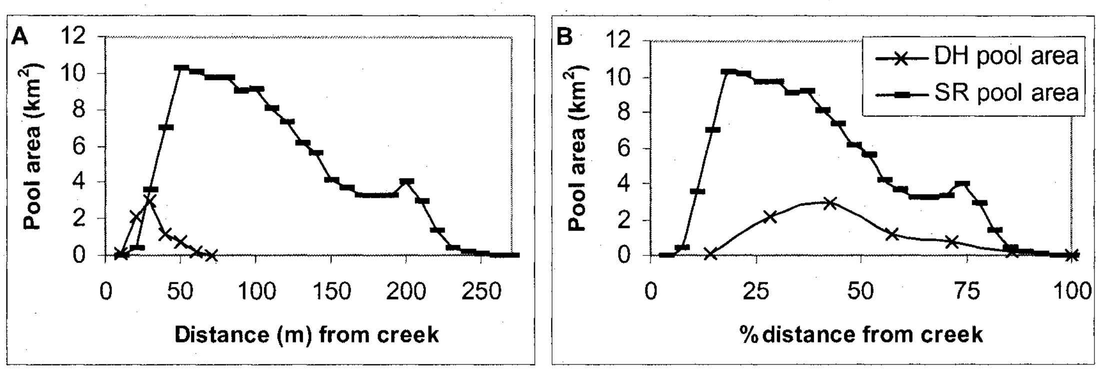

Figure 6: Results from buffer analysis of pool distribution at Saints Rest (SR) and Dipper Harbour. Total pool area (A) with distance (m) from creek and (B) as a percentage of distance from creek.

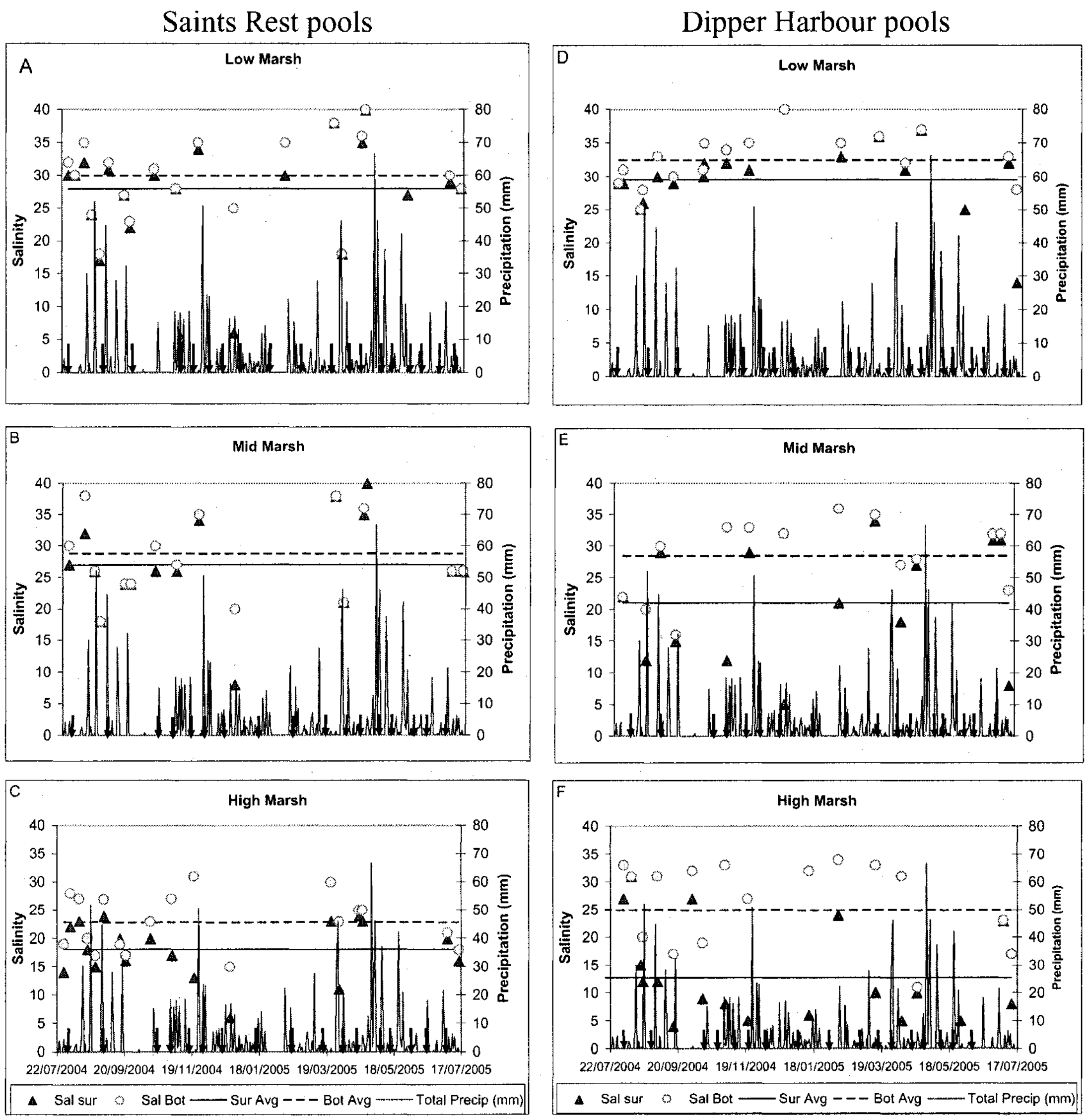

Figure 7: Surface (sur) and bottom (bot) salinity measurements of pools in Saints Rest and Dipper Harbour marshes in relation to average surface and bottom salinities, daily precipitation, and flood tides (indicated by black arrows).

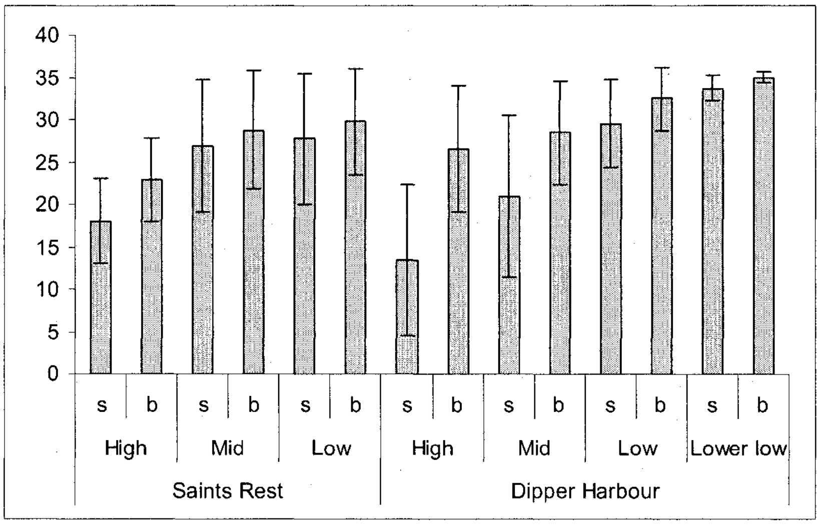

Figure 8: Average salinity and standard deviation of high, mid, low and lower low pools at both marshes. s = surface salinity, b=bottom salinity

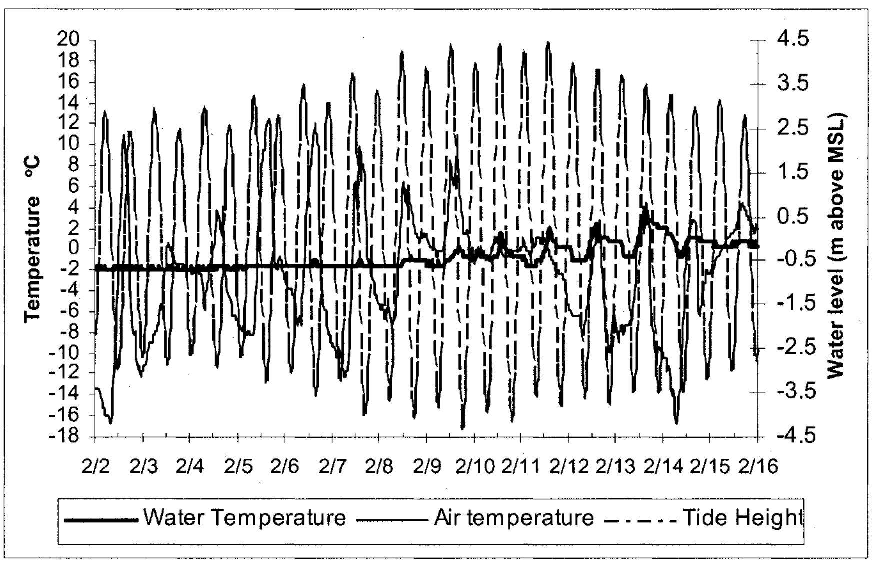

Figure 9: Water temperature of the high marsh study pool at Saint's Rest marsh and the corresponding air temperature and tide height.

