Understanding the ecological linkages between salt marsh ecosystems and nearshore fisheries

Authored by

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Abstract

Salt marshes are some of the most productive ecosystems on the planet however they continue to experience severe threats from human activities. These ecosystems have been increasingly recognized for their capacity to sequester large amounts of carbon and keep pace with sea level rise. Salt marshes provide numerous other ecosystem services including improving water quality and reducing flooding for coastal communities, however their importance for nearshore fisheries is often poorly understood and quantified. Many species of marine fish and crustaceans including those that hold commercial value utilize salt marshes at some point throughout their life history. Salt marshes offer refuge and an abundance of food resources making them ideal nursery habitats. Salt marshes contribute more to nearshore fisheries than just the direct export of juvenile fish. When fish and other nekton move between salt marshes and nearshore environments they act as biological vectors moving energy and nutrients mainly in the form of their biomass. Large amounts of detrital matter from salt marshes are moved by the tides providing another important source of energy and nutrients to nearshore food webs. This paper synthesizes existing research in relation to the ecological linkages between salt marshes and nearshore fisheries in order to better understand the importance of salt marshes for fish. An improved understanding of these linkages may provide support for undertaking salt marsh restoration and conservation efforts.

Keywords: Salt marsh, energy and nutrient linkages, fish, biotic vector, abiotic vector, tides

List of Abbreviations

CTZ	Critical Transition Zone
DIC	Dissolved Inorganic Carbon
DFO	Department of Fisheries and Oceans
DOC	Dissolved Organic Carbon
GPP	Gross Primary Production
MPA	Marine Protected Area
MSMB	Mont Saint Michel Bay
NPP	Net Primary Production
NSCPA	Nova Scotia Coastal Protection Act
NSDA	Nova Scotia Department of Agriculture
NSWCP	Nova Scotia Wetland Conservation Policy
OM	Organic Matter
POC	Particulate Organic Carbon
TA	Total Alkalinity

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1. Introduction

1.1 Background information

Nova Scotia's topography includes a coastline of approximately 7,400 km that supports a diverse array of coastal ecosystems. Among these coastal ecosystems are salt marshes that once covered an area of more than 30,000 hectares (Mackinnon & Scott, 1984). The majority of Nova Scotia's salt marshes are found within the Bay of Fundy, a water body that experiences the highest tides in the world and is bordered on three sides by the Canadian provinces of New Brunswick and Nova Scotia (Bleakney, 2004). Beginning in the 1630's, French settlers known as the Acadians, progressively drained and dyked approximately 60% of Bay of Fundy salt marshes (Mackinnon & Scott, 1984) converting them into rich arable farmland (Sherren & Verstraten, 2012). Building dykes with sod bricks and aboiteaux (also called tide gates) as drainage mechanisms, they were able to remove the water from the marsh at low tide to prevent it from re-entering the marsh at high tide. Rainwater naturally washes away the salt content and after three years the dyked marshland was ready for agricultural practices (Butzer, 2002).

While dyked salt marsh land in Nova Scotia is now used by humans for a variety of different purposes, including commercial and residential developments, historically dykelands were exclusively used for agriculture (Mackinnon & Scott, 1984). Drained salt marsh soil contains a rich and uniform distribution of nutrients making it ideal for growing crops while requiring no additional fertilizers. Salt marsh soils are aerated by plowing and do not need to be cleared of rocks and trees (Bertness et al., 2004). In contrast, land that is more typically cleared for agricultural purposes such as forests and other upland soils are variable in structure, nutrient and mineral contents, and pH. This is because of the constant leaching they have been experiencing in post-glacial times (Bertness et al., 2004). Salt marsh soils differ as they are essentially being re-formed annually with tidal waters bringing in organic and inorganic nutrients that get incorporated into the soil content. As a result of the tides, Bay of Fundy salt marshes have 6 times more potassium, 2.5 times more phosphorus, 3.5 times more calcium, and 4.5 times more magnesium than upland soils (Bleakney, 2004). Tidal mixing allows for the distribution of nutrients in marsh soils to be relatively uniform throughout. While the dyking of salt marshes has allowed for intensive agriculture and other human developments, after centuries of use and continuous pressures from natural causes (e.g., high tides and storm surges), many dykes have experienced some level of deterioration and in some cases have been breached (van Proosdij & Page, 2012).

Dykes currently protect more than just agricultural land including towns, transportation infrastructure, as well as commercial and residential developments. They also hold cultural significance by fostering a sense of place and identity while also supporting recreation and tourism activities (Sherren et al., 2016). The dykelands located along the Bay of Fundy are set within a dynamic environment that is already heightened by the extreme high tides that this region experiences (Sherren et al., 2019). All of the dykes that currently exist along the Bay of Fundy have been built within the last 100 years using modern machinery, with the majority being upgraded or built in the 1970s and are much higher than the original Acadian dykes (Bleakney, 2004). The Land Protection Section of the Nova Scotia Department of Agriculture (NSDA) is the body responsible for maintaining 241 km of dykes including 242 aboiteaux along Nova Scotia's coasts and waterways (NSDA, 2019). These dykes protect 17,400 ha of agricultural lands. Climate change impacts, especially sea level rise and storm surges are projected to intensify making these dykes more vulnerable (van Proosdij et al., 2018). Decisions need to be made regarding mitigation and adaptation strategies since the cost and maintenance requirements of raising all of the dykes in Nova Scotia to heights that will be able to withstand rising sea levels and intensified storm surges is high (Chen et al., 2019). In some cases, due to a variety of different factors it may make more sense to explore alternative options. As a result, the provincial government has been tasked with identifying which dykes to realign, reinforce, or remove entirely (Sherren et al., in press).

In situations where dykes are removed or breached, salt marshes, the ecosystems that originally occupied these areas, are given an opportunity to re-establish. Salt marsh restorations are being heavily considered in many circumstances throughout Nova Scotia (Sherren et al., 2019). After a lag time following their restoration, salt marshes are able to provide a vast array of ecosystem services (Smith et al., 2017). Salt marshes are highly productive and resilient coastal ecosystems that can withstand climate change impacts while also lessening some of the effects of sea level rise and storm surges to the adjacent terrestrial landscape (Singh et al., 2007). These ecosystems have also been shown to sequester large amounts of carbon, further mitigating climate change impacts (Wollenberg et al., 2018). In addition to these climate change related ecosystem services, salt marshes provide myriad other benefits. Some of these ecosystem services include water filtration, reduced flooding, shoreline stabilization, cultural and social services, and important habitat for many species (Weis et al., 2016; Rezaie et al., 2020; Sutton-Grier & Sandiger, 2019; Musseau et al., 2018). Their degradation and destruction, including through the creation of dykelands, is accompanied by the loss of these essential ecosystem services (Wollenberg et al., 2018).

Salt marshes provide important habitat to many organisms including a wide variety of different species of fish (Weinstein et al., 2011). Despite only being able to access the marsh platform during periods of tidal inundation, many species of fish are able to exploit the resources provided by salt marshes (Janes et al., 2020). Resident fish species occupy salt marshes throughout their entire life history, while transient species may utilize the marsh for only a certain part of their lives (Kneib, 2003). Salt marshes serve as important nursery grounds for many juvenile fish species including those that are commercially important, offering protection from larger predators and an abundance of food resources (Boesch & Turner, 1984). Detrital export from salt marshes is essential for adjacent estuarine ecosystems and other coastal areas as it provides an important nutrient subsidy for less productive estuarine and coastal food webs (Weinstein et al., 2011; Jinks et al., 2020). While other regions of the world have examined the importance of salt marshes for nearshore fisheries, the ecological linkages between these adjacent ecosystems have yet to be examined in Atlantic Canada. Understanding the value of salt marshes for nearshore fisheries has heightened relevance in Nova Scotia since fisheries hold cultural significance while also contributing to a major proportion of the local economy (Barnett & Eakin, 2015). Decisions about dykelands that are currently under consideration by the province may be directly affected by the evaluation and importance of the ecological linkages between salt marshes and nearshore environments. Gaining a better understanding of the ecological linkages and the associated benefits of salt marshes to nearshore fisheries may provide support for implementing salt marsh restoration in areas that are currently dyked.

1.2 Research questions

The understanding of ecological linkages that exist between salt marsh ecosystems and nearshore fisheries is an area of research that is severely lacking in Atlantic Canada. In order to be able to better conserve these linkages for the benefit of both salt marshes and fish it is critical that this knowledge gap be addressed. By answering the following three questions, I hope to begin to fill this knowledge gap that can be used to improve our understanding of the role that salt marshes have for fish.

To what extent are salt marsh ecosystems benefitting nearshore fisheries?

a) What ecological linkages currently exist between salt marshes and nearshore fisheries?
b) What is the direction and extent of these linkages? Is one direction weighted more than the other assuming two-way linkage exists (i.e., are more energy/nutrients being exported from salt marshes to nearshore fisheries, or is the net movement in the opposite direction)?

1.3 Methods

The majority of the information used for this project was obtained through a literature review synthesizing research that has examined any connections between salt marsh ecosystems and nearshore fisheries. The literature review can be broken down into two main components: the energy and nutrient linkages mediated by biotic vectors (e.g., fish and other nekton); and the energy and nutrient linkages mediated by abiotic vectors (e.g., the tides). The studies used for this literature review included data from salt marshes along the coasts of North America, Europe, and Asia (including Australia) and looked at salt marsh - nearshore fisheries linkages from an ecological and biological perspective, while others focused more on the economic significance of these linkages.

Another aspect of this project was a small pilot study conducted at two salt marshes (Kingsport and Hantsport) located within the Southern Bight of the Minas Basin, Bay of Fundy, in Nova Scotia. The purpose of the pilot study was to get a rough estimate of the amount of fish biomass entering each salt marsh with the flooding tide and leaving with the ebbing tide. This pilot study was carried out during an internship with CB Wetlands & Environmental Specialists (CBWES Inc.) and is discussed in detail in Chapter 4.

2. The salt marsh ecosystem

2.1 Background information on salt marsh ecosystems

Salt marshes are part of a group of intertidal habitats known as coastal wetlands, which include mangroves, seagrass beds, and brackish water reed swamps (Scott et al., 2014). Coastal wetlands are not only at the interface between the terrestrial and aquatic environments, but also the marine and freshwater, therefore are additionally influenced by fluxes of freshwater and saltwater (Silvestri et al., 2005). These fluxes in salinity are highly dependent on the location of the marsh in the estuary and the level of mixing that occurs between the freshwater and saltwater (Silvestri et al., 2005). Salt marshes located higher up the estuary are closer to freshwater inputs and therefore will experience lower salinity levels than those further down the estuary. Marshes closest to freshwater inputs can be described as freshwater tidal marshes (Odum, 1988). These ecosystems are still influenced by the tides; however, their salinity levels are on average less than 0.5 ppt. To compare, the mean salinity levels of salt marshes exist between 18.0 - 35.0 ppt. The transitional marshes that occur in between salt marshes and tidal freshwater marshes can be designated mesohaline or oligohaline depending on their salinity levels (Odum, 1988). Tidal influence also contributes to variations in pH, dissolved oxygen, and redox potential in salt marshes (Mackinnon & Scott, 1984). Salt marshes in arid areas are more susceptible to increases in salinity that can occur at low tide as a result of high levels of evaporation (Davy et al., 2011). Conversely, some of the salt marshes in Atlantic Canada experience the opposite due to the freshwater table dominating areas of the high marsh (Roberts & Robertson, 1986).

Globally, salt marshes are found along the coasts of every continent excluding Antarctica, and occur at temperate and high latitudes, however, they are known to dominate at latitudes greater than 30 degrees (Greenberg et al., 2006). It is estimated that approximately 435,000 km^2 of salt marshes remain worldwide, and it is important to note that this covers about 0.3% of the global surface area and comprises 5% of the global wetland area (Greenberg et al., 2006; Zedler et al., 2008). Just under half of global salt marshes occur on North American coasts in Canada and the U.S.A., with other large areas of these tidal wetlands occurring in China and Korea (Zedler et al., 2008). Salt marshes typically establish on low energy shorelines such as those along the coasts of estuaries, in lagoons or behind barrier islands. High energy coasts prevent adequate sediment deposition that is essential for various aspects of salt marsh ecosystems (Scott et al., 2014). The largest salt marshes tend to exist along shorelines with sand or mudflats. These protected regions allow for seedling establishment while the deposition of sediments creates sloping formations (Davidson-Arnott, 2002). Salt marshes receive sediment deposits that are primarily sustained from inflowing rivers; however, they are also obtained from the tides. Higher sedimentation rates generally occur in salt marshes that are exposed to higher tidal ranges (Davidson-Arnott, 2002). The Bay of Fundy experiences the largest tidal range in the world, which creates turbid waters and high levels of suspended sediment. Suspended sediment concentrations have been found to range between 0.12-12.67 g/L in the Cumberland Basin, an inlet located in the upper part of the Bay of Fundy (Amos & Tee, 1998). Salt marshes in this region therefore experience high levels of sediment deposition that is driven by the tides (Chmura et al., 2001).

2.1.1 Salt marsh zonation

Salt marsh zonation occurs largely as a result of salinity gradients, and differences in tidal flooding and elevation. The two main zones of salt marshes are the high and low marsh (Fig. 1) with different characteristics determining the species that occur in each (Davy et al., 2011). Eastern North American salt marshes are dominated by *Sporobolus spp. (*previously *Spartina spp*). with different species in different zones (Bertness, 1991). Smooth cordgrass (*Sporobolus alterniflorus*) is a halophyte that dominates the low marsh zone in salt marshes throughout eastern North America. The low marsh zone occupies the lowest elevations of the salt marsh and is inundated on every tidal cycle (Zedler et al., 2008). Macrophytes and other organisms inhabiting this region must be able to tolerate frequent flooding. The constant inundation of the low marsh zone makes it accessible to species of fish and other aquatic invertebrates such as molluscs and crustaceans (Teal, 2001). The marsh border closest to the terrestrial environment is often referred to as the “uplands” and receives little to no tidal flooding. *Sporobolus michauxianus* is found along the upland border of salt marshes and sometimes in areas of the high marsh zone that experience higher freshwater influences (Porter et al., 2015). The presence of *Sporobolus pumilus* is often an indication of high marsh zone in these salt marshes. The high marsh zone is generally only inundated during the monthly spring tides and the macrophytes found in this area are better adapted for drier conditions, however, still require some tidal flooding (Huckle et al., 2001). Aquatic species are able to access the greatest amount of high marsh zone during spring high tides, and terrestrial invertebrates and mammals utilize this zone when it is not flooded. Voles and raccoons are two species of mammals that use salt marshes for temporary refuge (Teal, 2001). Certain species of birds such as Nelson's sharp-tailed sparrow (*Ammodramus nelson subvirgatus*) rely on the high marsh zone for nesting (Shriver et al., 2007). It is important to note that the salt marsh ecosystem is a mosaic with various sub-habitats and often there is no clear boundary between low marsh and high marsh zones. Rather there is a gradual transition linked to elevation and flooding.

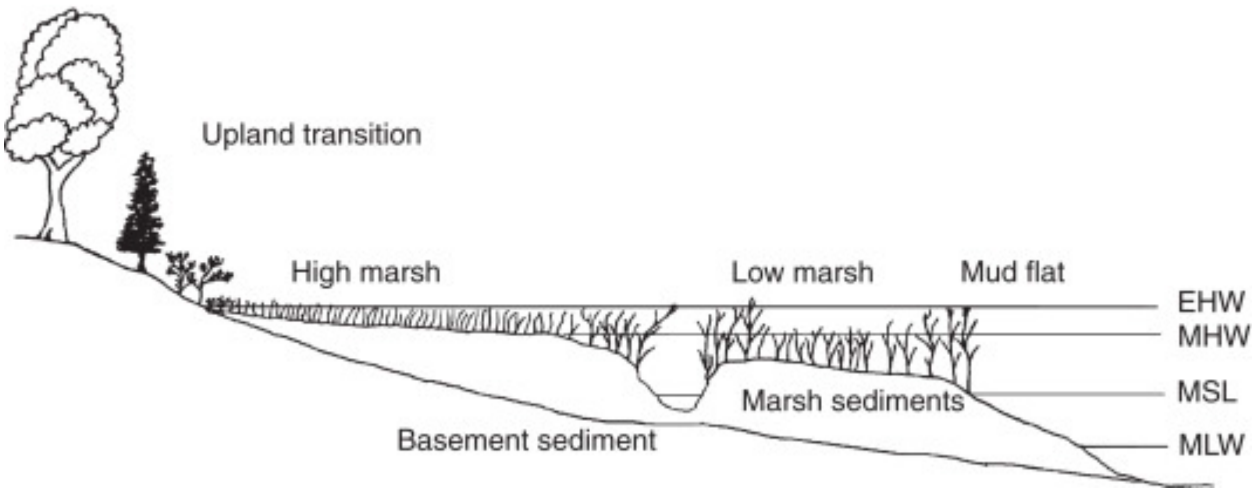

Figure 1. Basic diagram of an eastern North American salt marsh taken from Teal (2001) showing the low and high marsh zonation. The mean low water (MLW), mean sea level (MSL), mean high water (MHW) lines indicate what parts of the salt marsh are flooded at certain points of the tidal cycle. The extreme high water (EHW) mark demonstrates the water level that occurs with monthly spring high tides.