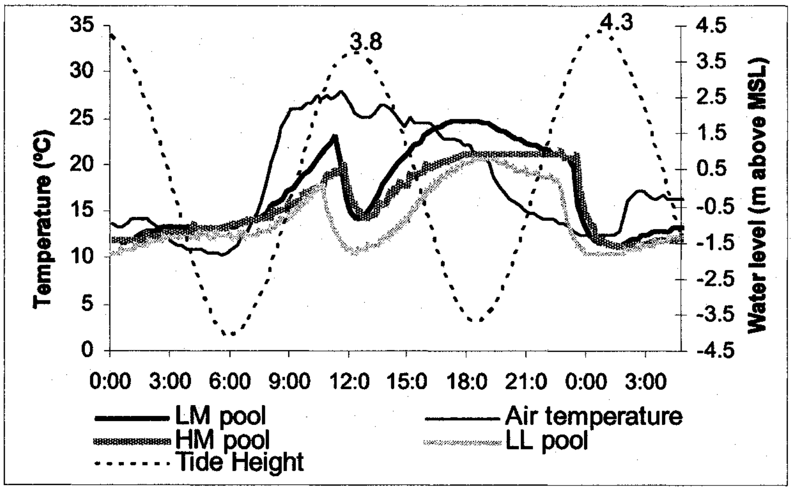

Figure 10: Example of the effects of flood tides on summer water temperature of 3 pools on Dipper Harbour marsh, July 22, 2005. Maximum tide heights (metres above MSL) noted on graph.

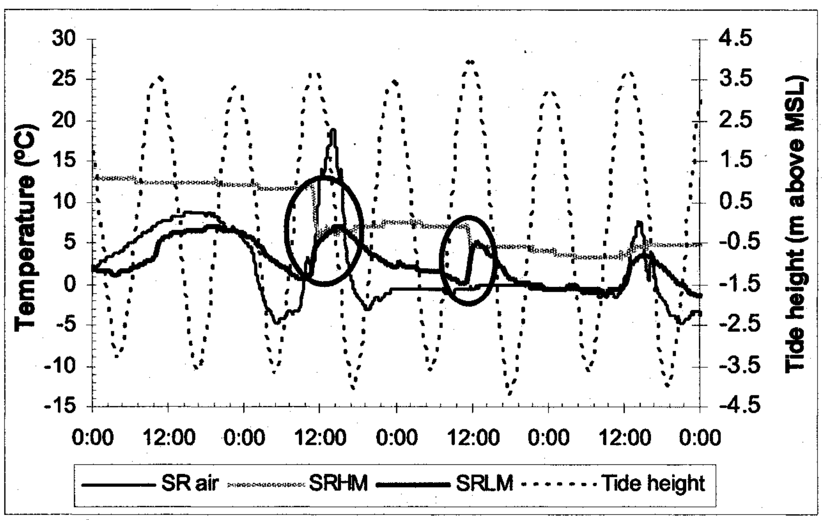

Figure 11: Effect of flood tides (circled) on water temperature in high and low marsh pools in Saints Rest Marsh, November 11-15, 2005.

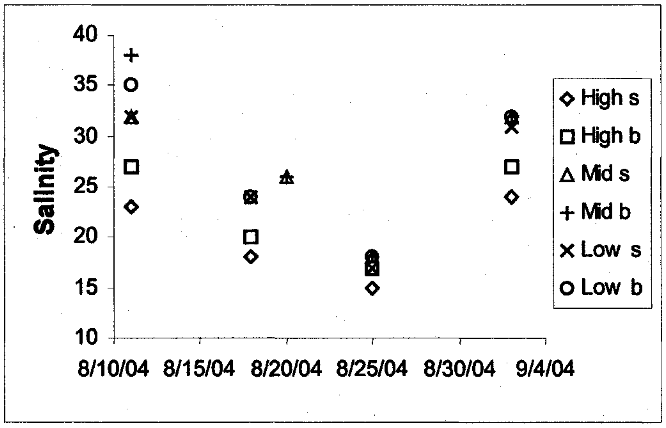

Figure 12: Variation in salinity in Saints Rest pools in response to major precipitation events: > 92 mm of rain fell from Aug. 12 to 21, 2004. Measurements made on Aug. 11, 18 (mid pool on Aug.20), 25 and Sept. 2. s =surface salinity, b =bottom salinity.

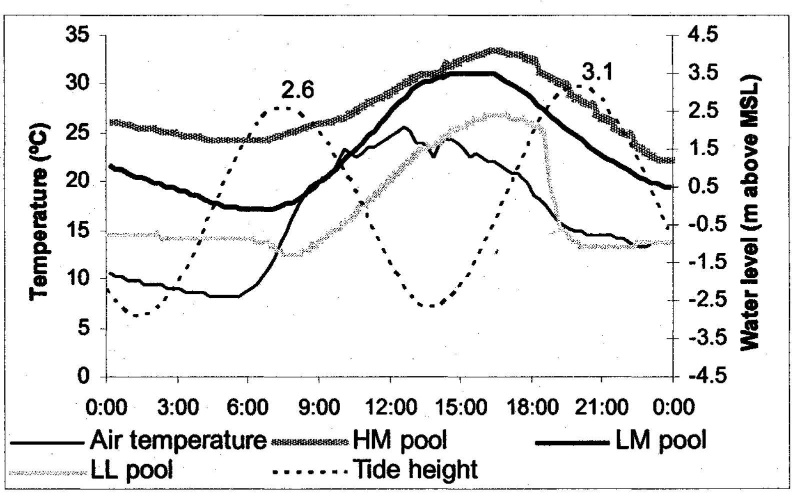

Figure 13: Example of water temperature of Dipper Harbour pools following air temperature with slight lag, July 17, 2005. Note that water temperature exceeds air temperature.

Connecting statement

Chapter 2 of this thesis examined and compared the spatial coverage and distribution of pool habitat and environmental variability of pools in the reference and recovering marshes. In Chapter 3 the results of the invertebrate surveys are reported with analysis of community and species patterns and their relation to pool distribution and environmental variability.

Chapter 3: Macroinvertebrate communities of salt marsh pools: comparison of a natural and recovering marsh

ABSTRACT: Salt marsh pools were monitored for one year with seasonal collections of invertebrate fauna in a recovering and a reference salt marsh on the lower Bay of Fundy. A total of 42 macroinvertebrate taxa were identified in the two marshes, with species richness (S) of individual pools ranging from 13 to 23. An estimated 50 years since dyke failure, the invertebrate fauna of pools in the recovering marsh is indistinguishable from that of the reference marsh. No significant differences in macroinvertebrate communities were detected between sampling dates, pool size or pool depth. Variability in pool flooding frequency and its effects on pool environmental conditions did not affect macroinvertebrate communities except for pools in the lowest parts of the marsh, which are flooded on all but the lowest neap tides. Average production of pool macroinvertebrates ranged from 1.8 to 4.0 g dry wt m^{-2}, depending on the amount of vegetation cover in the pools. The pools were characterized by low equitability in species abundance and biomass. The numerically dominant organisms of the pools were mites (Acarina), the gastropod *Hydrobia tottentei*, Tubificidae oligochaetes, and *Chironomus* sp. larvae as well as copepods and ostracods.

Introduction

Salt marsh pools complement the nursery and foraging values of marshes (Daiber 1982, Boesch and Turner 1984), serving as important habitat for fish (Smith and Able 1994, Adamowicz 2002) and invertebrates (Nicols 1935, Bromely and Bleakney 1979, Clark et al. 1984), and important feeding sites for birds (Burger 1982, Clark et al. 1984, Erwin 1996). Clarke et al. (1984) found a strong correlation between pool density and bird use in Massachusetts salt marshes, particularly for shorebirds, herons, and terns. As a result of the extreme tides in the Bay of Fundy, the surface of the salt marshes are flooded only intermittently, at extreme (spring) tides. Standing pools of water on the surface of the marsh provide a refuge for organisms, such as fish and aquatic invertebrates, which would not be able to survive on the marsh surface between flood tide events.

As feeding sites for fish and birds, pools are an important contributor to the secondary production of the salt marsh. Early researchers described the high level of primary production in salt marshes and theorized this production was exported as detritus to adjacent waters, supporting coastal fisheries (Teal 1962). Later work (Haines 1976, Nixon 1980, Odum 2000) partially refuted this outwelling hypothesis, but more recent research (Kneib 1997, Deegan et al. 2000) indicates that salt marshes are a major exporter of secondary production (rather than detritus) by harbouring large juvenile populations of estuarine species and by supporting a high rate of avian foraging.

Despite their apparent ecological importance in the salt marsh, few studies have focused specifically on the pools. Early studies found few species in pools (Nixon and Oviatt 1973, Campbell and Denno 1978), which may explain why further research was not pursued. The only published studies of marsh pools in the Bay of Fundy, however, reported 56 species of benthic macro- and meio-fauna (to species retained on a 0.233 mm mesh), including 18 new species records for the region (Bleakney and Meyer 1979, Bromley and Bleakney 1979). One objective of my research was to determine if Bay of Fundy pools have higher biodiversity than other regions, or if the higher diversity reported in Bromley and Bleakney (1979) is simply due to greater sampling effort employed in this study, which examined ten pools on five marshes sampled year-round for benthic and epiphytic fauna over two years.

Another objective was to compare the pool fauna of a recovering and an undisturbed marsh. In studies of restored marshes some components of the ecosystem recover more quickly than others. For instance creek use by nekton can return to the condition of an undisturbed marsh in as little as one year (Roman et al. 2002), however Allen et al. (1994) found that the forage value for mummichogs of a restored marsh had not recovered after 15 years. Others have reported that invertebrate communities of the marsh surface may take over 20 years to recover (Fell et al. 1991, Warren et al. 2002). In the Bay of Fundy, abandoned dykelands have been undergoing unmanaged recovery for more than 50 years. These sites can serve as natural laboratories to examine the long term outcome of salt marsh restoration.