2.1.2 Tides

Tidal inundation is perhaps one of the most important and distinguishing factors for salt marsh ecosystems. While the tides are extremely important for providing nutrients, they also remove and prevent the accumulation of toxic waste (Valiela et al., 1978). Toxic waste types include the build-up of metabolic by-products produced in salt marsh soils, heavy metals, and organic and inorganic substances from urban and industrial developments (Nelson & Zavaleta, 2012). Lunar tidal cycles are the mechanism that controls the water levels and periodicity of the tides. Depending on their location, salt marshes may experience one of four types of daily tides; semi-diurnal, diurnal, strongly semi-diurnal, and strongly diurnal (Bleakney, 2004). Semi-diurnal tides occur twice a day and include two high tides and two low tides, whereas diurnal tides include one high tide and one low tide per day. Strongly semi-diurnal tides consist of mostly semi diurnal tides and strongly diurnal tides consist of mostly diurnal tides, both with some variations (Bleakney, 2004). Tides are essential as they provide sediments and oxygen to the marsh, while transporting nutrients from the salt marsh to adjacent estuarine and nearshore coastal ecosystems. Tidal range differs significantly in salt marshes across the world and can range from 30 cm to almost 16 m; with the global average of tidal range falling between 2 and 3 m (Scott et al., 2014). Semi-enclosed microtidal seas include the Mediterranean, which experiences the smallest of tidal ranges. The coasts of North America experience vast differences in tidal ranges with microtides in Chesapeake Bay and the Gulf of Mexico with amplitudes of less than 1 m (Scott et al., 2014), while macrotides in the Bay of Fundy on Canada's east coast has the world's highest tides with amplitudes of up to 16 m. Differences in tidal ranges can create variations in factors such as structure, zonation, and vegetation even in salt marshes occurring at similar latitudes (Valiela et al., 1978).

2.1.3 Salt marsh primary producers

In addition to transporting nutrients and sediment, tides can also carry and deposit seeds, propagules, or portions of the rhizomes of plants to tidal flats which can facilitate the establishment of new or the expansion of existing salt marshes. Tidal flats gain elevation relative to mean sea level through the accretion of sediment that will support the colonization of pioneer salt marsh plants on the marsh surface (Bertness, 1991). Once salt marsh plants and algae have established themselves, they act as ecosystem engineers and will alter the environment resulting in more sediment deposition, further increasing elevation and supporting an array of other salt marsh species. Few plant families have evolved a tolerance to high salinities, periodic-submersion, and low oxygen that is characteristic of salt marshes (Flower & Colmer, 2015). Halophytes are salt tolerant plants that are characteristic of salt marshes and they have developed specific adaptations that allow them to thrive in this environment. Some species store salt in leaves or stems that will eventually be shed as dry tissue, while others have special glands that can excrete excess salt (Flower & Colmer, 2015). Some of the more widely distributed salt marsh plants include succulents such as the glassworts (*Salicornia, Sarcocornia* herbs, *Arthrocnemon* shrubs) and seablites (*Suaeda* spp.). Other common salt marsh plants include cordgrass (*Sporobolus* spp.), salt grasses (*Puccinellia, Distichlis*), sea lavenders (*Limonium* spp.) and orache (*Atriplex*). Salt marsh sedges (*Carex*, *Scirpus* spp.) and spikerushes (Juncus spp.) are less salt tolerant and tend to be found in the high marsh where rainwater dilutes the soil or in proximity to freshwater inputs (Scott et al., 2014). Salt marsh plants are grazed on by invertebrates including snails such as *Melampus bidentatus*, however, they contribute more to the salt marsh food web through decomposition. Salt marshes are known for serving as depositories for large amounts of organic matter that is a critical component of salt marsh and estuarine food webs (Boschker et al., 1999). Micro-organisms and invertebrates feed on decomposing salt marsh plants and begin the cycles that make energy and nutrients from the halophytes accessible to higher level organisms such as fish and birds (Boschker et al., 1999).

2.1.4 Salt marsh productivity and nutrient cycling

Salt marshes are some of the most productive ecosystems on the planet while also being substantial contributors in the coastal carbon cycle (Bauer et al., 2013; Najjar et al., 2018). Primary producers including salt marsh macrophytes and algae drive the productivity in these ecosystems. Estimates for gross primary production (GPP) rates in salt marshes range from 1900 g C m^{-2} yr^{-1} to 3600 g C m^{-2} yr^{-1} (Duarte et al., 2005). Aboveground net primary production (NPP) has been estimated to be in the range of 60g C m^{-2} yr^{-1} for salt marshes at more northerly latitudes and as high as 812 g C m^{-2} yr^{-1} at more tropical latitudes (Morris, 2007). This can be compared to a tundra ecosystem with a GPP rate of 122 g C m^{-2} yr^{-1} and a highly productive rainforest ecosystem with a GPP rate of 3125 g C m^{-2} yr^{-1} (Garbulsky et al., 2010). Due to their high level of connectivity with estuarine, riverine, and marine ecosystems, the biogeochemical processes of salt marshes are more similar to those of water bodies than purely terrestrial watersheds (Najjar et al., 2018). On the surface, salt marshes are dominated by vegetation, but microbial activity beneath the surface plays a key role in nutrient cycling. Microbial communities are responsible for the transformation of dissolved and particulate organic matter (Sousa et al., 2010). They exist in the sediments, soils and water of salt marshes and account for much of the energy and material flow in these ecosystems. Micro-organisms are highly important for the metabolism of the salt marsh since they decompose particulate organic carbon (POC) into dissolved organic carbon (DOC) making it readily available for higher level organisms (Wiegert et al., 1981). The contribution of DOC from marshes to adjacent coastal waters is largely through the leaching and decomposition of marsh plant biomass (Wang et al., 2014). In association with their high levels of productivity, salt marshes are a significant factor in the food chains of estuaries worldwide (Scott et al., 2014). Salt marshes function as nitrogen sinks and are important in denitrification. Nitrogen uptake occurs through the roots of macrophytes and is incorporated into the plant biomass, detritus, as well as sediments (Wiegert et al., 1981). While salt marshes trap and store nutrients, their high levels of productivity allow for large amounts of nutrients to be moved into coastal waters. The tides are largely responsible for the export of DOC to coastal waters and in certain regions this connection provides an essential nutrient subsidy that supports the functioning of less productive nearshore ecosystems (Lamberti et al., 2008).

2.2 Threats to salt marsh ecosystems

Despite their high levels of productivity and provisioning of ecosystem services, salt marshes have experienced significant losses as a result of human activities. Globally, it is estimated that between 25% and 50% of salt marshes have been lost (Crooks et al., 2011). Since these ecosystems occupy an area of less than 0.5% of the global surface area, any destruction of salt marsh area is impactful on a global scale (Zedler et al., 2008). Anthropogenic impacts that destroy or negatively affect salt marshes also reduce their capacity to provide ecosystem services and consequently threaten the species that depend on them (Himes-Cornell et al., 2018).

2.2.1 Humans: developments, coastal squeeze, alteration of tidal flow

Humans are highly reliant on the ocean and its resources, with more than half of the world's population living within 60 km of the coast (Scott et al., 2014). The location of salt marshes in the coastal zone has made them susceptible to human developments such as residential, commercial, and transportation infrastructure. The development of human infrastructure has been a main driver in the loss of coastal wetlands including salt marshes (Spalding et al., 2014). In some cases, marshes are being filled in to accommodate these developments, destroying the salt marsh ecosystem while creating other problems such as shoreline erosion (Spalding et al., 2014). Since salt marshes naturally occupy low lying areas, human infrastructure built over these areas is more susceptible to flooding especially with increasing sea levels. Hard materials, such as concrete, used in barrier walls do not have the same capacity to mitigate coastal flooding and storm surge impacts as salt marshes and other coastal wetlands (Torio & Chmura, 2013). Engineered infrastructure designed for flood and erosion control including seawalls, bulkheads, groins, and shoreline armouring may temporarily address a current problem, however they will wear over time, are unable to adapt to worsening conditions relating to climate change, and redirect wave energy rather than diffuse it often resulting in erosion elsewhere (Bowron et al., 2012).

Coastal squeeze presents another significant threat that is related to the development of human infrastructure adjacent to or within a salt marsh or other coastal ecosystem. Coastal ecosystems can naturally adapt to rising sea levels through vertical accretion and landward migration (Barbier, 2015). When hard or engineered infrastructure borders the landward boundary of a salt marsh, this severely limits any potential for the salt marsh to adapt with rising sea levels since there is no room to retreat (Borchert et al., 2018). This results in the coastal ecosystem essentially being "squeezed" between the rising water levels and infrastructure, causing the salt marsh to drown and/or erode. In attempts to prevent flooding and protect communities and cities, humans often build structures that will alter tidal flow and circulation (Gedan et al., 2009). Causeways, culverts, bridges, and engineered channels are some examples of structures that can alter the natural hydrology of an area and have adverse effects on salt marsh ecosystems (Bowron et al., 2012). As discussed in the previous chapter, many salt marshes have been converted for agricultural use through the construction of dykes and aboiteaux to prevent tidal flooding and drain the marsh surface (Butzer, 2002). While the alteration of tidal flooding may benefit humans in the short-term or in specified ways, it can also have unanticipated negative impacts on the salt marsh ecosystem. This may include the disruption of access for fish and other species as well as any energy and nutrient connections between the salt marsh and adjacent coastal waters (Gedan et al., 2009).

2.2.2 Climate change: Sea level rise and global warming

As mentioned in the section above, human developments are exacerbating the impact of sea level rise on salt marshes. Salt marshes accrete naturally, however, the rate at which salt marshes accrete is limited by sediment supply and the availability of space, therefore if sea level rise occurs too rapidly these ecosystems will not be able to keep up (Borchert et al., 2018). Through the alteration of hydrology and the development of human infrastructure on or adjacent to the landward edge of salt marshes, the ability of salt marshes to adapt to rising sea levels is limited (Crosby et al., 2016). Certain aspects of climate change and sea level rise are interconnected in terms of their impacts on salt marsh ecosystems (Chmura et al., 2011).

Thermal expansion of seawater is one factor contributing to sea level rise that can increase flood risks as well as increase the intensity of storms and waves. Melting glaciers as a result of the warming climate means that more freshwater is getting into the ocean altering salinities and circulation (Valiela et al., 2018). The Arctic Ocean in particular has been experiencing changes in salinity and water temperature, which is impacting plankton and fish populations. Permafrost upon which northern salt marshes are built on is also melting causing the shoreline to collapse and increasing the rates of coastal retreat (Valiela et al., 2018).

2.2.3 Pollution

Salt marshes in close proximity to human developments and activities are highly susceptible to pollution and oil spills. Nitrogen enrichment from human sewage, urban runoff such as road salt or gasoline from vehicles, and industrial wastes are all sources of pollution that salt marshes located close to cities are vulnerable to (Alvarez-Rogel et al., 2006). Agricultural runoff presents another significant source of pollution and can alter the nitrogen and phosphorus levels in estuaries and coastal wetlands. Eutrophication has also been shown to decrease the below ground root biomass that can cause the banks of salt marsh creeks to collapse (Deegan et al., 2012). While some sources and concentrations of pollution can kill salt marsh animals and plants, others can impact the composition of plant species and microbial communities in certain zones of the marsh (Alvarez-Rogel et al., 2006). The diversity of microbial communities has shown to be lower in salt marsh soils that have experienced metal or organic pollutants (Cao et al., 2006). The functioning of these microbial communities can also be altered by exposure to heavy metals and trichloroethylene, which can in turn impact the biogeochemical cycling of the salt marsh (Cao et al., 2006). Nutrient loading has been identified as one of the main contributors to the continued loss of coastal marshes in New England, U.S.A. (Gedan et al., 2011). Instead of putting down more roots and building up below ground biomass, plants will intake nutrients from surficial waters. While the overall productivity of the salt marsh remains high, the proportion of above ground biomass is much greater than the amount of below ground biomass. With few roots holding soils together, New England salt marshes have become extremely vulnerable to displacement and erosion (Gedan et al., 2011).

2.2.4 Oil spills

Salt marshes are also susceptible to pollution from oil spills. Salt marsh plants and animals are vulnerable to light oil spills as they are highly toxic while heavier crude oil spills will smother salt marsh plants and smaller animals (Lin & Mendelssohn, 2012). The severity of impact on vegetation can vary based on the degree of oil weathering, seasonality of exposure, soil type and exposure, and the extent of oil coverage of aboveground tissues (Hester et al., 2016). Soils that are contaminated by oil can impact belowground plant biomass through toxicity exposure. The presence of oil may also limit gas exchange and lower redox potential in soils, which may result in decreased plant growth (Pezeshki et al., 2000). Birds in particular are known to be highly impacted by oil spills in salt marshes since many different species utilize these ecosystems for breeding and habitat. Oil slicked feathers prevent birds from flying and the toxicity of the substance can kill the bird if ingested, which has a high likelihood of occurring when birds attempt to clean the oil from their plumage (Kingston, 2002). The Deepwater Horizon oil spill that occurred in 2010 is the largest marine oil spill recorded in U.S. waters (Hester et al., 2016). It is estimated that millions of gallons of oil were spilled in the Gulf of Mexico from a considerable distance offshore and in deep waters causing the oil to experience a higher degree of weathering once it reached the coast (McNutt et al., 2012). Louisiana's coast received some of the highest oiling from the spill causing the salt marshes to be highly impacted. Reductions in vegetation health index reflecting plant stress and impacts on photosynthetic processes as well as decreases in live aboveground biomass were seen in Louisiana marshes post spill (Hester et al., 2016). Areas that experienced high levels of oiling also saw reductions in belowground biomass by 76%, three and a half years following the initial spill (Lin et al., 2016). While salt marshes have been known to recover from smaller scale oil spills, the long-term impacts of large-scale oil spills on these ecosystems are poorly understood (Lin & Mendelssohn, 2012).

2.2.5 Biological invasions

Invasive species are becoming increasingly problematic for natural systems and salt marshes are no exception. Native salt marsh species are outcompeted for resources and space by non-native or invasive species (Gedan et al., 2009). Invasive species tend to be highly opportunistic with adaptations that allow them to establish and reproduce quickly and they often lack any natural predators in their new environments. Green crabs (*Carcinus maenas*) have been invading coastal ecosystems in North America for more than a century (Audet et al., 2003), however it is estimated that they did not reach the coasts of Atlantic Canada until the 1950s (Audet et al., 2003). They predate on bivalves and juvenile crabs and have been shown to outcompete native species including the mud crab (*Dyspanopeus sayi*) for habitat and resources. Furthermore, green crab burrowing has been shown to damage plant roots and rhizomes as well as destabilize creek banks in salt marshes contributing to their erosion (Aman & Grimes, 2016). Another example of a species that has become invasive in certain regions is smooth cordgrass, a common low marsh species native in salt marshes located along the Atlantic coast of the U.S.A. and Canada. Upon introduction to salt marshes located in the Pacific Northwest of North America it has become invasive and has threatened to displace the native California cordgrass *Sporobolus foliosa* (Callaway & Josselyn, 1992). On the Atlantic coast of the U.S.A., *Phragmites australis* is displacing native *Sporobolus alterniflorus* while also disrupting natural hydrological regimes in salt marshes (Weinstein et al., 2005). This species is able to raise the surface elevation of the marsh more rapidly than native species and may eliminate creeks and pools through decomposition. As the elevation of the marsh increases tidal flooding is reduced and the natural hydrological regime is further disrupted by the lack of creek networks throughout the salt marsh (Weinstein et al., 2005). *P. australis* has a lower salinity tolerance than typical salt marsh halophytes therefore salt marshes located in closer proximity to freshwater inputs or those that have already been hydrologically altered or disturbed are especially susceptible to invasions by this species (Chambers et al., 2003). The reduction in tidal flooding also disrupts other exchange processes (e.g., trophic relays, export of detrital matter), and allows *P. australis* to continue to extend its range (Weinstein et al., 2005). Invasive plant species are problematic because they can result in losses of floral assemblages that coincide with the animal and insect species that rely on them for food and refuge. Humans are facilitating the introduction of invasive species into salt marsh and other ecosystems both directly and indirectly, which in many cases is accidental (Gedan et al., 2009). Although indirect, climate change is causing species to move outside of their normal ranges while also placing stress on ecosystems resulting in a lowered resiliency and capacity to be able to respond to disturbances. Both of these factors are contributing to the increased occurrence of biological invasions (Gedan et al., 2009).

2.3 Ecosystem services

Coinciding with the high level of productivity and variety of functions that salt marsh ecosystems are known for is the array of ecosystem services that they are able to provide. Humans benefit directly and indirectly from these salt marsh services and in many cases are often unaware that these ecosystem services are the result of salt marshes (Himes-Cornell et al., 2018). These ecosystem services range from providing ecological, economic, social and cultural benefits with many of them falling into more than one of these categories. More recently, attention is being drawn to the climate change mitigating capabilities of salt marshes, especially in relation to their capacity to sequester carbon (Chmura et al., 2011). The economic value of ecosystem services provided by salt marshes is estimated to be $193,845 (in 2007 international dollars) per hectare per year (Davidson et al., 2019). Researchers are working to more accurately quantify the monetary value of these ecosystem services in hopes of increasing the urgency and occurrence of policy development for more effective protection of these ecosystems.

2.3.1 Water filtration

Salt marsh macrophytes and their characteristically dense root systems coupled with other primary producers make salt marsh ecosystems efficient water filtering systems. Salt marshes act as large sponges and are able to remove sediments, nutrients, contaminants and any other harmful pollutants out of the water column. Runoff from agricultural, industrial, and urban developments, presents a serious threat to the aquatic environment and can result in eutrophication (Weis et al., 2016). Salt marshes are an important buffer between terrestrial and estuarine environments since they regulate fluxes in nutrients while filtering, sequestering, and storing pollutants and excess nutrients (Levin et al., 2001). Water quality is an important factor for any species that utilizes the aquatic environment including humans. In this way salt marshes contribute to counteracting the effects of eutrophication in coastal areas (Sousa et al., 2012). Through the trapping and accretion of sediments, salt marshes reduce the amount of sediment in the water column, which also decreases the turbidity of the water. The reduction of suspended sediment increases the water quality of the estuary benefitting certain fish including salmonid species that are sensitive to turbid waters especially when in their larval stages (Wilber, 2001; Deegan et al., 2012).