Finally, given the zonation of vegetation in salt marshes (e.g., Miller and Egler 1950, Chmura et al. 1997) corresponding to elevation, it was hypothesised that pool fauna would show a similar zonation. It was expected that the larger the environmental fluctuations and the more frequent these fluctuations, the less diverse the community would be (Kneib 1984). In the lower marsh, where pools are flooded more frequently, the environmental parameters may be more constant compared to higher elevations, where flooding is infrequent and irregular. Pool size or depth may also be important as a larger, deeper pool in the high marsh may have more stable environmental conditions than a smaller, shallower pool in the low marsh. Sampling was conducted to examine such spatial patterns as well as seasonal changes.

Methods

Study Sites

Saints Rest marsh, located on the lower Bay of Fundy in Saint John, New Brunswick, has a long history of human use and alteration including dyking, ditching, construction of roads, use as a rifle range, and currently a sewage treatment plant discharges into the head of the creek. Dipper Harbour marsh, 28 km southwest of Saints Rest marsh, is a relatively undisturbed reference site. Both marshes have been described in detail elsewhere (Chapter 2, Thomas 1983a, Chmura et al. 1997). Three pools were selected in each marsh, based on initial salinity measurements and surrounding vegetation, to represent three marsh elevations; high, mid and low. These 6 pools were monitored for one year (July 2004 to July 2005). When it was observed that pools on the low marsh elevation were flooded only on spring tides, one additional pool regularly flooded except on the lowest neap tides (designated as lower low pools) were located in each marsh and added to the study. Five additional pools on each marsh were sampled for benthic invertebrates in late summer, 2004, bringing the total number of pools sampled to nine on each marsh.

Invertebrate Sampling

A Wildco™ hand corer with a diameter of 5 cm (surface area of 0.002 m^2) was used to collect sediment samples to a depth of 15 cm. The sample size was determined to be adequate after constructing a species area curve from repeated sediment samples (5) collected in one pool at Dipper Harbour, although large differences in abundance from sample to sample were noted. Other studies of marsh pools have used various methods to sample benthic invertebrates, collecting, from 1 (Bromley and Bleakney 1979, Stocks and Grassle 2003) to 5 (Nicols 1935, Ingolfson 1994) samples per pool, a surface area of 0.001 m^2 (Stocks and Grassle 2003) to 0.85 m^2 (Heck et al. 1995). Studies have also varied greatly in number of pools sampled, sampling frequency and times of year sampled. At the time of sediment sampling and on 2 other occasions a visual estimate of percent cover of aquatic vegetation was made.

Sediment samples were collected from the 6 main study pools July 28-30, 2004. Between August 25 and September 2 these pools were sampled again, along with 5 additional pools on each marsh, for a total of 8 pools per marsh. The 6 main pools and 1 pool at a lower low elevation on each marsh were sampled again in May 2005. In each pool, sediment samples were taken ~0.5 m and ~2.5 m in from the edge of the pool (termed 'edge' and 'mid' samples). The sediment samples were sieved through a 0.5 mm screen and the portion retained was placed in a 5% buffered formalin solution for a few days, then transferred to a 50% isopropyl alcohol solution for preservation until sorting and identification. The samples were transferred to a rose bengal staining solution for 1.5 hr to stain the invertebrates so they could be more easily sorted from roots and other debris in the sample using a dissecting microscope. Meiofauna (defined as those passing through a 0.5 mm screen), such as ostracods, forams and copepods, were quantified when encountered in the samples. However, due to the mesh size used these counts can not be considered complete and were not included in the final analyses.

In mid-August 2004 and again May 2005, 0.25 m^2 of aquatic vegetation (Widgeon grass, *Ruppia maritima*, and filamentous algae) was cut from each study pool at a randomly selected location within the pool, and removed carefully so as to not dislodge any invertebrates. Samples taken in August were rinsed repeatedly over a 0.5 mm mesh screen. The May samples were not rinsed, which allowed for accurate meiofauna counts as well as marcofauna. The algae and widgeon grasses were separated and the wet weight of each was determined for all samples. Weight of vegetation collected within 0.25 m^2 differed between samples, since vegetation surface coverage and depth was not consistent between pools or sample times, so invertebrate abundance was adjusted to number per 100 g wet weight of vegetation for analysis. The average weight of vegetation within 0.25 m^2 was then used to estimate total invertebrate abundance and biomass in pool vegetation per unit area.

The filamentous algae from the August samples were identified to genera using a compound microscope. Invertebrates in sediment and vegetation samples were hand sorted under a dissecting microscope. Small species and diagnostic features (such as chironomid heads) were mounted on slides and examined under a compound microscope. Invertebrates were identified to the lowest practical taxonomic level using the resources listed in Appendix A. Voucher specimens will be placed in the permanent collection of the Atlantic Reference Centre in St. Andrews, New Brunswick.

Dry weight was determined for species of macrofauna that comprised more than 10% of the total invertebrate abundance for 3 or more samples. To determine dry weight, specimens were randomly selected from samples containing a large number of individuals of the species to be weighed. With the exception of *Hydrobia tottentei* and *Gammarus micronutus* there was little variation in the size and wet weight of most species between samples. For this reason, a subset from the summer and spring sampling periods were weighed separately for only these two species. One to 100 individuals of each species representing more than 5% of total species abundance of samples from the 6 main study pools were dried and weighed. The number of individuals weighed was higher for smaller species. Specimens were soaked in distilled water overnight to remove alcohol, then placed in a drying oven at 120°C for 24 hr.

ANALYSES

To examine and compare diversity the Shannon-Wiener index of diversity ($H' = -\sum p_i \log p_i$, where p = the proportion of taxa i to total taxa count of sample) and evenness ($J = H' / \log S$, where S = species richness) were calculated for all samples and for combined data for each pool. Paired t-tests were used to compare diversity measures of edge to mid samples, seasons, and elevations.

Correlations between species and within species by marsh, season, and pool variables (depth, average salinity, elevation, and surface area) were examined to look for relationships between the invertebrates and with environmental parameters. High variances and many zero counts resulted in high skewness and kurtosis measures for all species. Transforming the data (log+1) did not produce a normal distribution for most species therefore Spearmans rank correlation, a non-parametric test was performed on the data. Some common species in the vegetation samples did display normal distribution after log transformation. For these species, Pearson's co-efficient of correlation was used. Kruskal-Wallis one way ANOVA was performed to test for differences in species abundance and dry weights between marshes, sampling times and pool elevation.

A combination of techniques were applied to look for spatial or temporal patterns in the vegetation and sediment samples. Bray-Curtis distance measures between samples were calculated from the abundance data. Cluster analysis was preformed on the samples using average linkage between samples and Bray-Curtis distance. For comparison to cluster analysis, non-metric multidimensional scaling (NMDS) was also performed to look for patterns in the samples through indirect gradients. NMDS is recommended by McCune and Grace (2002) as an appropriate ordination technique for non-parametric data. Cluster analysis and ordination were performed with Community Analysis Package software (Pisces Conservation Ltd., 2003). All other statistical analyses were performed in SPSS v. 13.0.

Results and Discussion

VEGETATION

The only vascular plant that grows in most pools is *Ruppia maritima*, though isolated stems of *Spartina alterniflora* frequently encroached into pools with sloping sides and pools often graded into stands of *Schoenoplectus robustus* near the upland. *Zostera marina* replaced *R. maritima* in a few of the lowest elevation pools, including the 'lower low' pool at Dipper Harbour. Thick mats of filamentous algae grew in virtually all pools from May to late fall (table 1). No attempt was made to quantify the abundance of each species of filamentous algae, though it was noted that *Cladophora* sp. was the dominant species of the algal mats and *Enteromorpha* sp. tended to occur in areas of the pool where water is moving (i.e., drainage channels). Less common algae identified from the pools included *Rhizoclonium* sp., *Cylindrocapsa* sp. and *Ectocarpus* sp. Blue green algae (Cyanophyceae) were epiphytic on other species of algae, on *R. maritima*, and were also found growing on bits of wood and rhizomes mixed in with the samples.

The percent cover of aquatic vegetation was generally much higher in Dipper Harbour than in Saints Rest marsh overall (table 1), likely due to much greater bird use (grazing) of the pools in Saints Rest marsh. Large flocks of Canada geese and black ducks were frequently observed in the pools at Saints Rest while birds observed at Dipper Harbour were generally in small groups or solitary. The low marsh pools had the least amount of vegetation, probably due to more frequent tidal flooding lifting algal mats and floating them out of the pools. The decrease in *R. maritima* coverage in the summer of 2005 may be due to the much drier summer weather in 2005 which resulted in extensive drying of the pools which was not observed in 2004. This was not observed in the mid marsh pool at Dipper Harbour in which, because of its steep sides, decreased water level exposed less sediment surface to the air.

Biomass

Dry weights were determined for species that comprised at least 5% of the total invertebrate macrofauna abundance in 3 or more samples from the 6 main study pools (table 2). There was no significant difference by marsh ($p=0.43$) or by sampling date ($p=0.24$) in total biomass based on dry weight (Kruskal-Wallis test). The average biomass of invertebrates in the pool sediment was 1.79 g dry weight m^{-2}. Fauna in pool vegetation averaged 0.86 g dry weight per 100 g of vegetation. The average weight of vegetation in a 0.25 m^2 sample was 65 g, which gives an average epiphytic macroinvertebrate biomass of 2.24 g m^{-2}, or potential total pool biomass (benthic and epiphytic macroinvertebrates) of 4.03 g m^2 if there is 100% vegetation coverage.

Hydrobia tottentei dominated the pools both in biomass and in abundance (table 3). The abundance of *H. tottentei* was lower in the sediment samples, due to the high abundance of mites (Acarina) (average = 35.6%). Mites were not included in biomass calculations because, despite their great abundance, their weight would be negligible.

DIVERSITY AND DISTRIBUTION

Species abundance data for samples by season are plotted in figures 1 and 2. Several species occurred in both the sediment and the vegetation samples while some species were restricted to one or the other (table 5). The number of invertebrate taxa identified in individual sediment samples (species richness) ranged from 2 to 14, with an average species richness of 6. Species richness was slightly higher in the vegetation samples, from 7 to 18 with an average of 13.5. When all sediment and vegetation samples from a repeatedly sampled individual pool were combined, species richness (of macrofauna) of the pools ranged from 13 to 23 (table 4). There were no significant differences between measures of diversity by marsh, mid or edge samples, season, or elevation.

The average Bray-Curtis distance between paired edge and mid sediment samples was 0.505, lower than the average distance of 0.719 for all sediment samples. However, distance between paired mid and edge samples ranged from 0.154 to 0.939, suggesting that variability within pools can be as great or greater than variability between pools. This conclusion is further supported when the paired edge and mid samples were combined and Bray Curtis distance calculated for the intensively studied pools. The average distance within individual pools over all 3 sampling periods (0.309) was only slightly lower than the average distance between all pools over all sampling periods (0.434).

Community Analysis

The only clear pattern to emerge in the cluster analysis of the sediment samples was the grouping of the 2 lower-low pools which had more typically marine species such as polychaete worms and the marine oligochaete *Peloscolex benedeni*. Apart from these two pools, samples showed no particular affinity by marsh, season or elevation (fig. 3). Paired t-tests on average species abundance also showed no significant differences between marshes or between seasons. The NMDS ordination reveals no clear gradient, except for an apparent separation of the lower low pool samples at each marsh (fig. 4). Given the high stress level (stress = 0.25), it is difficult to assume any real differences in the ordination (Clarke 1993). When NMDS was performed on the species a gradient appeared along axis 1 of the resulting ordination, with marine species (e.g. polychaetes, the anemone: *Nematostella vectensis*, *Littorina* sp.) on the left side of the axis and many of the insect taxa on the right (fig. 5).

There was similarly little evidence of patterns in the vegetation samples. The August samples from Saints Rest marsh are more closely related to each other than to other samples; however an August sample from Dipper Harbour is more similar to a sample from Saint Rest in May than any of the Saints Rest August samples are to each other (fig. 6). The NMDS ordination also shows a slight separation of the Saints Rest samples by season with August samples to the right on axis 1 (fig. 7). The Dipper Harbour samples are not as clear, but the samples from May appear grouped.

I hypothesized that even a small difference in position in the tidal frame and thus stability of environmental conditions would have a large effect on the invertebrate community of a pool. Yet small differences in flooding frequency seem to have no effect on the invertebrate community. In chapter 2 I showed differences in flooding frequency between high and low marsh pools. The high marsh pools at Saints Rest and Dipper Harbour were flooded on 6.4% and 16% of high tides in a year, the low marsh pools on 18% and 21% of high tides, respectively. Environmental variability of the pools however, was affected more by climate than tide. The exceptions to this were the lower low pools, where much higher flooding frequency resulted in lower variability. Since the majority of pools exhibit similar environmental conditions despite differences in flooding frequency, it is not surprising that the invertebrate communities are also similar.

While environmental conditions in the pools are extremely variable, the invertebrate communities appear to be stable. Macroinvertebrate species richness of individual pools is relatively consistent but there is low equitability with a few dominant taxa such as the ubiquitous Acarina, *Hydrobia tottentei* and Tubificidae oligochaetes. Vegetation in the pools is highly dominated by the one vascular plant, *Ruppia maritima*, and *Cladophora* sp., a filamentous green algae.

Bromley and Bleakney (1979) described 56 invertebrate taxa collected over a 2 year study. They also provided a checklist of 71 invertebrate taxa observed in salt marsh pools in Minas Basin over a 12 year period, the highest published diversity of any salt marsh pools. Only 50 of these were macrofauna however, which is more comparable to the 42 macrofaunal invertebrate taxa collected or observed in pools in this study. Bromley and Bleakney (1979) tentatively proposed that due to their high diversity compared to other regions, marsh pools in Minas Basin in the upper Bay of Fundy were "a unique and rich community component".

It is difficult to compare diversity of marsh pools to other studies or habitats as sampling effort, techniques, and taxonomic precision differ with investigator. In comparison with similar studies in other locations, salt marsh pools in the Bay of Fundy seem to have similar to slightly higher diversity of invertebrate macrofauna than those of the Gulf of St. Lawrence, the U.S. Atlantic coast, the UK, or Iceland, (table 5). However, studies of insect emergence have demonstrated that insect diversity is grossly underestimated in most studies, which identify insects only to the family or genus level. In PEI salt marsh pools Giberson et al. (2001) reported 43 species of nematocerous flies alone, while Mackenzie (2005) reported 33 taxa of insects emerging from marsh pools in southern Maine. It is not possible to draw conclusions about the biogeography of salt marsh pools until more studies utilizing the same collection and identification techniques are published.

Studies have been published on macroinvertebrate diversity in other estuarine habitats in the Bay of Fundy. Thomas et al. (1983) list 20 common species of macroinvertebrates on rocky shores in this region, though many other less common or perhaps less obvious species occur in this habitat (Gosner 1971). Tide pools on rocky shores are a somewhat analogous habitat to salt marsh pools and Thomas (1983b) summarized biota of a variety of types of tide pools. Zonation of biota is observed in tide pools of rocky shores, as with the shore substrate, with diversity decreasing as rate of tidal flooding decreases. Thomas (1983b) reported relatively low invertebrate diversity for ephemeral or brackish water pools high in the intertidal zone ($S = 3 - 4$) which he attributed to unstable and extreme environmental conditions while pools low in the intertidal zone can contain a more diverse community than the adjacent shore. Logan et al. (1983), summarized research on sublittoral hard substrate communities at 72 localities in the lower Bay of Fundy and reported 65 macroinvertebrate species as common, and 19 as rare species. Pohle et al. (2001) reported that species richness of sublittoral benthic invertebrates in the Bay of Fundy ranged from 30 to 45 ($H' \sim 2.7$-2.8) in an embayment in the lower bay. The 42 taxa reported in my study then, seem to be near the average species diversity of nearby littoral and sublittoral environments.

While estuaries in general, and salt marshes in particular, are considered areas of low diversity due to extreme fluctuations of environmental conditions (Day et al. 1989), salt marsh pools are similar in invertebrate diversity to other estuarine habitats and add to the overall diversity of salt marshes. If meiofauna is incorporated into diversity measures, species richness could increase substantially. However there are few comprehensive studies of meiofauna in saltmarshes or other coastal habitats to look to for comparison. In any case, their presence adds to the overall diversity and secondary production of a saltmarsh.

Species Patterns

Insects

Of the 14 families of insects observed in the pools only 3 were commonly collected in samples. Families well represented, both in occurrence in samples and abundance, were Chironomidae, Ceratopogonidae, Coroxidae and, to a lesser extent, Ephydridae.

Chironomidae were sometimes relatively abundant in both sediment and vegetation samples, but their diversity was low. Larvae of *Chironomus* sp. comprised >5% of the total invertebrate count in 18 of the 62 sediment samples and 3 of the 12 vegetation samples while only a few individuals of 2 species of Orthocladiinae chironomids were collected. Pupae of *Chironomus* sp. and Orthocladiinae were less abundant than the larvae. Ward and Fitzgerald (1983a) also reported high densities of *Chironomus* sp. larvae in Quebec salt marsh pools, but with pupae densities 100 to 1000 times lower, suggesting the larvae are an important prey item. There were no significant differences in Chironomidae between pools, marshes or sampling times. Larvae were found in higher abundance in vegetation samples, probably because most species of marine chironomids feed on algae or algal detritus (Hashimoto, 1976).

Though rare or absent from many sediment and vegetation samples, *Culicoides* sp. larvae and pupae (Ceratopogonidae) comprised >20% of the macroinvertebrates in the spring vegetation samples of the low and mid marsh pools at Dipper Harbour marsh. Empty pupae cases were found in most sediment samples and were often abundant in the Dipper Harbour samples. *Culicoides* sp. showed no significant correlation with any other common species of the pools; however one of their main food sources is nematode worms which, though present in all samples, were not enumerated. *Culicoides* sp. occurs in Quebec (Ward and Fitzgerald 1983a)and PEI (Giberson et al. 2001) marsh pools, although *Dasyhelea* sp. was much more abundant in PEI marshes. Bromley and Bleakney (1979) reported no Ceratopogonidae in salt marsh pools on the Minas Basin of the upper Bay of Fundy and this family is absent from Linkletter et al.'s (1977) checklist of flora and fauna of the Bay of Fundy.

Trichocorixa is the only coroxid genus in this region able to withstand the high salinity of the marsh pools (Scudder 1976). This genus was negatively correlated with pool salinity (r^2=-0.40, p=0.03). Potential prey items, including amphipods, chironomids and flatworms (Scudder 1976) were frequently collected in association with *Trichorixa* sp., however more samples are needed to confirm any positive correlations between these taxa.