2.3.2 Protection against sea level rise and storm surges

Salt marshes have the capacity to attenuate waves and reduce shoreline erosion and may buffer wind damages from hurricanes (Barbier, 2015). The topography and vegetation of salt marshes creates resistance that dissipates waves and provides some protection to the landward side of the marsh against storm surges. Salt marsh vegetation and wave attenuating capacity are also key factors in stabilizing shorelines that work to prevent coastal erosion (Van Coppenolle et al., 2018). Storm surges and sea level rise put coastal areas at increased risks of flooding. In a similar way that salt marshes act as large sponges to filter and store pollutants from landward runoff, they are able to hold flood water from storm surges and help to prevent excess flooding in low-lying coastal locations (Rezaie et al., 2020). Salt marshes have been found to reduce up to 14% of flood depth and associated property damage from storm surges (Rezaie et al., 2020). While flooding and storm surge intensity are expected to increase with rising sea levels, unlike human engineered flood defence structures, salt marshes are self-adaptive and have the potential to sustain themselves through sediment accretion (Van Coppenolle et al., 2018). This is however highly dependent on the rate at which sea level rise continues to occur and other factors such as sediment supply that contribute to the capacity of salt marshes to keep up (Crosby et al., 2016).

2.3.3 Habitat provision and the subsequent conservation of biodiversity

Salt marshes provide important habitat for a large variety of different species that depend on resources from these ecosystems for their survival (Pennings & Bertness, 2001). In addition to a diversity of resident species, salt marsh ecosystems support many transient species that only rely on this environment for part of their life history (Weinstein et al., 2011). Salt marshes have important ecological functions by providing important feeding grounds and nurseries for many species (Musseau et al., 2018). In addition to the diversity of the benthic invertebrate communities, other aquatic invertebrate species such as fiddler crabs (*Uca pugilator*) and common periwinkle (*Littorina littorea*) inhabit and feed in salt marshes (Garbutt et al., 2017). Insects such as various species of flies, beetles, and springtails utilize the exposed salt marsh macrophytes for habitat (Rochlin et al., 2011). Numerous bird species, including salt marsh sharp-tailed sparrows (*Ammodramus maritimus*) and willets (*Catoptrophorus semipalmatus*), use salt marshes for breeding, stopover grounds, or during moults that are particularly energy demanding events that occur for some species (Benoit et al., 2002). Adjacent mudflats support an abundance of benthic invertebrates and are often associated with salt marsh ecosystems, particularly in the Bay of Fundy. The Bay of Fundy mudflats are critical stopover grounds for migrating birds globally, as they offer an abundance of food resources (Hamilton et al., 2006). Semipalmated sandpipers (*Calidris pusilla* (L.)) feed extensively on the amphipod *Corophium volutator* during their stopover on these intertidal mudflats (Hamilton et al., 2006). Omnivorous mammals such as raccoons (*Procyon lotor*) and predatory bird species including red-tailed hawks (*Buteo jamaicensis*) feed on the molluscs, crustaceans, and fish that inhabit salt marsh ecosystems (Pennings & Bertness, 2001).

2.3.4 Salt marsh ecosystems as fish habitat

Salt marshes are also known to support a large diversity fish species that depend on them for nurseries or food resources. Many forage fish and commercially important fish species use salt marshes at some point in their life history (McCormick et al., 2019). Recreational fishery species such as the striped bass (*Morone saxatilis*) and smooth dogfish (*Mustelus canis*) utilize salt marshes as feeding grounds (Altieri et al., 2012). Nova Scotia salt marshes provide habitat to small species such as mummichogs (*Fundulus heteroclitus*), nine-spine sticklebacks (*Pungitius pungitius*), and Atlantic silversides (*Menidia menidia*) (Bowron et al., 2013). They also support commercially important species such as gaspereau (*Alosa aestivalus*) and flounders (*Pleuronectidae)* as well as indigenous fishery species like Atlantic tomcod (*Microgadus tomcod)* and American eels (*Anguilla rostrata*) (Dadswell, 2010). Salt marshes are often highly connected to other estuarine and nearshore environments. The export of nutrients through biological and physical vectors such as fish and tides provide important support to estuaries and nearshore ecosystems (Weinstein et al., 2011; Lafaille et al., 1998). The high marsh zone of most salt marshes is only fully accessible to fish during spring high tides while the low marsh zone floods at regular high tides. Despite the chances of being stranded at low tide, the lower predation levels and increased availability of prey resources make foraging in salt marshes a risk that many fish species are willing to take (West & Zedler, 2000).

2.3.5 Social and cultural ecosystem services

Salt marshes are recognized for their recreational and aesthetic values and serve as areas for ecotourism, recreation, and education. They can also provide myriad physical and mental human health benefits and similar to the other ecosystem services that salt marshes provide, these can be significantly impacted by the health of the ecosystem (Sutton-Grier & Sandifer, 2019). Trail systems adjacent or through salt marshes can not only serve as tourist destinations, they can also encourage physical activity such as walking, hiking, or running. Exposure to "green" spaces such as salt marshes may also reduce anxiety and stress, which are growing concerns in today's society (Sutton-Grier & Sandifer, 2019). Other recreational activities such as birding are also common and informative signs or boards near salt marshes can help to educate people on the importance of these incredible ecosystems. Salt marshes provide many research opportunities that further contribute to our understanding of the ecological and biological processes that they support (Weis et al., 2016). Indirectly, salt marshes can be linked to food security as they provide important habitat for a variety of fish species that humans harvest for food. Salt marshes also support numerous fish species that make up recreational fisheries including brook trout (*Salvelinus fontinalis*) and rainbow smelt (*Osmerus mordax*) and indigenous fisheries such as American eels and tomcod (Daborn et al., 2004; Dadswell et al., 2020). Salt marshes also provide numerous cultural services especially for First Nations communities. In Atlantic Canada, the Mi'kmaq First Nations utilize a variety of salt marsh plants for food and medicine. Many indigenous groups consider sweetgrass (*Hierochloe ordorata)*, a salt marsh grass species, to be a sacred plant (Shebitz & Kimmerer, 2005). The New Brunswick Mi'kmaq First Nations use sweetgrass for basket weaving, ceremonial purposes, to make ornaments as well as teas (Vasseur & Temblay, 2014; Shebitz & Kimmerer, 2005).

2.3.6 Carbon sequestration

Salt marshes have a key part in the global carbon cycle while representing a large portion of the biological and terrestrial carbon pool (Chmura et al., 2003). Tidal wetlands store a disproportionately large amount of carbon in relation to their total size, and it is estimated that salt marshes can store between 31-34Tg of carbon per year (Chmura et al., 2011). It has been estimated that tidal wetlands are able to sequester 10x the amount of carbon in comparison to peatlands and salt marshes sequester 4x more carbon than terrestrial forests (Chmura et al., 2003; Byun et al., 2019). This is largely due to the ability of the waterlogged peat of salt marshes to not only store large amounts of carbon, but also sequester it at a faster rate than terrestrial ecosystems (Byun et al., 2019). Excess carbon is also stored in salt marsh sediment which lowers the likelihood of it being aerobically metabolized and re-entering the atmosphere. Anaerobic decomposition is much slower in deep salt marsh soils than the aerobic metabolism that predominates near the surface of salt marshes and in terrestrial ecosystems (Chmura et al., 2003). These factors make salt marshes long-term storage units for organic carbon that will only be released back into the atmosphere through shoreline erosion or soil desiccation. Salt marsh plants are able to trap carbon from the atmosphere, the aquatic environment, and from other sources within the ecosystem. The carbon not only contributes to primary productivity but also ends up in the soils and peat of the marsh. It is important to note that when salt marshes are degraded, some of the carbon they store is released back into the atmosphere (Byun et al., 2019).

3. Energy and nutrient movement between salt marshes and nearshore fisheries

3.1 Aquatic trophic structure in the marsh

Estuaries and salt marshes are considered critical transition zones (CTZ) bridging the terrestrial and aquatic as well as freshwater and marine environments (Levin et al., 2001). In addition to a number of other ecological services they provide, salt marshes regulate fluxes of nutrients, water, particles, and organisms. Salt marsh macrophytes are a key structural component of these ecosystems while also being a crucial component in regulating the flux of energy and nutrients (Litvin & Weinstein, 2003). They are able to slow the flow of water creating more opportunity for deposition from the water column. Like other plants, salt marsh macrophytes take up nutrients from the sediment and recycle them back into the ecosystem (Weinstein et al., 2005). The high levels of productivity associated with salt marsh ecosystems are largely a result of the primary producers (Alongi, 2020). Salt marshes host many different types of algae with some growing on exposed and subtidal sediments in salt marsh creeks, while others occur in association with the extensive root systems of macrophytes (Sullivan & Moncreiff, 1990). These algae exhibit high levels of primary production and present a major food resource for numerous different invertebrates and some species of fish (Sullivan & Moncreiff, 1990; Kneib, 1997). Salt marsh macrophytes are generally not directly grazed on by aquatic organisms however their decomposition forms a significant component of the nutrients and energy in all salt marsh food webs (Levin et al., 2001).

Heterotrophic bacteria, deposit feeders, suspension feeders, shredders, and bioturbators are key functional groups in salt marsh ecosystems (Levin et al., 2001). These bacteria, fungi, and protozoans break down plant material into detritus providing a substantial source of organic matter. Detritus is consumed by a number of invertebrates ranging from amphipods to crabs and some of it is transported to adjacent ecosystems by the tides (Weinstein et al., 2005). Some species of fish will also feed on the detritus, however more fish will feed on the small detritivorous invertebrates that will be most accessible at high tide (Weinstein et al., 2011). Larger fish coming from other nearshore and estuarine environments also gain more access to salt marsh ecosystems at high tide taking advantage of the abundance of food resources in the form of invertebrates and smaller fish (Fig. 2) (Deegan et al., 2000). When fish and other nekton move between different ecosystems to forage or as part of ontogenetic migrations, they transport energy and nutrients mostly by the means of their biomass (Boesch & Turner, 1984). These are generally considered to be transient species and many of them hold commercial value making up a significant component of global fisheries (Meynecke et al., 2008). Species assemblages in coastal food webs undergo seasonal variation with significant changes occurring between summer and winter months (Abrantes et al., 2015). The seasonal influx of freshwater has been shown to alter species assemblages, with some species avoiding peak river discharge events (Rogers et al., 1984). The presence of ice in winter months can deter many transient species in salt marshes located at more northern latitudes and few species are known to overwinter on these marshes (Raposa, 2003).

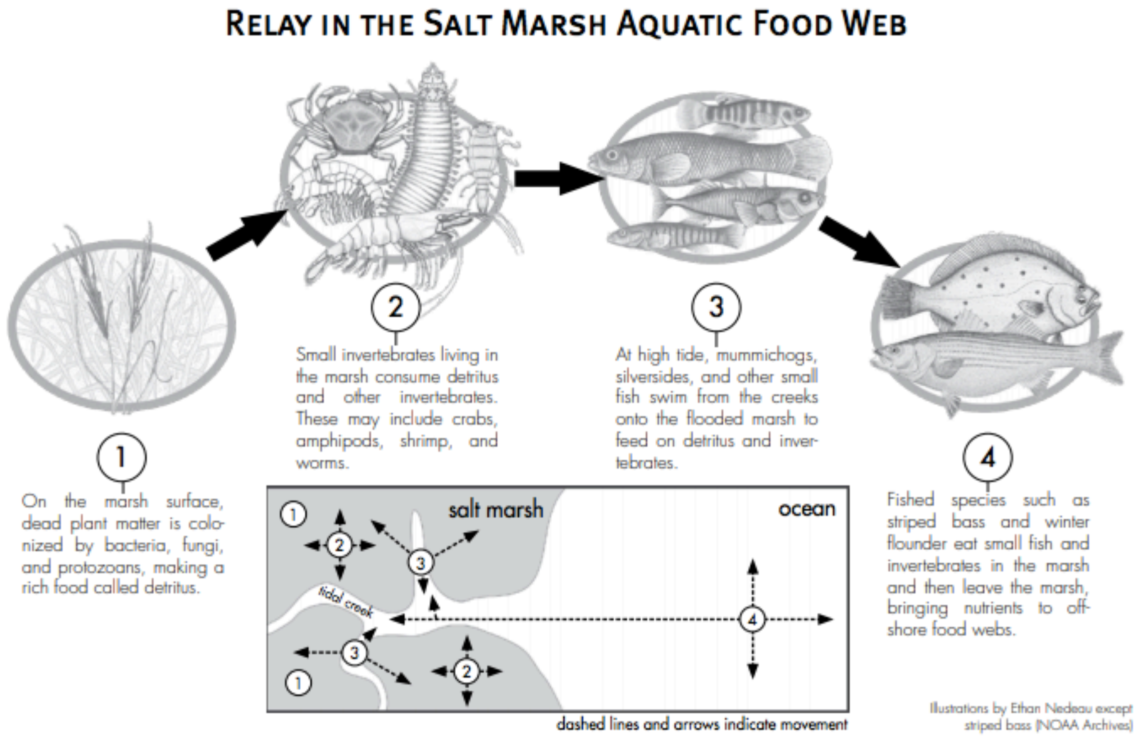

Figure 2. Diagram from Taylor (2005) showing a simplified trophic structure and movement patterns of species commonly found in a New England, U.S.A. salt marsh.

3.2 Fish usage of salt marsh sub-habitats

Fish are not distributed uniformly throughout salt marshes (Whitfield, 2016). Fish assemblages throughout these ecosystems vary with seasons, as transient species make up a substantial portion of salt marsh communities (Jin et al., 2007). Salt marsh ecosystems are comprised of an array of sub-habitats that support the diversity of fish species that utilize these ecosystems. The salt marsh platform, edge, channels and creeks, pannes, and peat (Fig. 3) may be used in various ways by different species (Jin et al., 2007; Able et al., 2018). The majority of the salt marsh platform is only accessible to fish at high tide, with the spring high tides of every month exposing all of it for fish use. While different studies report contradictory results, stranding may present a considerable risk for fish moving onto the marsh platform with the rising tide especially for larger individuals (Able et al., 2018). The deterrence of larger fish equates to a lower risk of predation to juveniles, smaller species and individuals, (Sheaves et al., 2014). This combined with the dense vegetation of the marsh platform may make it more attractive to smaller species. However, the willingness of larger fish to utilize the marsh platform demonstrates how valuable it is for foraging (McIvor & Odum, 1988).

The edge of the salt marsh that borders the main estuary or subtidal environment, offers more access to fish than the marsh platform. This is especially true in more southern marshes that experience lower tidal amplitudes which limits flooding and accessibility to fish on the marsh platform. As a result, studies have found the highest densities of fish along the edges of these salt marshes (Minello et al., 2003; Kneib, 2003). Fish species with a variety of life history patterns utilize the marsh edge, while the marsh platform tends to be dominated by resident species (Peterson & Turner, 1984). Salt marsh creeks and channels generally do not contain vegetation and therefore are not involved directly in primary production. Their presence does however enhance the value of salt marsh habitat for nekton (Minello et al., 1994). Salt marsh creeks and channels are critical for fish usage as they act as capillary networks with larger channels branching off into smaller creeks facilitating fish access into more areas of the marsh (Friedrichs & Perry, 2001). Salt marsh channels allow larger fish to move freely between salt marsh and adjacent coastal ecosystems when they are inundated with water (Able et al., 2012). Creeks are smaller in size and therefore limit the use of larger fish thus offering some protection for smaller fish and invertebrates (Rountree & Able, 2003). Both creeks and channels are important for the tidal export of organic matter and other nutrients, especially from the higher marsh zones, to nearshore ecosystems (Kneib, 2000).

Salt marsh pannes are permanent water bodies that are flooded during the spring high tides (Able et al. 2012). Pannes can have low oxygen levels and present risks relating to fluxes in temperature and salinity, especially those that are shallower and smaller in size (Valiela et al., 1977). Fish that utilize pannes tend to be resident species that possess unique physiological and behavioural adaptations that allow them to tolerate these harsher conditions (Smith & Able, 2003). Mummichogs are a common salt marsh resident species in eastern North American salt marshes that are often found in pannes (Bowron et al., 2013). This species is known to burrow itself in the mud in order to endure periods where evaporation levels are high. To cope with low oxygen situations in salt marsh pannes, some fish employ aquatic surface respiration which occurs when fish ventilate their gills at the air-water interface to improve oxygen uptake (Abdallah et al., 2015). Pannes often contain an abundance of food resources for fish such as algae, invertebrates, and larval fish (Valiela et al., 1977). While they are generally free of larger piscivorous species, pannes may provide fish with critical temporary refuge if they are unable to make it off the marsh platform with the ebbing tide (Able et al., 2012).

Peat in salt marshes results mainly from the decomposition of halophytes and accumulates at a greater rate than decomposition (Able et al., 2018). It is mostly stored as below ground biomass. However, erosional processes cause peat to be dispersed in a number of ways including through calving off the marsh edge or gets broken off during storms with ice rafting sometimes depositing the peat on the marsh surface (Able et al., 2018). In other cases, chunks of peat get deposited sub-tidally and can end up in channels throughout the marsh and are referred to as peat reefs. Peat reefs offer structured habitat for fish, bivalves, and even crustaceans including crabs and juvenile lobsters (Able et al., 1988). Tides can remove and erode peat reefs from salt marsh channels making their lifespan relatively short. A 2 m long peat reef was estimated to have a lifespan between 7.5 and 15 years, which would provide enough time for organisms such as ribbed mussels (*Geukensia* demissa) and grass shrimp (*Palaemonetes vulgaris)* to colonize it (Able et al., 2018). Barshaw et al. (1994) evaluated predation on settling post larval lobsters on three different substrates including peat reefs. The post larval lobsters settled quickly into the peat and cobble substrates. This quick settlement aids in predator avoidance while also suggesting that they preferred these two substrates over sandy substrates (Barshaw et al., 1994; Able et al., 1988).

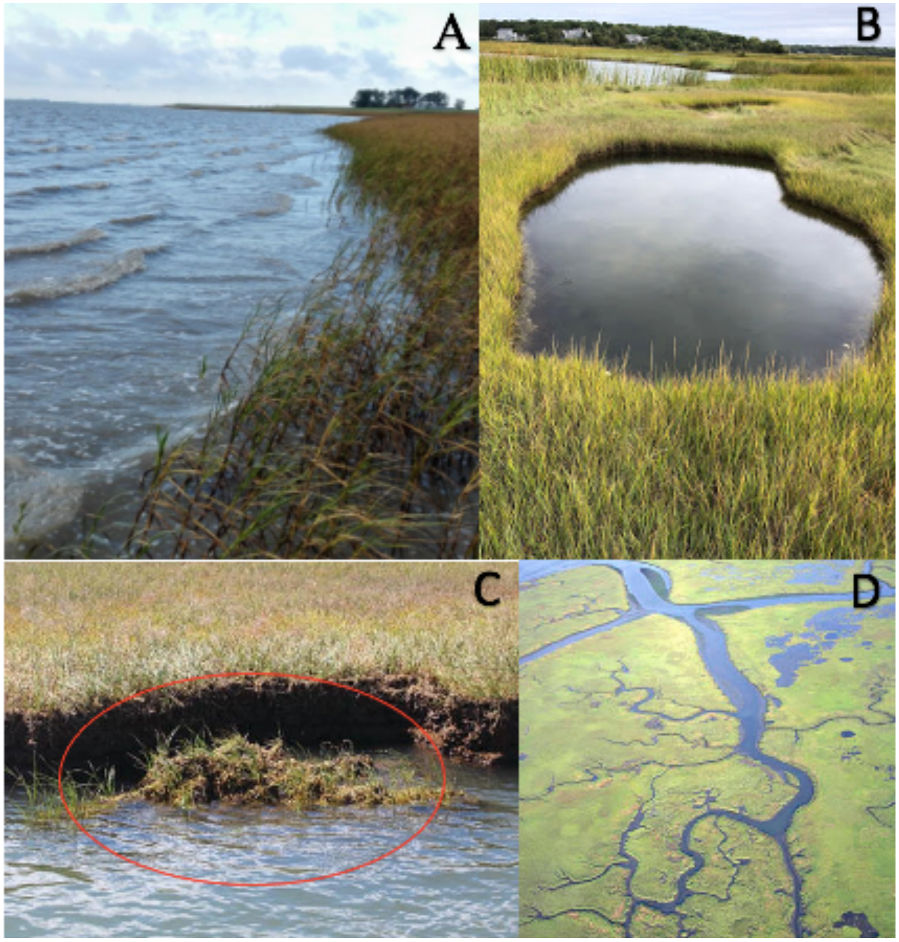

Figure 3. Photos showing the different sub-habitats within a salt marsh ecosystem, all of which are utilized by fish. Image A shows the salt marsh seaward edge (Zhu, 2019). Image B shows a salt marsh panne which is a permanent water body on the marsh surface (Cadrain, 2018). Image C shows a chunk of peat (red circle) that has been broken off from the main salt marsh, known as a "peat reef" (Able et al., 2018). Image D shows salt marsh channels branching off into smaller salt marsh creeks (Wechsler, 2017).

3.3 Nursery function of salt marshes

Coastal ecosystems, including salt marshes, are known to provide nursery habitat to an extensive list of fish and invertebrate species (Minello et al., 2003). The concept of a fish nursery has not been well defined and nursery value varies between different ecosystems and sub-habitats (Beck et al., 2003). The presence of juvenile fish in a habitat was once enough to designate that habitat as a fish nursery, however many researchers have argued that this is not an adequate indicator (Whitfield, 2016). Early work described the entire estuarine environment as a nursery however, more recent research has been directed towards the specific areas that provide a nursery function (Sheaves et al., 2015; James et al., 2019). Beck et al. (2001) described an area to constitute as a nursery if it contributed on average more individuals per unit area, that recruit to adult populations of a particular species than other habitats in which juveniles also occur. Salt marshes have been considered to be fish nurseries for their provisioning of food, refuge, favourable physical and chemical conditions, as well as advantageous hydrology (Boesch & Turner, 1984; Beck et al., 2001; Nagelkerken et al., 2013). Studies have also supported the notion that juvenile fish experience higher rates of growth and survival in salt marshes (Levy & Northcote, 1982; Mackenzie & Dionne, 2008). Estuarine environments including salt marshes generally experience warmer temperatures than offshore or deeper waters (Deegan et al., 2000). Temperature is a significant characteristic that influences the growth rates of organisms, and it is well understood that higher temperatures equate to higher levels of growth as long as that temperature does not exceed certain thresholds (Houde & Zastrow, 1993). Deegan (1990) also found Gulf menhaden (*Brevoortia patronus*) in warmer salt marsh creeks tended to have higher growth rates compared to those in open bays. These findings not only support the nursery value of salt marshes, but also highlight the inherent growth advantage of estuarine and coastal waters relative to cooler offshore waters (Deegan et al., 2000).

Another aspect of salt marsh ecosystems that contributes to enhanced rates of growth and survival for juvenile fish species is the availability of food resources and refugia (Boesch & Turner, 1984). Salt marshes are shallow and structurally complex, limiting access to larger predators while offering ample hiding places (Halpin, 2000). The differing sub-habitats within a salt marsh provide fish and invertebrates more opportunities to evade predators while also having access to an abundance of food resources. Mackenzie and Dionne (2008) found that male mummichogs with access to the entire marsh accumulated more biomass and higher growth rates than those that were restricted to pannes. Mummichogs with total marsh access exhibited 1.6 times greater production rates than mummichogs with access only to pools (Mackenzie & Dionne, 2008). This demonstrates that while the different sub-habitats may be preferentially selected by different species, having access to more areas of salt marsh ecosystems can provide a growth advantage.

Larvae and juvenile fish and invertebrates are a critical component in the energy transfer between salt marshes and nearshore fisheries (Fig. 4) as well as within the salt marsh food web (Kneib, 1997; Pittman et al., 2003). They grow and develop utilizing salt marsh resources before moving to nearshore environments where they contribute their accumulated biomass and numbers to nearshore fishery stocks (Boesch & Turner, 1984). The flooding tide facilitates movements into the salt marsh while the ebbing tide draws organisms including fish out into the subtidal environment (Whitfield, 2016). Salt marsh creeks and channels act as ecosystem corridors further helping to connect populations at various life stages (Able et al., 2012; Nagelkerken et al., 2013). Most individuals and a significant portion of their biomass do not survive to emigrate offshore (Sheaves et al., 2015). They may die of natural causes and undergo decomposition or are consumed by lower-level consumers eventually being recycled back through the salt marsh food web. Juvenile and larval fish and invertebrates may also be predated upon directly transferring energy and nutrients to their predators, which may be eventually translocated to other ecosystems (Pittman et al., 2003). This "sacrificial" component contributes to the energy and nutrient transfer within salt marsh ecosystems (Sheaves e al., 2015).

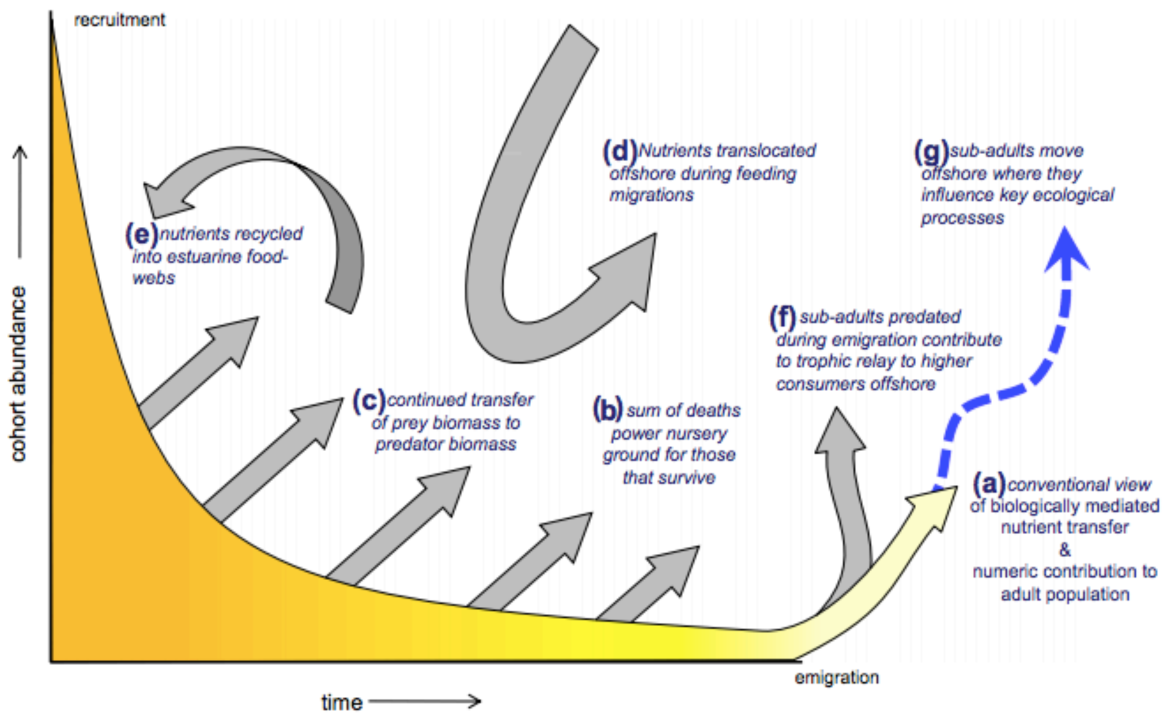

Figure 4. Diagram from Sheaves et al., (2015) listing the various ways in which the nursery function of salt marshes goes well beyond adding to adult stock numbers in supporting recipient ecosystems.

3.4 Fish and other nekton as biological vectors

Fish can act as biological vectors moving energy and nutrients between coastal wetlands such as salt marshes and other nearshore environments (Weinstein et al., 2011). The strict definition of a “salt marsh dependent species” has yet to be clearly defined determined, but fish are loosely categorized as being resident, transient, or migratory species. Resident species that inhabit salt marshes throughout their entire life history are an important part of the salt marsh food web feeding mostly on invertebrates and algae. They tend to be smaller in size but high in abundance and are included in the diets of many transient fish species (Kenneth et al., 2012). Transient fish are those that inhabit salt marshes for only part of their ontogeny. Some transient species may utilize salt marshes as hunting grounds or only during the periods of spring high tides or large influxes of freshwater (Weinstein et al., 2005; Rogers et al., 1984). Migratory fish that utilize salt marshes consist of catadromous and anadromous species. Catadromous fish species spawn in marine environments and migrate into freshwater at some point throughout their life history. Anadromous species undergo the reverse and spawn in freshwaters before moving into marine waters (Hering et al., 2010). Both catadromous and anadromous species access food resources and may utilize salt marsh habitat during some point of their migration (Hering et al., 2010) Many fish that hold commercial value are transient or migratory species that utilize salt marshes or other coastal wetlands during a portion of their lives (James et al., 2019).

While transient and migratory species may be the more direct linkage between salt marsh ecosystems and nearshore fisheries, resident fish species are also a significant component in estuarine food webs (Kenneth et al., 2012; Nemerson & Able, 2003). Resident species tend to be the first onto the marsh platform as it floods and the last to leave the marsh platform, thereby optimizing the time period that this part of the salt marsh is accessible. This allows them to directly exploit marsh resources while they are at a lower risk of being predated on by transient species that do not spend as much time on the marsh platform during each flood (Kneib, 2003). Mummichogs are the most prominent resident fish species in salt marshes along the east coast of North America (Kenneth et al., 2012). They are omnivorous and prey on diatoms, a range of invertebrates, fish eggs, and larva. Mummichogs are an important species in the movement of organic matter throughout salt marshes as they are found in abundance throughout pannes, intertidal creeks, as well as basin and subtidal creeks (Kenneth et al., 2012). The high abundance of both resident mummichogs and transient Atlantic silversides in salt marshes attract predators, many of which will move to adjacent ecosystems after feeding (Deegan et al., 2000; Able et al., 2007). While mummichogs overwinter in salt marshes, Atlantic silversides migrate offshore during the fall months to the inner continental shelf where they are particularly vulnerable to predators (Raposa, 2003; Fay et al., 1983). Atlantic silversides translocate energy and nutrients in the form of their biomass and are preyed on by piscivorous fish (Fay et al., 1983).

3.4.1 Evidence of feeding ecology

The high abundance and density of food resources available in salt marsh ecosystems is one of the main factors driving transient fish species to utilize salt marshes. Estuaries and salt marshes can provide more diverse diets to fish than neighbouring coastal environments (Able et al., 2018). It is important to note that utilization of salt marsh resources comes at the additional risk of stranding since the tides largely dictate when the marsh and marsh platform is accessible to fish. Various studies have demonstrated that the value of food resources out-weighs the risk of stranding as many different fish species feed in salt marshes (Able et al., 2018). Some species of fish are even able to make intensive use of the food resources in salt marshes along the Californian coast that are only accessible to fish for 16% of the tides (West & Zedler, 2000). Delaware Bay, U.S.A. salt marshes attract a variety of transient fish species that take advantage of the high levels of food resources. Predatory species including bluefish (*Pomatomus saltatrix),* weakfish *(Cynoscion regalis),* and white perch *(Morone americana)* have been found to prey on a number of different salt marsh invertebrates and resident fish species (Able et al., 2018). Striped bass move further into estuaries and feed in salt marshes assimilating nutrients and energy from the marsh ecosystem into the nearshore waters when they move back out of the estuary (Sheaves 2009). Salt marsh creeks are particularly important as they can make more areas of the marsh accessible to fish and some species preferentially recruit to marsh creeks to feed (Nemerson & Able, 2004; Jin et al., 2007). Nemerson and Able (2004) found that salt marsh creeks with high abundances of food resources were favoured over other sub-habitats and sites where more fish were found also generally had higher levels of stomach fullness. Juvenile sea bass (*Dicentrarchus* l*abrax*) rely on both the primary and secondary production provided by salt marsh ecosystems (Lafaille et al., 2001). Stomach analyses revealed that they feed mostly on the amphipod, *Orchestia gammarellus*, in salt marshes throughout Mont Saint Michel Bay, France (Lafaille et al., 2001). Fish moving out of salt marshes and into adjacent ecosystems following feeding are then translocating the energy and nutrients that they gained through their food in the form of their biomass.

3.4.2 Fish as vectors moving energy and nutrients between salt marshes and nearshore environments

The salt marshes along the coasts of Mont Saint-Michel Bay (MSMB) in northwest France have received attention from various researchers to get an improved understanding regarding the flows of organic matter to adjacent coastal ecosystems. Nekton are generally described as mobile organisms that are able to move independently against currents (Rountree & Able, 2007) Nekton presents a means of nutrient and energy flow, as crustaceans and fish move onto areas of the marsh to feed when it is flooded and then may move into adjacent ecosystems at low tide (Lafaille et al., 2001). Fish, in particular, have been shown to be important biological exporters of organic matter from MSMB salt marshes and may be important in the energy budgets of surrounding coastal environments (Lefeuvre et al., 1999). The biotic export of organic matter from these marshes to coastal waters is assumed to occur in three different ways: through gross output of ingested organic matter, net output that is excreted (non-assimilated organic matter), and the output of assimilated organic matter that is transformed into biomass and metabolism (Lefeuvre et al., 1999). Lafaille et al. (1998) determined that fish communities play an important role in the export of organic matter from these salt marshes despite only having access to them for 5-40% of tides. This provides them with 1-2 hours of foraging time depending on tidal amplitude (Lefeuvre et al., 1999). From 4000 hectares of salt marshes in MSMB, mullets (*Mugilidae*), gobies (*Gobiidae*) and sea bass (*Dicentrarchus labrax*) were found to transfer approximately 50 tonnes of dry mass particulate organic matter per year to other coastal environments (Lafaille et al., 1998). Mullets were the most abundant group in these fish communities accounting for 81% of the biomass. They were found to be responsible for exporting 8kg and 12kg of dry weight organic matter per hectare of salt marsh in 1996 and 1997 respectively (Lafaille et al., 1998).

Gulf menhaden are a common species in estuarine regions along the southern coast of eastern North America with some populations being known to migrate as far as south as the Gulf of Mexico (Robinson et al., 2015). To determine whether gulf menhaden are important vectors of energy and nutrients to coastal and marine systems Deegan (1993) examined changes in biomass accumulation relative to the migration pattern of this species. The study found that on average gulf menhaden from a Louisiana estuary were transporting 38g of biomass, 930kJ of energy, 22.5g of carbon, 3.1g of nitrogen, and 0.9g of phosphorus per meter squared to the nearshore of the Gulf of Mexico (Deegan, 1993). The export of biomass and nutrients by gulf menhaden was equivalent to roughly 5-10% of the total primary production of the estuarine areas from which they migrated. Estimates of dissolved and particulate nitrogen and phosphorus transport through tidal export were about the same as what was estimated to be transported by gulf menhaden (Deegan, 1993). Through the use of stable isotope analyses, Litvin and Weinstein (2004) found that primary production from salt marshes support the secondary production of juvenile weakfish (*Cynoscion regalis*) in Delaware Bay, U.S.A. The results of this study indicate that organic matter derived from salt marshes make up a significant proportion of weakfish biomass. This makes them important biological vectors of salt marsh macrophyte production in the estuarine food webs they are part of since they emigrate further down the estuary into coastal waters in the fall (Litvin & Weinstein, 2004). Stable isotope analyses have linked bay anchovies (*Anchoa mitchilli*) and white perch (*Morone americana*) to salt marshes since their prey (invertebrates) feed on salt marsh marcrophytes and algae (Weinstein et al., 2011). Individuals that were captured within the salt marsh or in the coastal waters up to several kilometers away from the coast were found to have carbon, nitrogen, and sulfur isotopes that could be traced back to macrophytes and benthic micro-algae likely originating from nearby salt marsh ecosystems (Weinstein et al., 2011).