Although the Ephydridae were not identified to species most appeared to be from the genus *Ephydra*. Relatively low numbers of larvae and/or pupae were collected in most samples. Other Diptera larvae collected or observed in the pools such as Stratiomyidae, Dolichopodidae, Tabanidae, and Syphyridae, were relatively rare, however, given that they are larger than many other taxa in the pools they may be a preferred prey item of birds or fish. Mosquito larvae (Culicidae) were very rare; only 2 were collected. There were numerous small depressions near the upper edge at both marshes that contained extremely large numbers of mosquito larvae and appeared to contain no fish, however, because of frequent drying, these were not considered pools in the terms of this study.

Molluscs

Hydrobia tottentei was one of most common and most evenly distributed species in all samples. This small gastropod was generally most abundant in samples from the high marsh pool in Saints Rest, the deepest pool in the study, which may indicate depth offers some protection from predation by birds for this species. *H. tottentei* was not correlated with any other common species of the pools.

Gemma gemma is a small bivalve collected only in sediment samples from Saints Rest. Treating the samples with formalin seemed to damage the thin shell of *G. gemma* and may have destroyed smaller specimens, resulting in an underestimate of its abundance in the pools. It occurred in highest abundance in the lower low marsh pool and was not present in the high marsh pool.

Amphipods

Gammarus micronutus is a common species of marsh pools, associated with *Cladophora* algal mats (LaFrance and Ruber 1985). It was extremely abundant in most pools, but its ability to escape capture by most techniques used to sample marsh pool invertebrates probably resulted in underestimation of its abundance. It was collected in all vegetation samples and in 25% of the sediment samples. In the lowest marsh pools with regular flooding this species appears to be replaced by *Gammarus duebenai*. *Corophium volutator*, an important prey item of shorebirds (Hicklin and Smith 1984), was found in small numbers in some samples from May 2005, but may be a transient species washed into the pools on a spring tide.

Polychaetes

Manayunkia aestuaria, a small, tube dwelling polychaete, was collected in all of the main study pools except the mid marsh pool at Dipper Harbour. Though not technically meiofauna, it is likely that some smaller specimens were lost during seiving. *Manayunkia aestuaria* is an infaunal species and its presence in vegetation samples probably came from mud incidentally collected with the vegetation. Three other species of polychaete, *Pygospio elegans, Streblospio benedicti* and *Polydora cornuta* were present only in the lowest marsh pools and were associated with the other more 'marine' species. *Hediste (Neresis) diversicolor*, reported as a common species of salt marsh pools in some locations (Nichols 1935), was rare in Saint's Rest and Dipper Harbour marshes.

Oligochaetes

Tubificidae oligochates were present and often abundant in most samples. *Peloscolex benedeni*, which was present only in the lowest marsh pools, was easily identified by distinctive papillae covering the body (Cook and Brinkhurst 1973). At least two other species of Tubificidae oligochaetes were collected, one of which occured often in large abundance in all pools, but these were only identified to the family level.

Platyhelminthes (class Turbellaria)

Turbellarians were uncommon in sediment samples but abundant in some vegetation samples. At least 3 species were collected in the vegetation, however these were not identified further.

Meiofauna

After samples were sieved, some nematodes, ostracods, copepods and forams were still retained. Ostracods, copepods and flatworms were the most abundant organisms in the unsieved vegetation samples collected in May, often exceeding 1000 individuals per 100 g of vegetation. Though not sorted by species it was noted that

Cytherois spp. was the most common ostracod collected. Both harpacticoid and calaniod copepods were collected and species identified included *Pseudocalanus sp., Eurytemora affinis, Calanus cyclopagis,* and *Calanus hyperborius.* At least 3 species of calcareous and 1 species of agglutinated forams were collected.

IMPORTANCE OF POOLS TO WILDLIFE

Over the course of this study, migrating shorebirds were frequently observed feeding in the marsh pools at high tide at Saints Rest marsh in the fall of 2004 and greater yellowlegs (*Tringa melanoleuca*) were observed in pools at both marshes from early spring to fall. Mudflats in the upper Bay of Fundy are highly valued as a feeding ground for migrating shorebirds because of their high productivity of *Corophium volutator.* Given the high density of this amphipod at its peak fall population (Hicklin and Smith 1984) and average dry weight of individual *C. volutator* (Boates and Smith 1979), production of this species on mudflats is likely 6.35 g m^{-2}. The average biomass (dry weight) of macroinvertebrates in marsh pools in this study ranged from 1.79 to 4.03 g m^{-2}, depending of the percent cover of vegetation. Invertebrate production of the marsh pools is not dependent on season, unlike that of the mudflats (Hicklin and Smith 1984) and some species of shorebirds feed primarily in the marsh on the return migration in spring (Hicklin and Smith 1979). In the lower Bay of Fundy where *C. volutator* is not as abundant, Gratto and Thomas (1984) reported prey species of sandpipers included species characteristic of marsh pools such as *H. tottentei* and Chironomid larvae and pupae. Daiber (1982) notes that several species of waterfowl depend on the marsh pools for feeding and Ferringno (1961) found that draining marsh pools had a drastic effect on waterfowl. A correlation between bird use of salt marshes and the amount of open water (pools) has been shown by Burger (1982) and Clarke et al. (1984). In addition to direct foraging in pools insects emerging from pools are a food source for passerines, such as the salt marsh sharp-tailed sparrow, *Ammodramus caudacutus* (Greenlaw and Rising 1994).

The importance of marsh pools and other shallow littoral habitats to fish as nursery, foraging and refuge sites is the subject of high interest and ongoing research (e.g., Raposa and Roman 2001, Adamowicz 2002, Raposa 2003, Able et al. 2005). Though not quantified, I observed mummichogs (*Fundulus heteroclitus*) in all sampled pools in all seasons and frequently in high abundance. Important prey items of mummichogs, such as amphipods, tanids, copepods and polychaetes (Kneib and Stiven 1978), were collected in all of the pools sampled. In pools on a St. Lawrence salt marsh, Ward and Fitzgerald (1983b) found the preferred prey items of sticklebacks (Gasterosteidae) were coroxids, chironomid pupae and copepods, which also were common species in the pools of this study. Despite heavy feeding they found the fish had no effect on the invertebrate community of the pools. The finding in this study, that the invertebrate communities of the pools were stable over time despite observed fluctuations in fish density, suggests this may be the case in these salt marshes as well.

The abundance of several species of meiofauna observed, particularly in the un-seived vegetation samples demonstrates that much of the diversity and production of these pools may be missed when meiofauna is not captured. For instance, marsh pools have been shown to have very diverse copepod communities, relative to macroinvertebrate diversity (Ruber et al. 1994). Some species of meiofauna are important prey items to fish (Ward and Fitzgerald 1983, Kneib and Stiven 1978), some species of birds (Gratto and Thomas 1984, Gaston 1992), and are important in transferring energy to higher trophic levels as prey for macroinvertebrates.

CONCLUSION

The apparent gradient of species collected in sediment samples (fig.5) is probably related to the ability of the individual species to withstand broad, fluctuating environmental conditions. The gradient itself could be interpreted as increasing environmental variability from left to right along axis 1. The insect families found in these pools are able to survive in environments with extreme fluctuations in temperature and salinity (Cheng 1976). Although these taxa should be able to physically survive in the conditions of the lower low pools, they are likely limited by competition in these more stable environments. The gradient in the species data and the separation of sediment samples from the regularly flooded (lower low) pools in the community analysis (figs. 3-5) supports the separation of pool invertebrate communities from this study into those occurring in regularly flooded pools and those occurring in irregularly flooded pools. Further sampling would help to determine at what elevation pools change between these two types. The presence of eelgrass (*Zostera marina*) may be an indicator of the regularly flooded pools. The small ephemeral pools at the upland edge of the marsh that appear to be dominated by mosquito (Culicidae) larvae are likely a third pool type with a unique invertebrate community. Typical salt marsh fish, like fundulids and gasterosteids show a preference for pools higher up marsh creeks which are flooded irregularly (Raposa and Roman 2001, Raposa 2003). This is the dominant pool type in the marshes in this study. The more saline pools may provide opportunistic feeding areas for estuarine fish and nekton at flood tides.

After an estimated 50 years since dyke failure, the invertebrate fauna of pools in the recovering marsh is indistinguishable from that of the reference marsh. In fact, pools of the recovering marsh tended to have slightly higher species richness than the reference marsh (table 4), though this was not significant. Three species: *L. saxatilus, G. gemma* and *N. vectensis* were collected only in pools at the recovering marsh. The pool habitat has been shown here to be a resilient (as defined by Grimm and Wissel 1997) component of a salt marsh, capable of returning to an equivalent state of a reference site following an unmanaged restoration.

Table 1: Percent cover of aquatic vegetation in high (H), mid (M), and low (L) marsh pools from July 2004 to July 2005

Dipper Harbour		July 30	Aug.20	Sept.16	May 23	July 5
	Ruppia	90	90	90	5	45
H	Algae	5	5	<10	5	25*
	Bare	5	5	0	90	35
	Ruppia	80	90	55	<1	80
M	Algae	20*	30*	<10	10	30*
	Bare	15	10	45	90	<5
	Ruppia	35	40	40	<1	15
L	Algae	15	15	15	15	40
	Bare	50	45	45	85	45
Saints Rest						
	Ruppia	-	25	**	**	**
H	Algae	-	10	**	**	**
	Bare	-	65	**	**	**
	Ruppia	-	<5	<5	0	0
M	Algae	-	35	<10	25	45
	Bare	-	60	85	75	55
	Ruppia	-	5	<1	0	0
L	Algae	-	20	25	40	30
	Bare	-	75	75	60	70

*total >100% due to cover of algae growing epiphytically on *Ruppia*.
** no bottom visibility.