Salt marshes found along the coasts of South Asia and Australia grow much higher in the intertidal zone and experience tidal flooding less frequently than North American marshes (Connolly, 1999; Janes et al., 2019). Consequently, the salt marsh plants in these regions tend to be less productive than their North American counterparts (Janes et al., 2019). Even so, Australian salt marshes have been shown to have a substantial influence, especially in areas that lack seagrass, on some crustacean and finfish species that make up large fisheries. Jinks et al. (2020) sampled banana shrimp (*Fenneropenaeus merguiensis),* mud crab *(Scylla serrata),* javelin grunt (*Pomadasys kaakan),* king threadfin (*Polydactylus macrochir),* trumpeter whiting (*Silago maculate),* and yellowfin bream (*Acanthopagrus australis)* in subtropical Australian estuaries to estimate trophic contributions from key primary producers. The majority of fisheries catches in coastal waters comes from unvegetated soft-sediment bottoms, indicating that the support of primary production is likely coming from coastal wetlands (Jinks et al., 2020). Jinks et al. (2020) examined the source of organic matter coming from nearby coastal wetlands in the diets of various inshore finfish and crustacean species with commercial value. The study found that macrophytes were contributing approximately 75% to secondary fish production while the remaining 25% was coming from benthic algae. The salt marsh grass (*Sporobolus virginicus)* contributed between 18-88% of the organic matter to inshore fisheries (Jinks et al., 2020). Another study conducted by Raoult et al. (2018) examined the contribution of primary productivity to commercially important fish and crustacean species in two Australian estuaries. Stable isotope analyses revealed that the salt marsh grass *Sporobolus virginicus* was a significant nutritional source and supported the largest mean proportion (47-63%) of the diet of all consumers that were evaluated other than yellowfin bream (Raoult et al., 2018). Taken together, these studies from Europe, North America and Asia support the notion that transient fish species act as biological vectors that export organic matter out of salt marsh and estuarine environments to nearshore waters.

3.4.3 Migrations

Some species of fish undergo intense seasonal or ontogenetic migrations that can span hundreds, sometimes even thousands of kilometers (Maier & Simenstad, 2009). These journeys are energetically taxing and usually involve the movement through multiple ecosystems before the end point is reached. As fish pass through different environments, they utilize the resources that are readily available while also providing energy and nutrients in the form of their biomass and excretions (Maier & Simenstead, 2009). Chinook salmon (*Oncorhynchus tshawytscha*) are an anadromous species that spawns in freshwater rivers while adult populations inhabit marine waters. Tagging technology has indicated that juvenile Chinook salmon spend time in salt marshes during their migrations through estuaries (Hering et al., 2010). Hering et al. (2010) found that some juveniles occupied salt marshes on successive tidal cycles while others intermittently entered salt marsh channels over periods of up to 109 days. American eels (*Anguilla rostrata*) are a catadromous species that undergoes a remarkable migration from freshwater systems located along the eastern coast of North America to the offshore Sargasso Sea. Juvenile eels inhabit freshwater habitats and estuaries before reaching maturity and migrating further into marine waters (Giles et al., 2016). While the majority of our knowledge in terms of the foraging ecology for this species comes from freshwater systems, it has been suggested that estuaries (especially in more northern locations) are preferential (Eberhardt et al., 2015). Despite being migratory, eels have been considered to be salt marsh residents since their biomass often makes up a significant component of catches in salt marshes along the northeast coast of North America. Gut and muscle tissue analyses for carbon and nitrogen stable isotopes have revealed that American eels function as top predators in New England, U.S.A. salt marsh ecosystems (Eberhardt et al., 2015). They feed primarily on fish, crustaceans, and polychaetes found throughout these salt marshes. Catadromous species are known to be an important source of energy and nutrients for freshwater systems. As semelparous organisms, species that undergo only one reproductive cycle they will enter the detrital food web of the Sargasso Sea upon completing their spawning migration (Giles et al., 2016). Eel migrations represent a large-scale movement of energy and nutrients to open water environments, however more research is required to determine what proportion is coming from salt marsh ecosystems (Eberhardt et al., 2015).

3.5 Physical vectors linking salt marshes and nearshore fisheries

3.5.1 Energy and nutrient transfer mediated by abiotic vectors

While there is no doubt that fish and other nekton play an essential role in the movement of energy and nutrients from salt marshes to coastal environments, physical vectors offer an alternate mode of transport (Childers et al., 2000). Salt marsh macrophytes generate high amounts of biomass throughout their growing season, aligning with the high levels of productivity for which these ecosystems are known. Following senescence, salt marsh plants start to decay and are broken down into organic matter (Valiela et al., 1978). The organic matter that is not incorporated back into the salt marsh food web through decomposition or consumption is exported by tides and currents to other nearshore environments. This concept is known as outwelling and was first described by Odum (1968). Outwelling can also be related to the concept of source-sink energetics where the excess production from one ecosystem (the source) gets exported and supports a less productive ecosystem (the sink) (Odum, 2000). Salt marshes are considered to be a source of dissolved and particulate organic matter for adjacent nearshore and estuarine ecosystems (Wolaver & Spurrier, 1988). In this way salt marshes have been found to subsidize nearshore ecosystems and their production can benefit fish that are not occupying them (Litvin & Weinstein, 2004).

Earlier research demonstrated that this concept is largely system dependent. Factors such as the level of estuarine production, tidal amplitude, and the geomorphology of the estuary can impact the amount of outwelling and nutrient fluxes that occur (Valiela et al., 1978; Nixon, 1980). Nixon (1980) found no evidence of outwelling in New England salt marshes which was likely attributed to the fact that they are less extensive and have lower tidal amplitudes. Their connection with the ocean is somewhat restricted and as a result, New England salt marshes were found to typically be importing carbon (Nixon, 1980). In contrast, salt marshes in Louisiana and along the North Atlantic Bight are known to be heavy exporters of organic material. These salt marshes are highly productive and much more extensive while also experiencing higher tidal amplitudes than those in New England (Odum, 2000). Large salt marshes have been able to form in the upper portion of the Bay of Fundy in part due to the extremely high tidal amplitudes, gently sloping shores, and high sediment supply. Despite having a shortened growing season in comparison to more southerly marshes, these salt marshes haven been found to accumulate carbon at rates as high as 184 g C m^{-2} yr^{-1} (Connor et al., 2001). While other salt marshes in North America have been found to export as much as 45% of their organic matter (Teal, 1962), the unique tidal regime of the Bay of Fundy contributes to nearly 100% of organic matter from salt marshes being exported (Gordon & Cranford, 1994). Salt marshes have also been found to experience intermittent levels of outwelling with weather events such as storm tides and rainstorms leading to more outwelling of nutrients and OM (Odum, 2000). The nutrient uptake by consumers in coastal waters is largely supported by the outwelling of detrital particulate organic matter coming from adjacent ecosystems (Duarte et al. 2017).

In order to get a better understanding of how organic matter originating from salt marshes is interacting with nearshore environments, researchers have attempted to quantify the amount of organic matter that these ecosystems are producing. Salt marshes along the Atlantic and Gulf coasts of the U.S.A. have been found to produce up to 8kg/m^2 of plant material in the form of macrophytes, benthic algae, and phytoplankton (Kneib, 2003). While more northern marshes generally have a higher diversity of plant and animal species, they generally produce less organic matter (Roberts & Robertson, 1986). Creeks and channels throughout these salt marshes move organic matter and nutrients into neighbouring bays. Salt marsh detritus gets deposited in seagrass beds and forms an important part of the food web for salmonid species inhabiting seagrass beds (Levy & Northcote, 1982). High spring tides result in the movement and flux of organic matter to be bidirectional and balanced (Troccaz, 1996). Above ground production of smooth cordgrass (*Sporobolus alterniflorus)* demonstrates a reduction from south to north. Georgia salt marshes produce 2883g/m^2 and salt marshes in the Bay of Fundy producing

900g/m^2 (dry weight) in smooth cordgrass each year (Roberts & Robertson, 1986). Huiskes (1988) examined 3300 hectares of Westerschelde salt marshes in the Netherlands and estimated that they are contributing 8% of the organic matter and as much as 25% of the nutrients incorporated into adjacent estuarine environments. The amount of below ground salt marsh biomass that gets exported or the way in which it contributes with nearshore environments is not well understood. However, Troccaz & Giraud (1996) determined that between 0.7-5.8g/m^{2}y of total nitrogen was being exported by the tides from salt marshes in Mont Saint Michel Bay, France. This study also estimated that these same salt marshes exported between 83.3-114.2g/m^{2}y of detritic carbon (Troccaz & Giraud, 1996).

Other studies have examined the various zones of salt marshes and their relative contributions of organic matter to nearshore waters. Bouchard and Lefeuvre (2000) found that the organic matter produced in the high marsh was mostly kept within the marsh with very little being exported to coastal waters. This study found that although the low marsh was less productive than the other two marsh zones, almost 90% of the organic matter was either exported by the tides or redistributed within the marsh. The fate of the remaining 10% was decomposition within the low marsh zone (Bouchard & Lefeuvre, 2000). In some salt marshes, the middle marsh zone has been found to produce large amounts of plant biomass that are rapidly available to food webs in coastal waters (Bouchard & Lefeuvre, 2000). A common plant in salt marshes in the Wadden Sea is *Puccinellia maritima*, which is essentially the equivalent species to the highly productive *S. alterniflorus* of eastern North American salt marshes. Ketner (1972) estimated that middle marsh vegetation, mostly consisting of *Puccinellia maritima* produced 463g/m^2 in live biomass and 277g/m^2 of dead biomass. A study conducted by Wolff et al. (1980) examined the same vegetation in Oosterschelde, Netherlands salt marshes and estimated live biomass production to be around 576g/m^2 and dead biomass to be approximately 384g.m^2. While the low marsh zone is the most exposed to tidal inundation, the middle marsh zone gets flooded at least at every high tide. More tidal influence translates into a higher potential for more organic matter to be moved from salt marshes to coastal waters (Bouchard & Lefeuvre, 2000). Salt marshes are constantly experiencing tidal forces; however, spring and neap tides provide different opportunities for the export of energy and nutrients. Duarte et al. (2017) investigated the difference in the movement of plant detritus during spring and neap tides in salt marshes throughout the Tagus estuary on the western Portuguese coast. This study found that the spring tides of every month significantly increased the export of plant detritus to the main channel and the ocean, while neap tides resulted in most of the plant detritus being retained within the inner estuary (Duarte et al., 2017). It is important to consider these differences in tidal influences and ranges throughout the world.

3.5.2 Abiotic and biotic vectors functioning together in energy/nutrient transfer

Some organisms depend on the tides as a critical factor in their life history, particularly those that undergo a zooplankton stage (Mazumder et al., 2006). Zooplankton are small organisms that are unable to swim or navigate themselves against the tides and therefore will end up wherever the tide takes them. Many different invertebrates go through a zooplankton stage and these organisms act as an important trophic linkage since they consume phytoplankton and are heavily preyed on especially by juvenile fish (Kneib, 1997). In Australian salt marshes, spring tides initiate a synchronised spawning event by burrowing crabs every month (Mazumder et al., 2006). The newly hatched larvae are transported by the tides where they undergo further development in the main estuary. Mazumder et al. (2006) found significantly higher levels of crab larvae in the outgoing tide compared to the incoming tide. Stomach analyses revealed that crab larvae were being consumed by fish, including those with commercial value, within the salt marsh as well as further out in the estuary (Platell & Freewater, 2009; Mazumder et al., 2006). This spawning event presents a unique and highly efficient transfer of energy from salt marshes to nearby estuarine environments in the form of crab larvae mediated by the tides (Mazumder et al., 2006). Nekton face limited accessibility to Australian salt marshes due to the fact that they are located higher up in the intertidal zone and are flooded less frequently than salt marshes in other regions (Janes et al., 2019). Australian salt marshes are however able to export large amounts of organic matter through physical vectors as shown by their significant nutritional input to the prawn fishery (Janes et al., 2019). While being part of a commercial fishery, prawns inhabit coastal waters and are also a food source for a variety of fish species acting as an important ecological link between salt marshes and other coastal ecosystems (Cattrijsse et al., 1997). Similarly to Australian salt marshes, those in Atlantic Canada are located higher up in the intertidal zone, however, depending on their location they experience vastly different tidal regimes (Bleakney, 2004). The substantial tidal range within the Bay of Fundy results in high flushing of the salt marshes, disturbing the sediment and drawing out additional food resources that can be consumed by fish (Imrie & Daborn, 1981). Stomach analyses revealed that salt marsh arthropods are an important component in the diets of various juvenile fish species in the Minas Basin, Nova Scotia (Imrie & Daborn, 1981). When biotic and abiotic vectors function synergistically, evidence suggests that the ecological linkages between salt marshes and nearshore environments are strengthened.

3.5.3 Biotic vs abiotic vectors

While it is clear that energy and nutrients are transported between salt marshes and other nearshore environments through the movement of nekton and tidal forces, there are apparent differences between these two modes of transport. One difference that is important to note is the quality of the energy and nutrients that are transferred by biotic vectors in comparison to those moved by abiotic vectors (Lefeuvre et al., 1999; Deegan, 1993). The organic matter transported through abiotic vectors is in dissolved, particulate, and detrital forms. It gets incorporated into nearshore food webs differently and much slower than the organic matter that is moved by biotic vectors. Even though abiotic vectors are constantly transporting organic matter between salt marshes and nearshore environments at no energetic cost, the quality is lower than that being moved by fish and other biotic vectors (Deegan, 1993). Fewer species are able to directly utilize the organic matter being moved by abiotic vectors and it gets incorporated into nearshore food webs differently (Litvin & Weinstein, 2003). Decomposers and saprophagous species use detritic organic matter that has a particularly low energetic value and is rapidly deposited (Nixon, 1980). Filter feeders utilize particulate organic matter while primary producers integrate dissolved organic matter into nearshore food webs. Fish and other biotic vectors that obtain energy and nutrients in salt marshes accelerate the turnover of organic matter through digestion and directly return it to nearshore environments where it can be integrated into food webs (Lefeuvre et al., 1999).

3.5.4 Conclusions

Biotic and abiotic vectors have been found to facilitate the movement of energy and nutrients between coastal and nearshore ecosystems (Deegan, 1993; Lafaille et al., 1998; Lefeuvre et al., 1999). Many species of fish and other nekton are highly mobile and may utilize various coastal and nearshore habitats throughout their life history (Litvin & Weinstein, 2003).

Their movement between various ecosystems transfers energy and nutrients mostly in the form of their biomass (Pittman et al., 2003). The tides largely dictate the accessibility of intertidal ecosystems for fish while also mediating the movement of particulate organic matter and planktonic between intertidal and nearshore environments (Odum, 2000; Mazumder, 2006). Flood tides carry and deposit organisms and particulate organic matter into intertidal ecosystems while the ebbing tide draws organisms and nutrients in the form of detrital matter out into nearshore waters (Odum, 2000; Mazumder, 2006). In these ways abiotic and biotic vectors support bidirectional ecological linkages between intertidal and nearshore environments.

3.6 Linking salt marshes to fisheries economics

The ecological benefits of salt marshes for a variety of different fish and invertebrate species have been studied for decades while attempts to understand the connection between salt marshes and other coastal wetlands to fishery values have been more recent. Attempts to quantify the economic value these ecosystems provide to fisheries have mainly been done as part of promoting the conservation and restoration of salt marshes and coastal wetlands (Taylor et al., 2018). It is difficult to quantify because many fish species are highly mobile and utilize salt marshes in many different ways. Global estimates have been made in terms of what proportion of fisheries landings can be attributed to coastal wetlands (Barbier et al., 2011). Approximately 46% of the 11,300 extant fish species are considered to be coastal, utilizing estuaries, lagoons, deltas, and not moving beyond the outer continental shelf (Meynecke et al., 2008). Meynecke et al. (2008) estimates that these coastal fish species make up more than 90% of the global fish catch. A model presented by Bell (1997) estimated that salt marshes along the coasts of Florida U.S.A. were contributing between USD$5,592-USD$36,902 hectare per year (in 2015 dollars) in recreational fishery value. This could be broken down to USD$2,620 and USD$397 per hectare of salt marsh on the east and west coasts of Florida, U.S.A. respectively (Barbier et al., 2011). Blue crab and some species of penaeid shrimp are salt marsh residents while also being important fisheries species in North America. Zimmerman et al. (2000) estimated that salt marshes may account for 66% of the shrimp and 25% of the blue crab production in the Gulf of Mexico.

A more recent study estimated that 95% of the world's commercially important fish species are supported by coastal ecosystems, largely for their role as nurseries (Janes et al., 2020). A paper by de Groot et al. (2012) proposed that the fish nursery function of coastal wetlands could be valued at $194 (based on the 2007 international dollar value) per hectare of coastal wetlands per year. Janes et al. (2020) looked to quantify fisheries enhancements from different coastal vegetated habitats in Australia through a systematic literature review. Larger and longer-lived fish that are commonly targeted by fisheries accounted for the highest biomass and economic value (Meynecke et al., 2008). Even though small non-commercial fish species were more abundant in coastal ecosystems, they provide an important dietary component and ecological link for these larger fish (Janes et al., 2020). In comparison to unvegetated seabed, tidal marshes were found to provide 1700 more fish, which is equivalent to 64kg of fish per hectare per year (Janes et al., 2020). Other estimations of the fishery value of coastal wetlands have been based on trophic energy flows through the use of stable isotope analyses. Janes et al. (2019) focused on 96 commercially important species in the waters of Australian states and found that 49,000 tonnes of commercial fish catch (total annual landings for Australian fisheries are 14 million tonnes) were supported by coastal ecosystems including tidal marshes, mangroves, and seagrass beds. This study also estimated that salt marsh ecosystems were contributing AUD$31.5 million per year to Australia's fisheries (Janes et al., 2019).