Table 2: Dry weights of select macrofauna of Saint's Rest and Dipper Harbour saltmarshes, Bay of Fundy.

Species	#	Total (mg)	mg / individual
Trichorixa verticalis	34	2	0.06
Gammarus micronutus (May)	36	36	1.00
G. micronutus (August)	40	16	0.40
Chironomidae larvae	30	3	0.10
Culicoides sp. larvae	50	7	0.14
Culicoides sp. pupae	50	7	0.14
Tubificidae	100	1	0.01
Hydrobia tottenti (August)	50	72	1.44
H. tottenti (May)	50	143	2.86
Manayunkia aestuarina	43	0	0.00
Turbellaria	50	1	0.02
Ephydridae	1	1	1.00

Table 3: Summary of average percentage weight and abundance of common pool macroinvertbrates in sediment and vegetation samples from Saint's Rest and Dipper Harbour saltmarshes, Bay of Fundy.

	Vegetation samples				Sediment samples			
	% dry weight		% abundance		% dry weight		% abundance	
	Avg	Range	Avg	Range	Avg	Range	Avg	Range
H. tottentei	90.40	50.5-100	43.92	1-93.5	85.82	0-100	27.83	0-99
G. micronutus	0.04	0-0.5	10.03	0.5-49	4.19	0-100	1.64	0-50
T. verticalis	0.31	0 – 2	1.78	0-5	2.23	0-75	2.44	0-36
Chironomidae	1.74	0-13	7.49	0-44	4.47	0-100	6.78	0-80
Culicoides sp.								
larvae	0.45	0-3	2.51	0-13.5	0.06	0-2.5	0.07	0-1.5
pupae	0.56	0-4	3.11	0-19	0	0	0.02	0-1
Tubificidae	1.57	0-6.5	15.49	0-74.5	1.21	0-25	11.78	0-77
Turbellaria	2.04	0-16	10.19	0-48	0.47	0-25	0.90	0-33
Ephydridae	2.89	0-27	0.28	0-1.5	1.54	0-71.5	0.31	0-11

Table 4: Diversity expressed as taxa richness (S), Shannon-Weiner (H'), and evenness (J) of macroinvertebrates Saints Rest and Dipper Harbour marsh pools.

Marsh	elevation	S	H'	J
Saints	High	20	1.258	0.967
Rest	Mid	23	0.810	0.595
	Low	20	0.794	0.610
	Lower	19	0.764	0.597
Dipper	High	17	1.390	1.130
Harbour	Mid	16	0.687	0.570
	Low	21	1.294	0.978
	Lower	13	3.002	2.695

Table 5: Macroinvertebrate taxa in salt marsh pools in this study and in salt marshes found on to the Bay of Fundy: 1 (this study), 2 (Bromley and Bleakney 1979), St. Laurence River Estuary: 3 (Ward and Fitzgerald 1983), Narragansett Bay RI: 4 (Nixon and Oviatt 1973),Rowley MA: 5 (Clarke et al. 1984), Nauset Marsh, MA 6 (Heck et al. 1995), 7 Delaware National Estuarine Research Reserve (Stocks and Grassle 2003), 8 Aberlady Bay, UK (Nicols 1935), Western Iceland 9 (Ingolffson 1994).

	Bay of Fundy		QC	RI	MA	MA	DE	UK	Iceland
	1[a]	2	3	4	5	6	7	8	9
Phylum Cnidaria									
Nematostella vectensis	s	+		+			+		
Protohydra leukarti		+						+	
Syncoryne sp.								+	
Phylum Platyhelminthes									
Turbellaria	vs	++		++					
Phylum Rhynchocoela							+		
Amphimporus angulatus		+							
Lineus sp.		+						+	+
Prostomatella obscura		+							
Phylum Mollusca									
Gastropoda									
Littorina littorea	s	+						+	
Littorina saxatilis	vs	+	+			+		+	+
Hydrobia sp.	vs	+	+		+	+	+	+	+
Ilyanassa obsoleta		+							
Skeneopsis planorbis									+
Sacoglossa									
Alderia modesta		+						+	+
Elysia chlorotica		+							
Limopontia sp.								+	
Stiliger fuscatus		+							
Nudibranchia									
Tenellia sp.		+						+	
Bivalvia									
Gemma gemma	s	+							
Geukensia demissa		+							
Hiatella striata		+		+					
Macoma balthica								+	
Mercenaria sp.				+					
Modiolus sp.				+					
Mya arenaria	o	+		(+)				+	+
Mytilus edulus	o	+						+	+
Phylum Annelida									
Polychaeta					+				
Arenicola marina			+					+	+
Capitella sp.				+		+	+		
Eteone heteropoda		+							
Eteone longa		+							
Eulalia viridis								+	
Fabricia sabella						+			+
Hediste diversicolor	s	+	+					+	+
Heteromastis filiformis		+							
Leitoscoloplos sp.						+			

Table 5 continued

	Bay of Fundy		QC	RI	MA	MA	DE	UK	Iceland
	1[a]	2	3	4	5	6	7	8	9
Manayunkia aestuarina	s	+						+	+
Pygospio elegans	s	+						+	+
Polydora cornuta	s	+	(+)	(+)					(+)
Scolecolepides sp.				+					
Scoloplos sp.		+							+
Streblospio benedicti	s	+		(+)					
Oligochaeta						+			+
Tubificidae	vs	+	+				+		
Phylum Arthropoda									
Acarina	vs	+							
Isopoda		+			+			+	+
Chirodotea coeca						+			
Edotea montosa						+			
Erichsonella attenuata						+			
Idotea sp.						+			+
Jaera marina		+						+	(+)
Amphipoda					+				
Corophium volutator	v	+		(+)				+	
Corophium bonelli									+
Gammarus mucronatus	vs	+							
Gammarus duebeni	vs							+	+
Gammarus lawrencianus			+						
Gammarus oceanicus			+						+
Orchestia grillus		+							
Pseudalibrotes littoralis									+
Decapoda									
Carcinus maenus	o	+		+		+		+	
Callinectes sapidus				+					
Crangon sp.	o					+		+	
Palaemontes sp.					+	+			
Hemiptera								++	
Trichorixa verticalis	vs	+	+		+				(+)
Saldidae	s								
Homoptera									
Notonectidae					+				
Trichoptera	o							+	
Diptera					+				
Ceratopogonidae	vs		+						
Chironominae	vs	+	+	+			+		+
Orthocladiinae	vs								+
Tanypodinae								+	
Culicidae	v		+						
Dolichopodidae	vs		+						
Ephydridae	vs	+	+						
Stratiomyiidae	vs		+						
Syrphidae	o		+						
Tabanidae	vs	+	+						
Coleoptera									+
Enochrus hamiltoni	v	+	+						

\+ Species / family reported. (+) indicates only reported to genera

[a] Coding in column 1: vs = collected in both vegetation and sediment samples, v = in vegetation only, s = in sediment samples only, o = observed in pools but not collected