Taylor et al. (2018) used stable isotope analyses to define habitat-fisheries linkages in the context of harvest in two Australian estuaries. Salt marshes were found to have the greatest value-per-unit-area in comparison to mangroves and seagrass beds. Salt marshes had an average estimated total economic output from fisheries harvest of AUD$25,741 and AUD$2,579 per hectare per year in the Clarence River and Hunter River estuaries respectively (Taylor et al., 2018). In terms of gross value of production (GVP), these values were equivalent to AUD$1,305,002 and AUD$222,449 in the Clarence River and Hunter River estuaries respectively (Taylor et al., 2018). These values accounted for a small proportion of the total GVP of AUD$1.79 billion that is generated by Australian wild capture fisheries on an annual basis (Australian Government Department of Agriculture, Water and the Environment, 2020). One of the challenges that arises when attempting to quantify the value of coastal wetlands for fisheries is that species of fish depend on these ecosystems differently throughout their life histories (Janes et al., 2019; Sheaves et al., 2020). McCormick et al. (2019) took a different approach to address this issue. They developed a residency index to quantify the economic value of salt marsh habitat for fish species with commercial value. The residency index incorporates the life history along with the estimated time spent in the salt marsh during juvenile and adult stages of a specific species to assess the relative importance of salt marshes for a given species throughout its lifecycle (McCormick et al., 2019). McCormick et al. (2019) estimated that between 22.2-24.7% of the ~8800 tonnes of total UK landings in 2015 for European bass (*Dicentrarchus labrax*), European plaice (*Pleuronectus platessa*), and common sole (*Solea solea*) can be attributed to salt marshes.

The residency index described in McCormick et al. (2019) may be a useful tool for quantifying the relative contribution of salt marshes to the lobster fisheries since they utilize these ecosystems as juveniles. Two studies (Able et al., 1988; Barshaw, 1994) identified the importance of peat reefs associated with salt marshes to juvenile lobster survival in eastern U.S.A. salt marshes suggesting additional research on this topic in Atlantic Canadian salt marshes would be prudent. The Canadian lobster fishery is particularly lucrative and accounts for the highest earnings of all fished species in Canada (DFO, 2019). In 2017, lobster landings for Atlantic provinces totalled at CAD$1,461,661,000, which accounted for 38% of the revenue of total landings among all commercial species for all of Canada (DFO, 2019). The American eel is another species with fishery value in Canada that is known to utilize salt marshes (Eberhardt et al., 2015). The American eel commercial fishery accounted for a combined value of CAD$1,355,000 in 2017 (DFO, 2019). This value does not include the revenue generated from the juvenile eel fishery which was estimated to be USD$2.9 million (2012 dollars) in 1997 (Pendleton et al., 2014). American eels are also an important species for an indigenous fishery holding high sociocultural value (Giles et al., 2016). Another important indigenous fishery species in Nova Scotia that utilizes salt marsh ecosystems is the Atlantic tomcod. Tomcod are an important species for Mi'kmaq people since they migrate through estuaries into freshwater streams during the months of December and January. This time of year is significant as most other fish species in this region migrate offshore during winter months (Dadswell et al., 2020). Despite the difficulties associated with placing an economic value on non-commercial indigenous fisheries, the high sociocultural value of indigenous eel and tomcod fisheries needs to be incorporated into any efforts evaluating the conservation value for this species.

4. Pilot study - Evaluating the direction and relative weight of fish movement in two Nova Scotia salt marshes

4.1 Introduction

It is important to note that ecological linkages vary between ecosystems and studies have shown that they are largely system dependent (Duarte et al., 2017). Salt marshes are intertidal ecosystems with strong ecological linkages to nearshore fisheries primarily through their nursery role (Whitfield, 2016). Their high levels of productivity are considered to be sources of organic matter that support adjacent nearshore ecosystems (Odum, 2000). In certain cases, salt marshes have been shown to be sinks for particulate organic forms and some invertebrates (Wolaver & Spurrier, 1988; Mazumder et al., 2009). Variables such as geography, connectivity, and hydrology have been shown to affect the amount of energy and nutrients being imported and exported from salt marsh ecosystems (Lefeuvre et al., 1999). This demonstrates the need for system specific studies in order to gain an understanding of the ecological linkages between a salt marsh and a nearshore environment.

Hydrology is one of the main factors that influences the significance of ecological linkages, especially those mediated by fish between salt marshes and nearshore ecosystems (Litvin & Weinstein, 2003). It is therefore surprising that this area of research is lacking in the Bay of Fundy, a region that experiences the most significant tidal range in the world (Bleakney, 2004). The purpose of this pilot study was to estimate the number of fish and the associated biomass entering salt marsh habitat on the flooding tide and leaving on the ebbing tide in this region. I hypothesized that similar numbers of fish will be moving into and out of the salt marsh, however those leaving on the ebbing tide will account for more biomass as a result of feeding during the flood tide. The results will help to provide insight into the ecological linkages that exist in the Bay of Fundy and the relative importance of salt marshes for fishes in this region.

4.2 Methods and materials

4.2.1 Study sites

The first two sampling days took place within a salt marsh covering approximately $0.13km^2$ less than 1km south of Hantsport Nova Scotia (45.0616590, -64.1715087) on a section of salt marsh at the mouth of the Halfway River. The Halfway River branches off the southwest side of the Minas Basin and experiences the tidal range of the Bay of Fundy. An old railroad runs parallel to the salt marsh on the landward side with several residences and a manufacturing plant that produces pulp fibre drink trays are located adjacent to the site (Fig. 5). The final two sampling days took place at a salt marsh (45.1586674, -64.3720679) on the west side of the Minas Basin approximately 1km west of the town of Kingsport, Nova Scotia. The Kingsport salt marsh covers an area of approximately 1.55km^2. Agriculture is a common land-use in the area and a main road runs parallel to part of the landward side of the salt marsh (Fig. 5). The dominant vegetation at both sites were *Sporobolus alterniflorus* and *Sporobolus pumilus*. Sampling took place throughout the months of August and September during the weeks of high tides. Sampling at the Hantsport site occurred on August 20, 2020 and August 21, 2020 and sampling took place at the Kingsport site on September 4, 2020 and September 21, 2020.

4.2.2 Fyke nets

On each sampling day two fyke nets were set up in different channels approximately three hours before the predicted high tide time. Both nets had 6mm mesh with the large fyke net frame dimensions being 1m by 0.7m and the small fyke net frame measuring 0.5m by 0.5m. Nets were deployed with the frame sitting flush with the bottom of a channel with the wings extending up onto the vegetated high marsh. Nets were set approximately 3 hours before the predicted high tide and were secured using a combination of rebar and wooden stakes being held in place using plastic zip ties. Both nets were set in smaller channels branching off of one of the main channels within the two study sites. Tidal channels were selected based on appropriate width for the fyke net frame to lie flush with the bottom of the channel with the wings extending onto the high marsh platform. The channels also needed to be long enough with numerous branching creeks further up in order to ensure that sampling would encompass a significant portion of the salt marsh.

One net was set with the opening facing downstream (seaward facing) to catch fish coming into the salt marsh with the flooding tide and the other facing upstream (landward facing) to catch fish leaving with the ebbing tide (Fig. 6). With the exception of the August 20, 2020 sampling day, the larger fyke net was set facing seawards while the smaller fyke net was set facing landward. While both nets were set at similar distances from one of the main marsh channels, it was necessary to set one net slightly higher in the marsh in order to have enough time to retrieve the nets before there was no water in the channels and fish were at risk of suffocation. Nets were pulled approximately 3 hours after the predicted high tide time and fish were quickly removed from the nets and placed in holding buckets before they were identified down to the species level and measured.

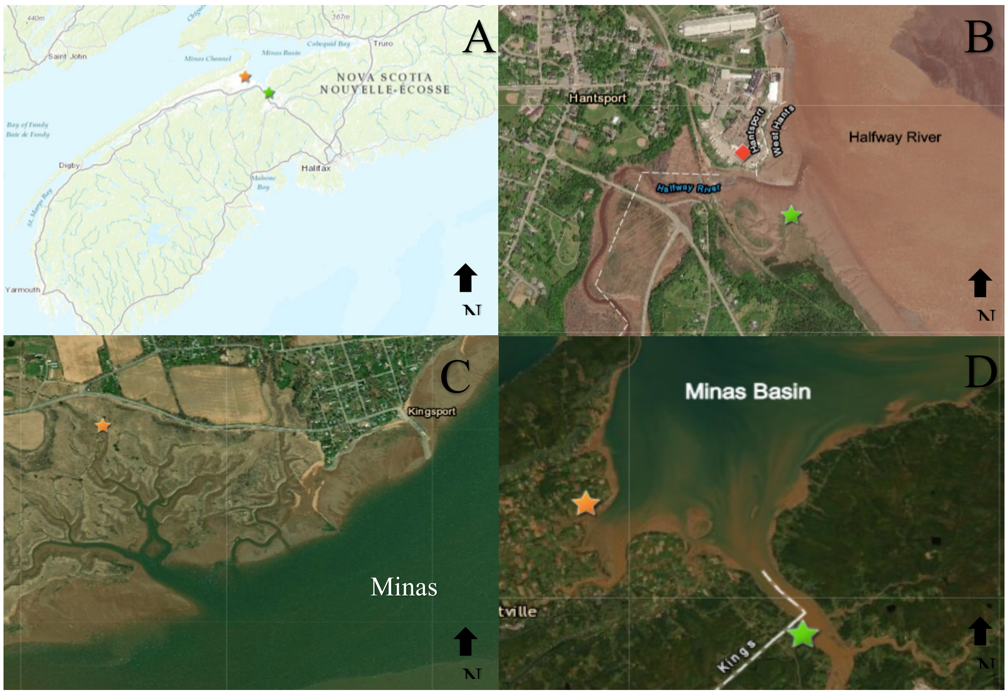

Figure 5. Maps showing the locations of the study site. Image A shows the Kingsport site (orange star) and the Hantsport site (green star) on a map showing the majority of Nova Scotia. Image B shows a closer view of the Hantsport sampling site (green star) with the red diamond showing the manufacturing facility. Image C displays the Kingsport sampling site (orange star) from a closer view. Image D shows both sites relative to one another within the Minas Basin, which is the main water body that the two salt marshes.

Figure 6. Images of one of the fyke nets used to capture fish coming onto or off the salt marsh. Left - Close up view of the small fyke net deployed in a channel at the Kingsport saltmarsh just as flood tide began to come in. Right - View of the small fyke net deployed in the landward facing direction (not easily visible, however, a main salt marsh channel is located behind the fyke net shown by the red arrow). The fyke net wings extend onto the high marsh platform (shown by the yellow arrow) on both sides to allow for a greater area of the salt marsh to be sampled.

4.2.3 Measurements

The wet weight of the first 15-20 fish of each species was taken and recorded. At the Hantsport site, a VWR® P-Series Portable Balance with a precision of 0.001g was used to weigh fish. A Starfrit High Precision Pocket Scale with 0.1g precision was used at the Kingsport site in an attempt to mitigate the limitations of using a highly sensitive scientific scale in an unpredictable field environment. When using both scales an empty container was tared on top of the scale before a fish was weighed to the nearest 0.1g. Following measurements, all fish were placed in a holding bucket before being returned to the nearest tidal channel that retained a sufficient amount of water that would allow fish to move further down river with the ebbing tide.

4.2.4 Statistical analysis

The weight and abundance data from the two fyke nets were statistically analyzed using *Microsoft Excel 2018*. A one-way analysis of variance (ANOVA) was run for each factor to determine if fish weight and numbers differed significantly between the landward facing fyke net and seaward facing fyke net. Significance was determined by a p-value ≤ 0.05.

4.3 Results

Throughout all sampling days a total of 121 fish were caught in both fyke nets representing six different species from five families (Appendix C1). The total fish biomass caught in the seaward facing net was 24% higher than the total fish biomass caught in the landward facing net (Fig. 7). The average weight of a fish caught in the seaward facing net (mean=10.9g, SE= 4.33, df= 26) at both sites was more than double the average weight of a fish caught in the landward facing net (mean= 5.15g, SE=1.11, df=26) at both sites (Fig. 7). At the Hantsport site, fish biomass between the seaward (mean=22.5g, SE=5.0, df=2) and landward (mean=7.12, SE=2.28, df=19) facing fyke nets did differ significantly (p=0.05, F=4.46). It is important to note that this difference in fish biomass was largely influenced by the low number of samples. Fish biomass at the Kingsport site did not differ significantly (p=0.181, F=1.85) between the seaward (mean=9.80, SE=4.65, n=22) and landward (mean=3.44, SE=0.51, n=22) facing fyke nets. The average fish weights for both sites and net orientations were not necessarily representative of the samples. The median weight of fish caught in the seaward facing net when combining data from both sites was only 1g more than fish caught in the landward facing net from both sites (Fig. 7). The biomass of fish caught in the landward facing fyke net compared to the seaward facing fyke net at both sites did not differ significantly (df=1, p=0.118, F=3.99).

On average, 1.75 times more fish were caught in the landward facing net (mean= 22, SE= 0.485, n=4) than in the seaward facing fyke net (mean= 8, SE= 0.202 n=4), but mean fish abundance did not differ significantly between the two nets at both sites (df=1, p=0.379, F=0.903) (Fig. 8). Fish abundance at the Hantsport site did not differ significantly between the landward and seaward facing nets (p=0.423, F=0.999). It is important to note that these results are being largely influenced by a low number of samples since it is apparent that more fish were caught in the landward (mean=30.5, SE=29.5, df=1) than in the seaward (mean=1, SE=1, df=1) facing fyke net. Fish abundance at the Kingsport site also did not differ significantly between the two nets (p=0.955, F=0.00410) with similar numbers of fish being caught in the landward (mean=14, SE=12, df=1) and seaward (mean=15, SE=10, df=1) facing fyke nets.

4.3.1 Experimental error

VWR® P-Series Portable Balance was switched out with a Starfrit High Precision Pocket Scale after the sampling days at the Hantsport salt marsh. This was largely due to the high level of sensitivity of the VWR scale with any gust of wind resulting in the scale reading to fluctuate. In order to mitigate stress on fish by reducing their time on the scale, the less sensitive Startfrit scale was used for the Kingsport salt marsh sampling days. Another source of experimental error stemmed from the effectiveness of the fyke net in the seaward facing direction. When using fyke nets for fish sampling in salt marsh creeks and channels they are designed to be set landward facing. This is because as the tide begins to drop, fish that are leaving the marsh platform are essentially guided into salt marsh creeks and channels to avoid being stranded on the salt marsh at low tide. With the fyke net being set in a salt marsh creek/channel facing in the landward direction, the fish exiting the marsh using that creek/channel cannot easily avoid the net and most will get caught. In contrast, fish are able to easily avoid the seaward facing net by swimming over or around it to access the high marsh since the water level on the flooding tide allows for it.

The limited number of sampling days did not capture the seasonality differences in fish assemblages that occur in Bay of Fundy salt marshes throughout the year. During spring and fall months, many migratory species are undergoing transitions from freshwater to salt water or vice versa, passing through estuaries and salt marshes on their way. The present study did not take into account the migration times of fish species when selecting sampling days and the short duration of the project limited the ability to begin sampling in the spring and end later in the fall months. Consequently, the majority of the fish caught could be classified as resident species or transients that remain close to the salt marsh boundary during the summer and early fall months. The exclusion of seasonality and thus the majority of migratory species, narrows the scope of the conclusions that can be drawn from the results.

Both of the sampling days at the Kingsport salt marsh resulted in numerous green crabs (*Carcinus maenas*) ending up in both fyke nets (Appendix A7). On the first day of sampling at the Kingsport salt marsh 7 Atlantic silversides were found dead with evidence suggesting green crab predation as the cause, in the seaward facing net. On the second day of sampling at the Kingsport salt marsh only one banded killifish (*Fundulus diaphanous*) casualty was found in the seaward facing net. Fish that experienced green crab predation were counted, however weight measurements could not be taken as they were not entirely intact after predation took place. Green crabs were not weighed and were therefore not included in statistical analyses. In terms of abundance, green crabs dominated in the seaward facing net (Appendix C4) and were the second most numerous species in the landward facing net (Appendix C5). Sand shrimp were also found in abundance in the seaward facing net on the first sampling day at the Kingsport marsh, however they were not weighed as they were too small and light. In future studies all nekton including invertebrates should be accounted for since they represent an important ecological linkage between salt marshes and nearshore environments.

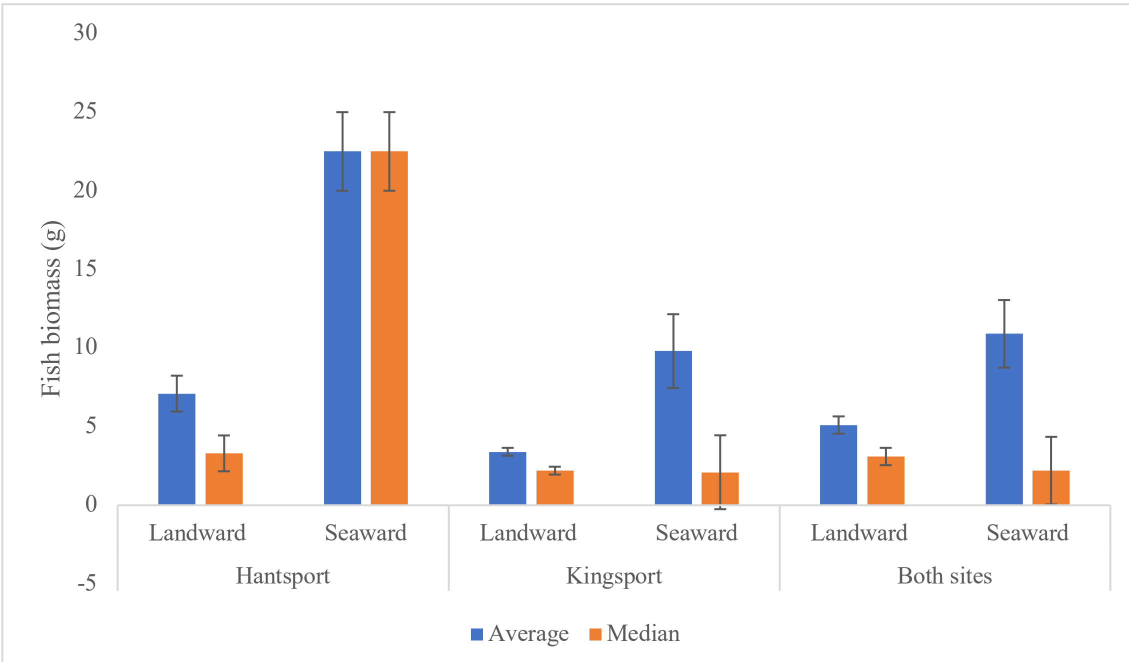

Figure 7. Average and median fish biomass (g) values for fish caught in opposite fyke nets deployed in two salt marshes (Hantsport and Kingsport) within the Minas Basin, Nova Scotia. Fish caught in the seaward facing net were assumed to be moving into the salt marsh with the rising tide and those caught in the landward facing net were thought to be leaving the salt marsh with the ebbing tide. Fish biomass between the seaward (mean=22.5g, SE=5.0, df=2) and landward (mean=7.12, SE=2.28, df=19) facing fyke nets at the Hantsport site did differ significantly (p=0.05, F=4.46). At the Kingsport site, fish biomass did not differ significantly (p=0.181, F=1.85) between the seaward (mean=9.80, SE=4.65, df=22) and landward (mean=3.44, SE=0.51, df=22) facing fyke nets. Fish biomass did not differ significantly between the seaward (mean=10.9g, SE= 4.33, df= 26) and landward (mean= 5.15g, SE=1.11, df=26) facing fyke nets at both sites (p=0.118, F=3.99). Mean and median values for fish biomass between the two fyke nets are presented to show that the mean value of fish biomass is not necessarily representative especially for the seaward facing net. Large biomass ranges occurred between individual fish in samples from both nets, making the median biomass more representative of what most fish weighed.

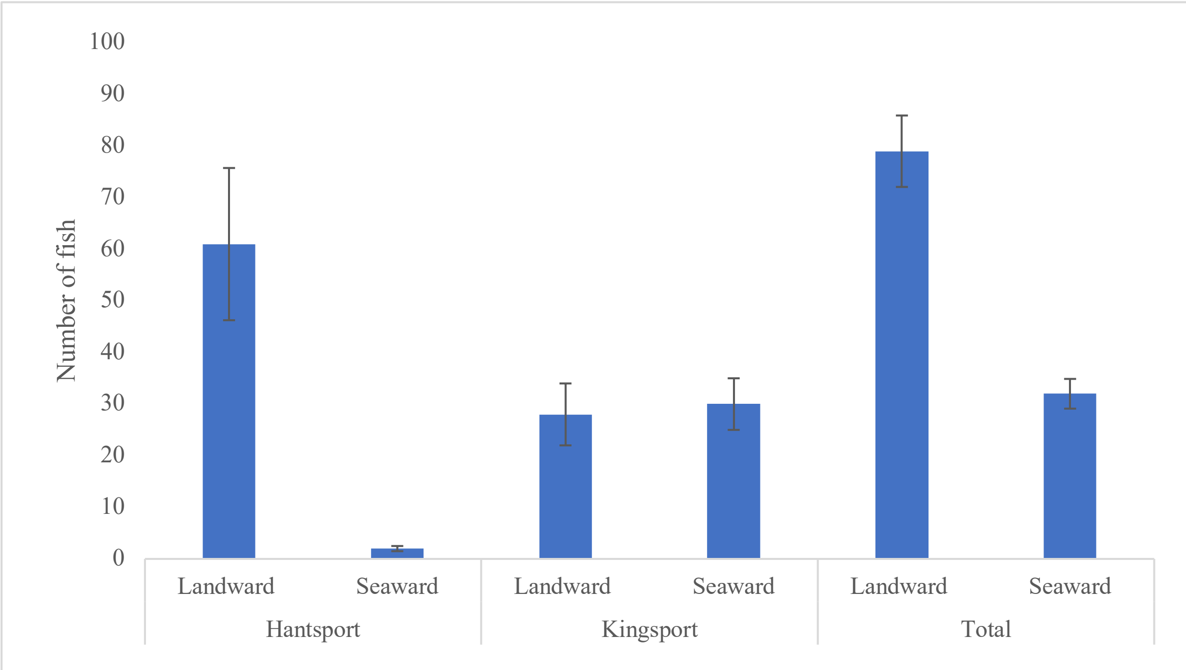

Figure 8. Average number of fish caught in seaward facing and landward facing fyke nets from two sampling days at the Hantsport and two sampling days at the Kingsport salt marshes. The landward facing net was assumed to be catching fish leaving the salt marsh on the ebb tide while the seaward facing net was catching those moving into the marsh with the flood tide. When combining the data from both sites, on average, more fish were leaving the salt marsh than entering it with more fish having been caught in the landward facing net (mean= 22, SE= 0.485, df=4) than in the seaward facing fyke net (mean= 8, SE= 0.202 df=4). Fish abundance was not found to differ significantly between the landward and seaward facing nets at both sites (p = 0.379, F=5.99). At the Hantsport site, fish abundance did not differ significantly between the two nets (p=0.423, F=0.999), however this is being largely influenced by a low number of samples since it is apparent that more fish were caught in the landward (mean=30.5, SE=29.5, df=1) than in the seaward (mean=1, SE=1, df=1) facing fyke net. Fish abundance at the Kingsport site also did not differ significantly between the two nets (p=0.955, F=0.00410) with similar numbers of fish being caught in the landward (mean=14, SE=12, df=1) and seaward (mean=15, SE=10, df=1) facing fyke nets. It is important to note that issues with the sampling method were influential in creating differences in fish abundance as the seaward facing net was not as effective at catching fish as the landward facing fyke net.

4.4 Discussion

After analyzing the results of fish weight and abundance, there are no clear differences between the biomass and number of fish coming onto the salt marsh with the rising tide and leaving with the ebbing tide. These findings negate the initial hypothesis in that fish moving off the salt marsh with the ebb tide would be heavier than those moving in the opposite direction. The results do, however, support the assumption that similar numbers of fish would be moving in both directions since many fish take advantage of salt marsh resources during the flood tide, although few species stay within the salt marsh at low tide. Since 78% of fishes sampled in the landward facing net weighed 5g or less, it is possible that the additional biomass that could be attributed to a full stomach in fish leaving the salt marsh was negligible and not picked up by either scale. It is important to note that sample size was small and previous fish sampling in the Bay of Fundy has revealed seasonal variation in both species and abundances (Bowron et al., 2012; Gratto, 1980). The range of fish weights caught between both nets at both sampling sites was also large, with the heaviest fish weighing 169 times more than the smallest fish in the sample, and 11% of the fishes accounting for more than 50% of the total biomass. Although further research and larger sample sizes across all seasons will be required to provide firmer conclusions, prior research has indicated that the ecological linkages, including those mediated by fish, are bidirectional between salt marshes and other nearshore environments.

The nursery function of salt marshes for fish and invertebrate species exemplifies this bidirectional linkage with nearshore environments (Whitfield, 2016). Larval and juvenile species that occupy salt marshes contribute to the salt marsh food web as they are a food source for numerous species (Sheaves et al., 2015). Whether they are predated on or die of natural causes the energy and nutrients in the form of their biomass gets recycled back into the salt marsh food chain. Those that survive through their juvenile life stages and emigrate into nearshore waters form the main linkage in this direction as they contribute to stock numbers and biomass (Sheaves et al., 2015). Salt marshes are also known to support numerous species of juvenile and larval invertebrates such as crabs and lobsters (Kneib, 1997; Able et al., 2018). Mazumder et al. (2009) compared zooplankton samples taken on the flooding and ebbing tides in an Australian salt marsh. The results indicate that the salt marsh was functioning as a net exporter of crab and gastropod larvae while acting as a sink for copepods and amphipods (Mazumder et al., 2009). While mean zooplankton densities were substantially higher in ebb tide samples, this study demonstrates linkages between salt marshes and other estuarine environments. The export of crab and gastropod larvae may be delivering an important nutritional subsidy for fish inhabiting less productive areas of the estuary, while also providing an important trophic link (Mazumder et al., 2009). These findings support the notion of two-way linkages in that organisms are moving both into and out of salt marsh ecosystems.

Many predatory fish species that utilize salt marshes have commercial or recreational value are important in keeping populations of herbivorous species and their grazing levels under control (Bertness et al., 2014). An interesting study by Altieri et al. (2012) looked at the effects of overfishing key top predators on a salt marsh ecosystem. The study found that the overexploitation of striped bass, blue crab (*Callinectes sapidus)*, and smooth dogfish (*Mustelus canis*) by recreational fishers resulted in a trophic cascade in a Massachusetts salt marsh. Without the presence of these predators, populations of the herbivorous crab, *Sesarma reticulatum* exploded resulting in overgrazing of salt marsh vegetation causing large amounts of die off (Altieri et al., 2012). Bertness et al. (2014) excluded the same predatory species listed by Altieri et al. (2012) with the addition of green crabs from a Massachusetts salt marsh and found that herbivorous grazing increased by more than 100%. This resulted in macrophyte die off and bare ground to increase by more than 150% in the salt marsh (Bertness et al., 2014). This demonstrates the importance and existence of bidirectional ecological linkages between salt marshes and nearshore fisheries. Predatory species utilize salt marshes as hunting grounds subsequently keeping primary consumer populations under control (Bertness et al., 2014). When these linkages are disrupted, both ecosystems ultimately suffer.

While vegetated habitats such as salt marshes have been shown to be preferentially selected by fish and other nekton in comparison to unvegetated habitats, research has also shown that there can be synergistic effects when two or more vegetated habitats are in proximity to one another (Sheaves, 2005). Fish moving between adjacent vegetated habitats expend less energy while also being at a lower risk of predation in comparison to having to move through unvegetated habitat that separate vegetated habitats (Sheaves, 2005). Irlandi and Crawford (1997) examined pinfish (*Lagodon rhomboides*) to gain an understanding of linkages between salt marshes and neighbouring subtidal environments. Pinfish exhibited higher levels of movement between salt marshes and seagrass beds than they did between salt marshes and unvegetated mudflats (Irlandi & Crawford, 1997). Pinfish were also found to be longer and 90% heavier when they had access to salt marsh and vegetated subtidal ecosystems, suggesting that these two ecosystems provided a growth advantage (Irlandi & Crawford, 1997). In addition to fish, Rozas and Minello (1998) found decapod crustaceans to be more attracted to salt marshes when they are nearby seagrass beds in certain cases. Decapod crustaceans are a food source for numerous species of fish, therefore their abundance in salt marshes enhances the value of this habitat for fish. Baillie et al. (2015) found higher catch rates of commercial and recreational fish species in habitats where there was connectivity between salt marshes and seagrass beds in comparison to habitats without connectivity between salt marshes and seagrass beds. This further supports the case that fish benefit from having access to multiple habitats and these advantages can be seen in fisheries data. However, examining the subtidal environment surrounding the two study sites was outside the scope of this project, but this may be an important variable to consider in future work within the Bay of Fundy region.

While the results of this pilot study provide some evidence of bidirectional linkages between salt marshes and nearshore environments, not enough data was obtained in this pilot study to be able to draw meaningful conclusions. In order to get a more accurate representation of the amount of fish biomass moving into salt marshes with the flooding tide and leaving with the ebbing tide in this region, this type of study should be carried out on a much larger temporal scale (at least a year) with more replication. This would allow for more data to be collected and the differences in fish assemblages and numbers that occur with seasonality to be captured. This is an area of research that has been lacking in Atlantic Canada and should be continued and built upon in order to gain a better understanding of salt marsh-fishery linkages in this region. This research area is of particular importance to fisheries management efforts as well as decisions regarding the implementation of marine protected areas in coastal waters. It also supports the case that salt marshes are utilized by various species of fish and should be considered fish habitat in decisions relating to salt marsh restoration and conservation.

5. Conclusions and recommendations

It is evident that ecological linkages exist between salt marsh ecosystems and nearshore fisheries, however the extent of these linkages is largely system dependent and varies based on a multitude of factors. Macrophytes form the basis of the salt marsh food web and their detrital matter also comprises an important component of the trophic structure of nearshore food webs (Currin et al., 1995). Tides function as abiotic vectors moving planktonic organisms as well as dissolved and particulate organic matter between salt marshes and nearshore ecosystems (Lefeuvre et al., 1999; Mazumder, 2006). Fish and other nektonic organisms function as biotic vectors transporting energy and nutrients in the form of their biomass when they move between systems. Ontogenetic and seasonal migrations of these organisms can represent mass movements of energy and nutrients from originating to recipient systems (Deegan et al., 2000). Hydrology appears to be the main factor affecting both abiotic and biotic vectors of nutrient and energy transport (Litvin & Weinstein, 2003). Higher tides draw organic matter out from higher areas of salt marshes while also making the ecosystem more accessible to fish. Many species of nekton have adapted their behaviours to take maximum advantage of seasonal variations in tidal flow such as timing migrations and spawning to take place during monthly spring high tides (Mazumder et al., 2009). The hydrogeomorphic setting of salt marshes affects the connectivity with nearshore ecosystems and the extent of energy and nutrient linkages between salt marshes and nearshore ecosystems (Lefeuvre et al., 1999).

It remains unclear as to which vector type (biotic or abiotic) is more important in terms of mediating energy and nutrient linkages between salt marshes and nearshore environments. The value of both biotic and abiotic vectors is system and species specific, as salt marshes in different regions vary in their exchange of dissolved and particulate organic matter and nekton with the nearshore environment. While the quality of energy and nutrients is higher and the trophic transfer is more direct with biotic vectors (Deegan et al., 2000), it is not necessarily true that biotic vectors outweigh abiotic vectors in terms of importance. Outwelling provides a substantial source of organic matter to nearshore ecosystems in some regions, especially those where salt marshes are extensive with large tidal amplitudes (Odum, 2000). Nearshore fisheries that interact with salt marshes benefit from having energy and nutrient linkages mediated by both vector types even though it is difficult to separate the relative contribution from abiotic or biotic vectors.

Several recommendations can be made in relation to acknowledging the presence of these ecological linkages and by having a better understanding of what can affect these energy and nutrient linkages mediated by biotic and abiotic vectors:

1. **MPA/MPA network planning**

Being at the interface of the terrestrial and aquatic environments has often meant that salt marshes and other coastal wetlands are considered to be a challenging management zone in marine protected area planning (Ruttenberg & Granek, 2011). The landward side of salt marshes is often the area that presents the most difficulty in setting boundaries for marine protected areas (Ruttenberg & Granek, 2011). The IUCN recommends that the highest astronomical tide or high water mark should designate the landward boundary of an MPA, especially in regions with high tidal ranges (Day et al., 2018). These designations have proven to be problematic both legally and administratively especially in estuarine environments. This is largely due to the fact that the principles defining high or low water marks are unclear and there may be confusion regarding what bays and channels are actually part of an MPA (Day et al., 2018). This is complicated further with sea level rise as these recommendations do not account for the movement of these ecosystems landward in the future. Unfortunately, this is not only the case for MPA regulations, but coastal wetland protection in general. While fish are only able to utilize the area of coastal ecosystems that are flooded, the remainder of these ecosystems still contribute to the provisioning of habitat and other services. Therefore, it would be prudent for MPA boundaries to encompass the entire salt marsh area including a buffer zone to provide more protection to coastal wetland ecosystems. The protection of the entire ecosystem will enhance the quality of ecosystem services that it provides (Weinstein et al., 2014).

While MPAs have been used as an ecosystem-based management (EBM) strategy for fisheries management, a common criticism of MPAs is the notion that a fixed area cannot adequately protect species that move during different periods of their life history (Sunblad et al., 2010). The majority of fish species move widely across different regions and ecosystems, therefore the current set up of MPAs likely only offers protection for a certain life stages of many fishes (Sunblad et al., 2010). MPA networks can be more effective especially if appropriately placed movement corridors are considered for the protection of more mobile species (Sunblad et al., 2010). MPA networks that cover multiple vegetated habitats within close proximity to one another may also help promote the synergistic effects they have on fish. Life histories should be more heavily considered in the design process of MPAs in order to protect species during multiple ontogenetic stages. Salt marshes and other coastal wetlands that function as nurseries should be incorporated into these MPA networks for their nursery function as well as all of the additional benefits they provide to nearshore ecosystems. Other connectivity indices should also be considered in MPA planning in design, with areas that have high connectivity receiving priority in terms of protection.

2. Consideration of bidirectional linkages in fisheries management

It is important to acknowledge the bidirectional linkages as nearshore fish stocks directly influence the trophic structure of coastal ecosystems. As shown in studies described in Chapter 4, overfishing has been shown to have a direct correlation with a salt marsh ecosystem collapse in

Massachusetts, U.S.A. (Altieri et al., 2012). Fish species targeted in recreational fisheries are often top predators that play an important role in nearshore as well as coastal ecosystems. While many of these species benefit from the high food abundances and provisioning of nursery habitat provided by salt marshes, they also regulate the populations of herbivores through predation (Altieri et al., 2012). Without the presence of top predators, overgrazing by herbivorous crabs resulted in mass die-offs of salt marsh macrophytes (Altieri et al., 2012). Since salt marsh macrophytes are the main structural component of salt marsh ecosystems, it is not surprising that the overgrazing resulted in the collapse of the ecosystem. This sort of collapse will greatly impact the other species that rely of those salt marshes (Green et al., 2012). Some of these species may hold commercial or recreational value therefore resulting in adverse impacts on other fisheries. The existence of these bidirectional linkages makes it imperative that decisions regarding fisheries management take coastal ecosystems into account. Fishing quotas and stock levels of target species in both recreational and commercial fisheries should therefore not only reflect the numbers required to maintain a sustainable fishery. They should also reflect population numbers required to maintain lower-level consumers at levels that mitigate trophic cascades in adjacent connected ecosystems.