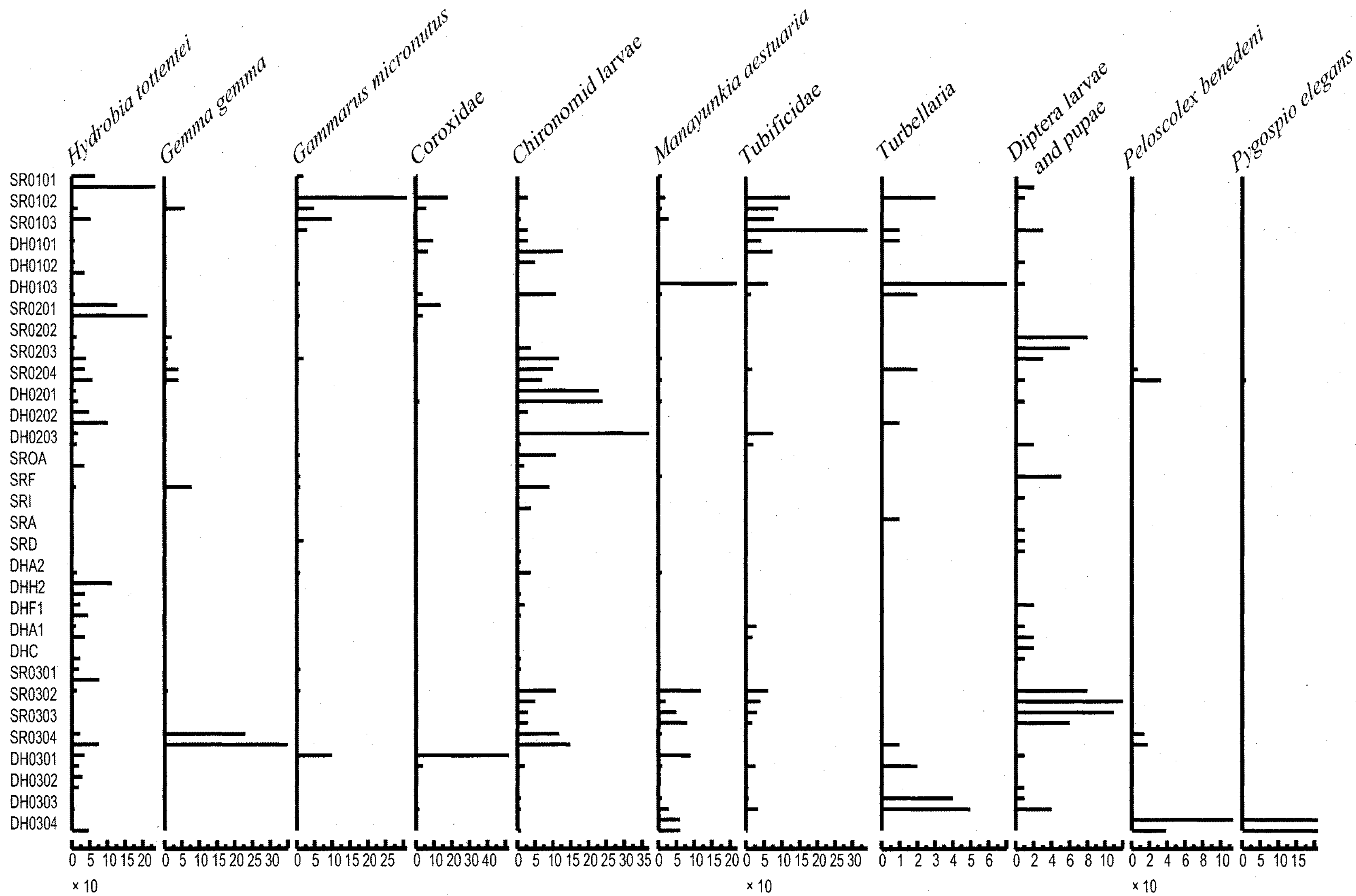

Figure 1: Summary of abundance data for macrofauna taxa representing at least 10% of the total abundance of invertebrate macrofauna in sediment samples. Main pool samples are coded by marsh, Saints Rest (SR) or Dipper Harbour (DH), sampling period; July 2004 (01), August/September 2004 (02) May 2005 (03), and location on marsh; high marsh (01), mid marsh (02), low marsh (03), lower-low marsh (04). For example: Sample SR0102 is the July sample from the mid marsh pool at Saints Rest marsh. Additional pools are labelled by marsh code and letter.

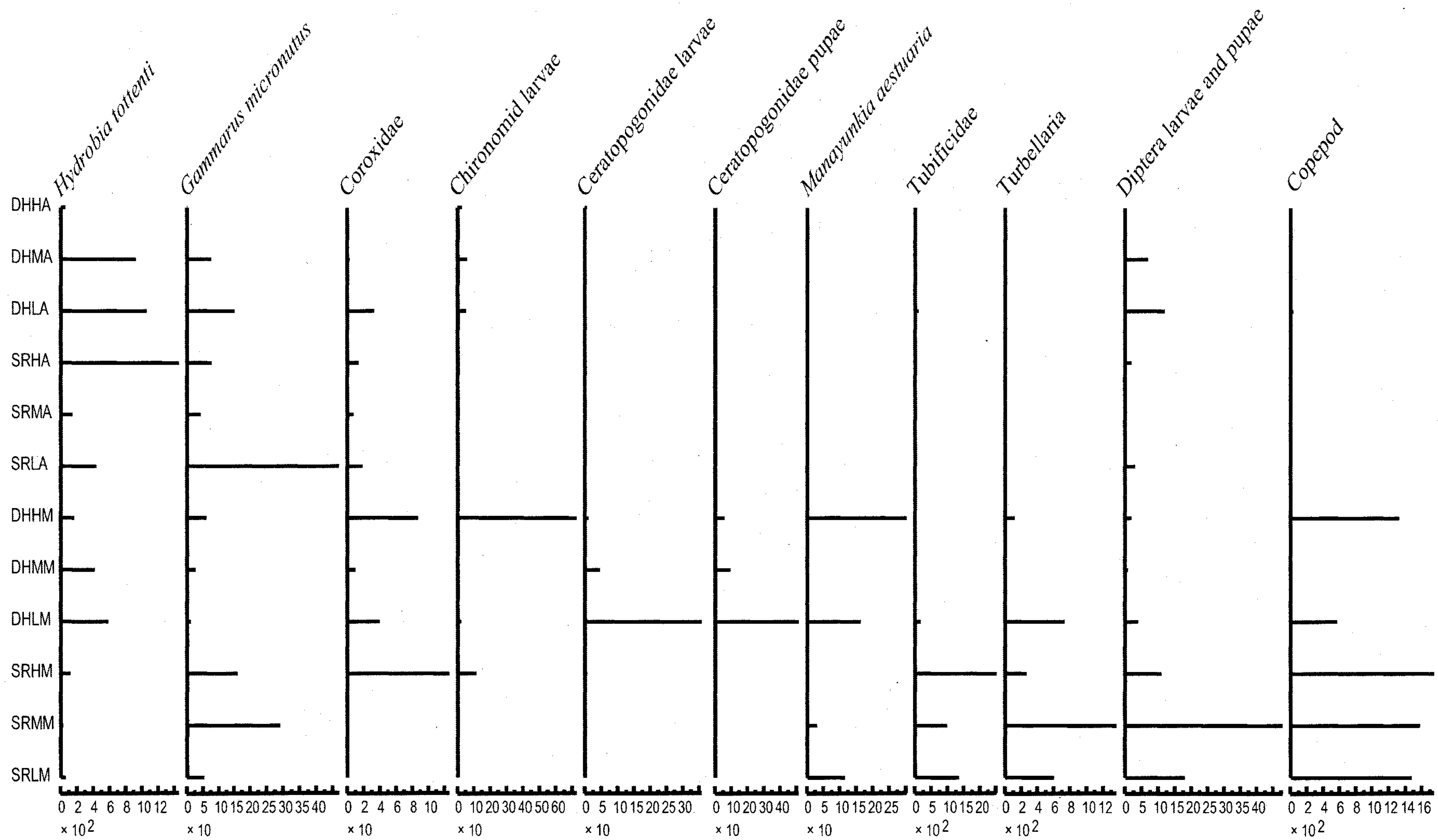

Figure 2: Summary of abundance data for macrofauna taxa representing at least 10% of the total abundance of invertebrates in vegetation samples collected in August 2004 and May 2005. Sample coding: SR = Saint Rest, DH = Dipper Harbour, H, M, L indicate high, mid and low pools and the last letter indicates sample date (A = August 2004, M = May 2005).

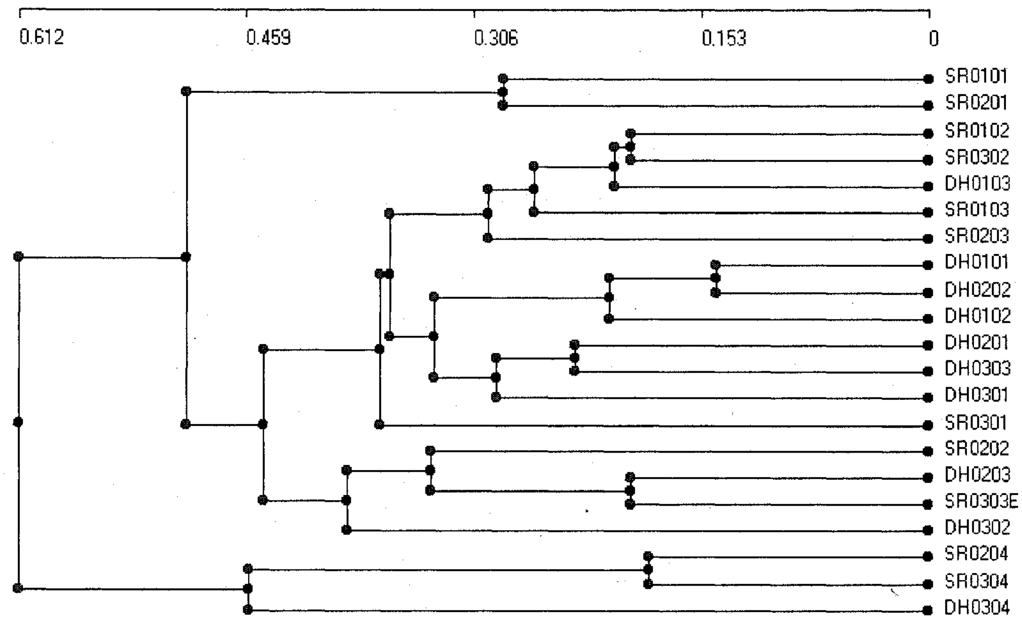

Figure 3: Dendrogram produced through cluster analysis of abundance of invertebrates in combined edge and mid sediment samples of intensively studied pools using average linkage, Bray-Curtis distance. Sample coding follows figure 1.

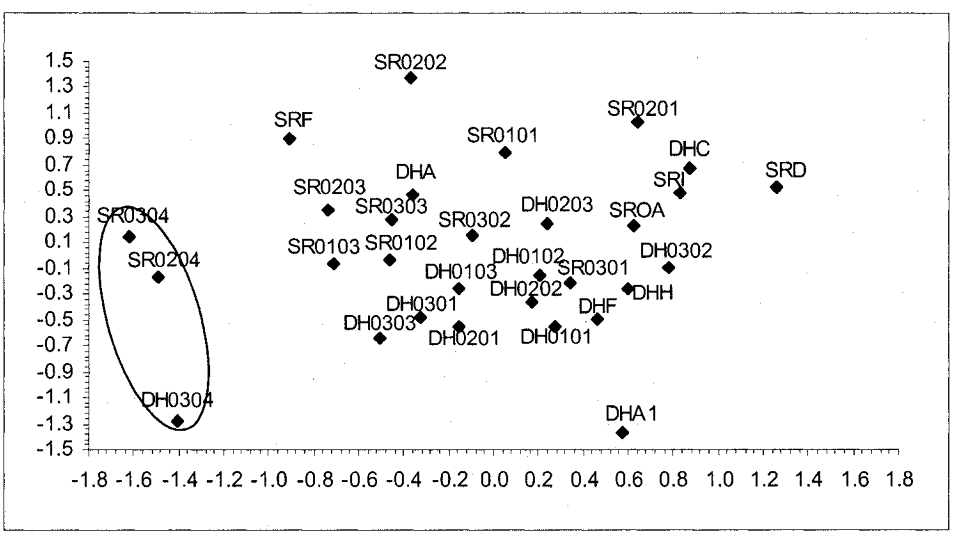

Figure 4: Non-metric multidimentional scaling (NMDS) ordination of sediment samples. Sample coding follows figure 1. The three points to the left of axis 1 are the samples from the lower-low pools at Saints Rest marsh and Dipper Harbour marsh.

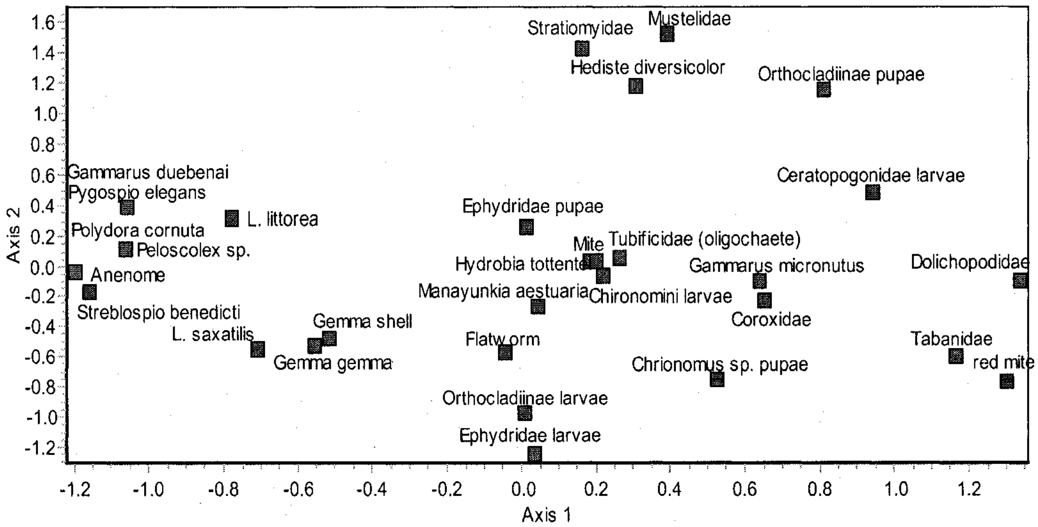

Figure 5: NMDS ordination of species in sediment samples.

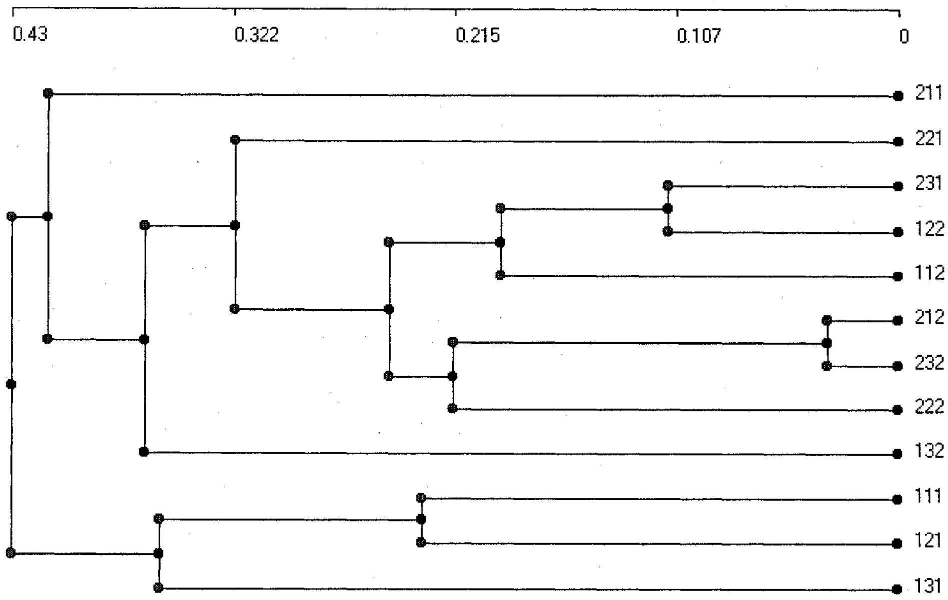

Figure 6: Dendrogram produced through cluster analysis of log transformed invertebrate abundance in August and May vegetation samples of intensively studied pools using average linkage, Bray-Curtis distance. First number in samples code represents marsh (Saints Rest = 1, Dipper Harbour = 2), second number represents pool elevation (1=high marsh, 2=mid marsh, 3=low marsh), third number represents sampling date (1=August, 2= May).

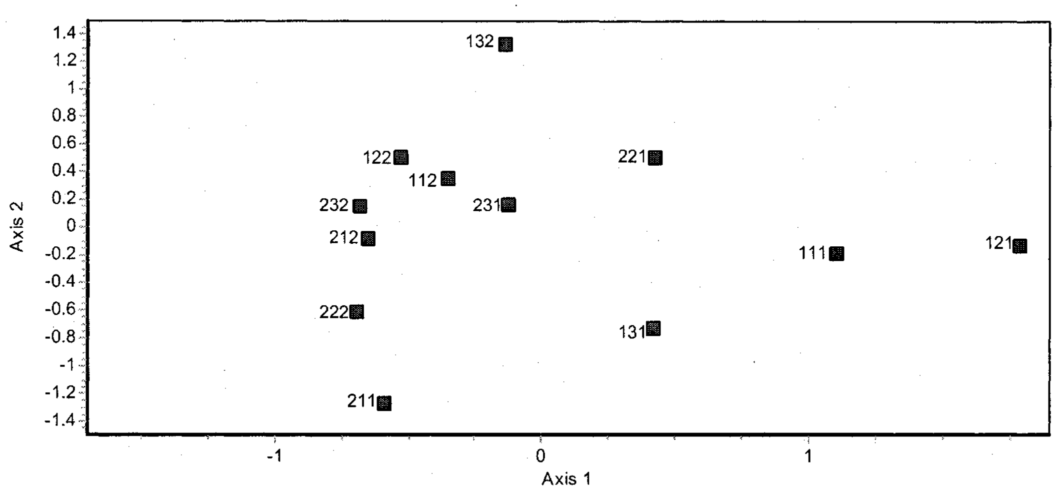

Figure 7: NMDS ordination of vegetation samples. See fig. 6 for sample coding.

Chapter 4: Summary Conclusion

Grimm and Wissel (1997) define resilience as a property of ecosystem stability that refers to a system "returning to the reference state (or dynamic) after a temporary disturbance". As habitat within a salt marsh pools show resilience both in form, by their re-emergence on a recovering salt marsh with no human intervention and in function, as the invertebrate fauna of pools in the recovering marsh is indistinguishable from that of the reference marsh.

More than 50 years after the dyke breached, the recovering marsh has nearly 3 times as much pool area (as a proportion of vegetated marsh surface) as the reference site. The greater pool area on a recovering marsh lends support to Redfield's (1972) hypothesis that they are a more common component of a younger marsh. However, given the extent of human alteration on Saints Rest marsh, some of the increase may be attributed to pools forming in failed ditched and borrow pits as Miller and Egler (1950) suggested occurs in recovering marshes, or in sections of the original creek network that did not become reactivated when tidal flooding returned to the system. Observations from this study suggest that ice is a driver in forming and enlarging pools in Bay of Fundy marshes.

Environmental variability was extreme in most pools, with salinity ranging from brackish to hypersaline and temperature changing rapidly when tidal water flooded the pools. Differences in flooding frequency between the marshes and between the intensively studied high and low marsh pools did not cause significant differences in the average temperature and salinity of the pools examined, with long term environmental conditions being affected more by climate than tide. The only pools that had significantly different temperature and salinity were pools at the lowest elevations, where much higher flooding frequency resulted in lower variability. Regularly flooded pools were uncommon in the marshes examined.

Forty-two macroinvertebrate taxa were identified from the pools, which is near the average species diversity of nearby littoral and sublittoral environments (see studies in Thomas 1983, and Pohle et al. 2001). Unlike the zonation observed in vascular plants in a salt marsh, small differences in flooding frequency seem to have no effect on the invertebrate community, rather the constant high level of environmental variability in most pools seems to be the determinant of what invertebrates could use the habitat. Non metric multidimentional scaling and hierarchical cluster analysis supported separating the pool invertebrate communities of this study into those occurring in regularly flooded pools, and those occurring in irregularly flooded pools. Species with broad environmental tolerances are able to survive in the irregularly flooded pools while they are replaced, probably through competition, by more typical estuarine species in the regularly flooded pools.

Generalist bird species populations have been found to be significantly higher in restored or created saltmarshes than in nearby pristine marshes and this increased use has persisted in some marshes for more than 20 years (Brawley et al. 1998, Fell et. al. 2000, Warren et. al. 2002). This increase in bird usage might be attributable to greater pool coverage if this is a common feature of a recovering marsh. In terms of habitat value, an increase in pool area on a marsh with equivalent invertebrate production results in increased feeding habitat for birds and fish. As such, in the Bay of Fundy, recovering marshes may be more attractive to wildlife than unaltered marshes.

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Appendix A: Chapter 3 Taxonomic References

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