3. Salt marsh restoration as a potential fisheries management tool

These ecosystems provide crucial habitat for various species of fish and have been shown to contribute substantially to stock numbers (Janes et al., 2020). Despite this, salt marshes have been heavily degraded with global estimates being as high as 50% of salt marshes being lost. In certain regions these numbers are higher, for example in Nova Scotia 60% of salt marshes are thought to have been destroyed province wide with 85% of Bay of Fundy salt marshes having been lost (Mackinnon & Scott 1984; Hanson & Calkins, 1996). The restoration of coastal wetlands, including salt marshes, has been considered to be a tool for helping to rebuild and maintain healthy stocks (Schulz et al., 2020). While overfishing is often the main factor, there are often numerous contributing factors resulting in the decline of fish stocks. Loss of access and habitat destruction are often key factors in these declines, and coastal ecosystems are facing some of the highest rates of degradation among all ecosystems (Himes-Cornell et al., 2018). Restored salt marshes have been shown to provide important habitat and are utilized by various fish species. As a bonus, salt marshes and other coastal wetlands also provide numerous other ecosystem services to humans especially in the context of climate change mitigation (e.g., carbon sequestration, storm surge protection) (van Proosdij & Page, 2012; Barbier, 2015). The restoration of salt marshes should therefore be considered as a nature-based solution in regions that are currently experiencing or expected to face climate change.

4. Policies to limit salt marsh loss

While salt marsh restoration has proven to be successful in restoring fish habitat in areas where these ecosystems have been destroyed, it is better that the destruction of salt marshes and other coastal ecosystems not occur in the first place (Schulz et al., 2020). Reference salt marshes have been shown to support higher abundances of fishery species in comparison to restored salt marshes (Rozas et al., 2005; Virgin et al., 2020). Certain regions have implemented policies to limit the degradation or loss of salt marsh ecosystems however, globally these ecosystems are still being destroyed at a significant rate (Himes-Cornell et al., 2018). Salt marshes in Nova Scotia are protected by federal and provincial policies with some including compensation and offsetting requirements to limit the net loss of salt marshes. The Fisheries Act from the Department of Fisheries and Oceans (DFO) prohibits the harmful alteration and destruction of fish habitat (Canada Fisheries Act, 2019). While it is widely accepted that salt marshes provide important habitat for fish, issues with this Act arise with what area of a salt marsh constitutes fish habitat. The Nova Scotia Wetland Conservation Policy (NSWCP) and the Nova Scotia Coastal Protection Act (NSCPA) are two examples of provincial polices that protect salt marshes. The NSWCP aims to prevent the net loss of wetlands including salt marshes (Government of Nova Scotia, 2011) and the NSCPA targets the prevention of developments and activities that may harm coastal areas (Bill 106, 2019). Future climate change impacts are predicted to have adverse effects on salt marshes and other coastal ecosystems. While salt marshes have shown potential to accrete at the same rate as sea level rise, this is largely system dependent with the health of the ecosystem and having adequate space to migrate landwards being important factors (Himes-Cornell et al., 2018). For these reasons it is important that policies be put in place to protect salt marshes globally with a focus on adaptive capacity to account for predicted future climate-related changes in coastal areas.

5. Recommendations for additional research

The Bay of Fundy is one region that would benefit from further research regarding the energy and nutrient linkages between nearshore fisheries and salt marshes. This is mainly due to the lack of research in terms of the importance of salt marshes as support for nearshore fisheries in this area and the unique tidal regime that the Bay of Fundy experiences. Another area that would benefit from further research is in relation to the economics associated with salt marsh-fishery linkages. The development of a clear definition for a salt marsh-dependent species would also be particularly useful in emphasizing the importance of these ecosystems for certain species. Attempts have been made to define estuarine-dependent species, however no such efforts have been made specifically for salt marshes. This information would help fill data gaps in terms of the degree to which salt marsh ecosystems are essential for the survival of certain species. Research into how these ecological linkages may change with increasing climate impacts would also be useful.

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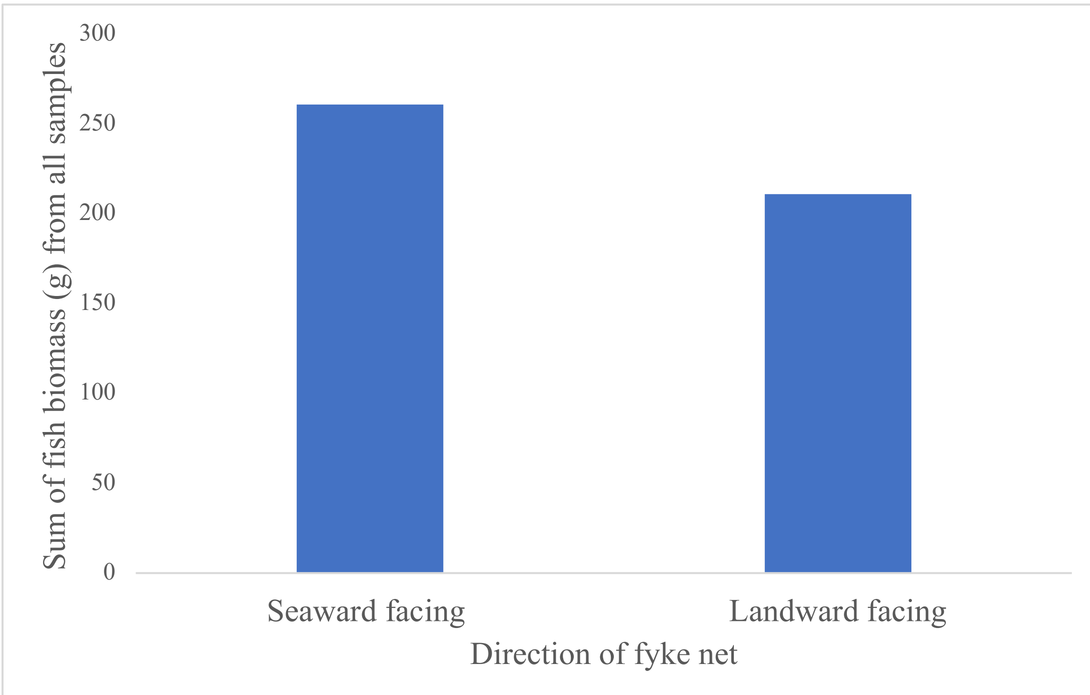
Appendix A
Fish biomass data

Appendix A1. The total sum of biomass (g) of fish caught throughout all sampling days did not differ significantly between the two fyke nets (p=0.118).



Appendix A2. Statistical output of the one-way ANOVA results for fish biomass data from all samples.

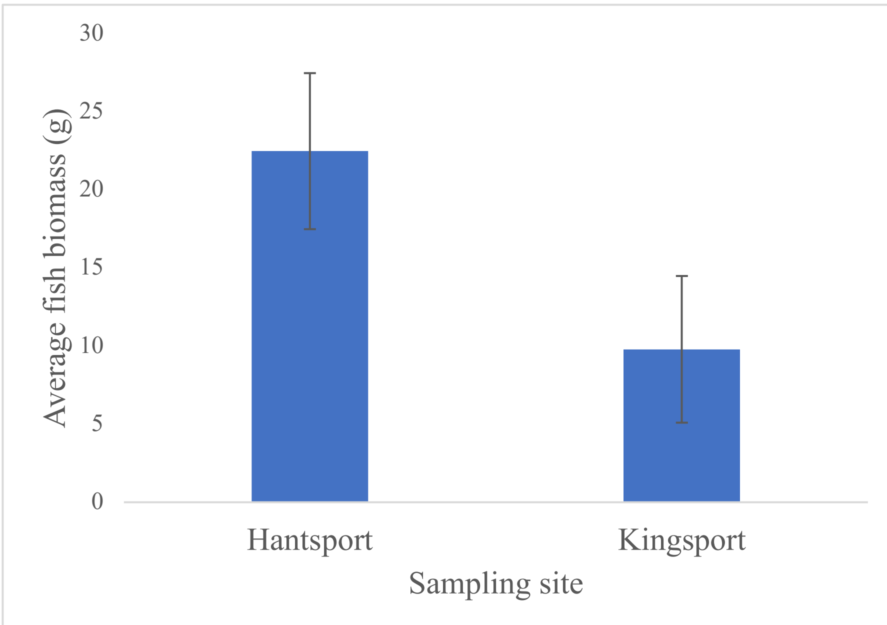
SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	24	260.7	10.8625	450.025924
Column 2	41	211	5.14634146	50.8000488

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	494.641183	1	494.641183	2.5166281	0.1176582	3.99336492
Within Groups	12382.5982	63	196.549178			
Total	12877.2394	64				

Appendix A3. Average fish biomass caught in the seaward facing fyke net throughout all sampling days at the Hantsport (mean= 22.5, SE=5, n=2) and Kingsport (mean= 9.80, SE=4.65, n=2) salt marshes. Fish biomass in the seaward facing net at the Hantsport site was not significantly higher than the fish biomass caught at the Kingsport site (df=3, t-stat= 1.86, p=0.0800).



Appendix A4. Statistical output from a one-way ANOVA of fish biomass from the seaward facing fyke nets at both sampling sites.

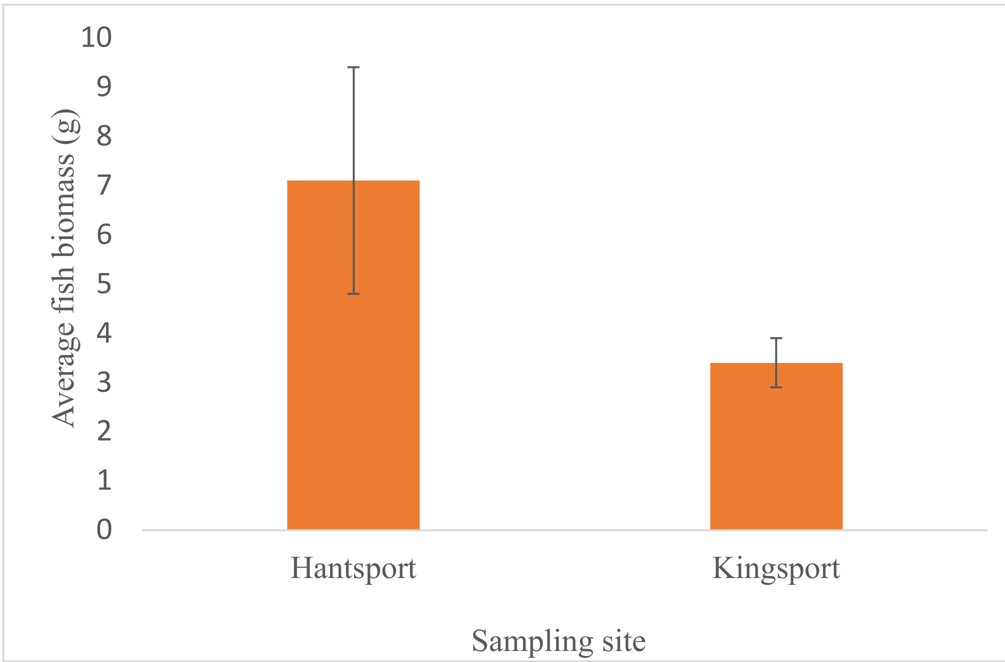
SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	2	45	22.5	50
Column 2	22	215.7	9.80454545	476.433788

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	295.486705	1	295.486705	0.64650787	0.42996719	4.3009495
Within Groups	10055.1095	22	457.050434			
Total	10350.5963	23				

Appendix A5. Average fish biomass caught in the landward facing fyke net throughout all sampling days at the Hantsport (mean=7.12, SE=2.3, n=2) and Kingsport (mean=3.4, SE=0.5, n=2) salt marshes. Fish biomass in the landward facing net at the Hantsport site was not significantly higher than the fish biomass caught at the Kingsport site (t-stat=1.58, p=0.07).



Appendix A6. Statistical output from a one-way ANOVA of fish biomass from the landward facing fyke nets at both sampling sites.

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	19	135.3	7.12105263	98.5273099
Column 2	22	75.7	3.44090909	5.73491342

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	138.07719	1	138.07719	2.84330747	0.09974049	4.09127856
Within Groups	1893.92476	39	48.5621734			

Total	2032.00195	40

Appendix A7. Tables with raw data from all sampling days.

Site	Sample #	Direction of fyke net	Species	Weight (g)
Hantsport	1	Landward	Atlantic silverside	3
			Atlantic silverside	3.5
			Atlantic silverside	4.1
			Atlantic silverside	3.6
			Atlantic silverside	3.5
			Atlantic silverside	4.4
			Atlantic silverside	3
			Atlantic silverside	1.5
			Atlantic silverside	2.9
			Atlantic silverside	2.5
			Atlantic silverside	3.1
			Atlantic silverside	3.2
			Atlantic silverside	3.3
			Atlantic silverside	3.0
			Atlantic silverside	2.0
			Gaspereau	6.5
			American eel	40
			American eel	16
Notes: 41 additional silversides were caught and not weighed, 1 additional American eel was caught, however it escaped from the weighing container and could not be recovered to be weighed.				
Hantsport	1	Seaward	*No fish were caught during sampling	

Site	Sample #	Direction of fyke net	Species	Weight (g)
Hantsport	2	Landward	American eel	26.2
		Seaward	American eel	17.5
			American eel	27.5

Site	Sample #	Direction of fyke net	Species	Weight (g)
Kingsport	3	Landward	Mummichog	6.7
			Mummichog	5.0
			Mummichog	0.9
			Mummichog	2.1
			Mummichog	3.4

			Mummichog	1.1
			Mummichog	4.2
			Mummichog	1.8
			Mummichog	2.0
			Mummichog	8.3
			Mummichog	0.9
			Mummichog	8.3
			Mummichog	2.0
			Mummichog	1.9
			Mummichog	1.9
			Mummichog	3.9
			Mummichog	1.4
			Mummichog	6.7
			Mummichog	1.7
			Mummichog	2.3
Notes: 35 green crabs were caught in the seaward facing net and they were not weighed or included in the total catch numbers 6 additional mummichogs were caught in the landward facing net, however they were not measured.				
Kingsport	3	Seaward	Atlantic silverside	1.1
			Atlantic silverside	2.1
			Atlantic silverside	2.0
			Atlantic silverside	2.2
			Atlantic silverside	1.9
			Atlantic silverside	0.9
			Atlantic silverside	1.2
			Atlantic silverside	0.5
			Atlantic silverside	1.4
			Mummichog	8.6
			Mummichog	4.4
			Mummichog	1.3
			Mummichog	0.5
			Mummichog	4.9
			Mummichog	6.1
			Mummichog	7.3
			Mummichog	1.1
			Banded killifish	4.3
Notes: 29 green crabs were caught in the seaward facing net and they were not weighed or included in the total catch numbers; 7 dead Atlantic silversides were caught in the seaward facing net and were not measured as their full bodies were not intact likely as a result of green crab predation.				

Site	Sample #	Direction of fyke net	Species	Weight (g)
Kingsport	4	Landward	Banded killifish	2.9
			Mummichog	6.3

Notes: 10 green crabs were caught in the landward facing net and they were not weighed or included in the total catch numbers.				
Kingsport	4	Seaward	Tomcod	68.0
			Tomcod	84.5
			Banded killifish	1.3
			Mummichog	10.1
Notes: 29 green crabs were caught in the seaward facing net and they were not weighed or included in the total catch numbers; 1 dead banded killifish was caught in the seaward facing net and was not measured as it was not fully intact likely as a result of green crab predation.				

Appendix B

Fish abundance data

Appendix B1. Statistical output from a one-way ANOVA showing results for fish abundance from all samples.

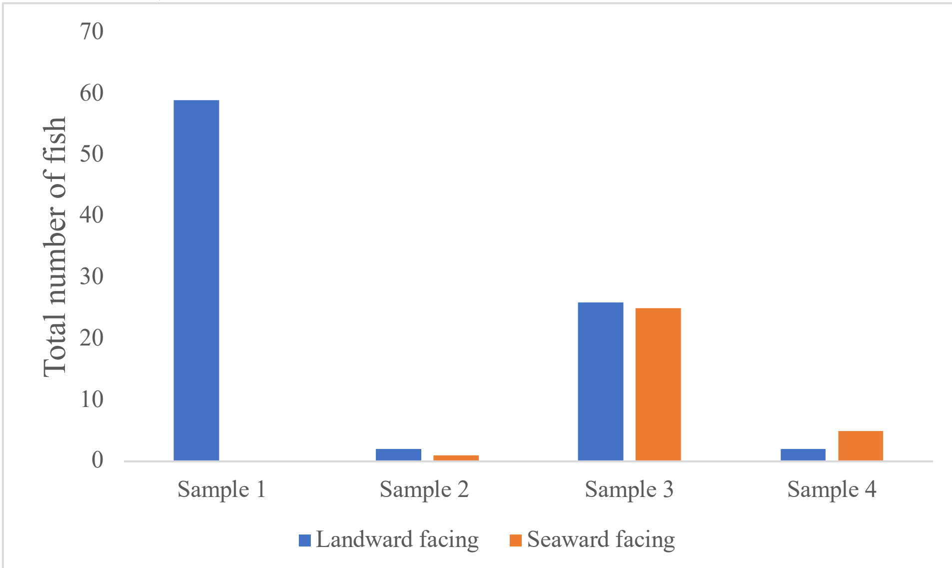
SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	4	89	22.25	766.916667
Column 2	4	32	8	132.666667

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	406.125	1	406.125	0.90291802	0.3786891	5.98737761
Within Groups	2698.75	6	449.791667			
Total	3104.875	7				

Appendix B2. Bar graph showing the total number of fish caught in each net during all sampling days. Sampling days 1 and two were conducted at a salt marsh in Hantsport, Nova Scotia, while sampling days 3 and 4 occurred at a salt marsh in Kingsport, Nova Scotia. The number of fish caught at both sampling site did not differ significantly based on the direction of the fyke net (df=1, p=0.379, F=5.99).



Appendix B3. Statistical output from a one-way ANOVA of data of fish abundance from both the landward and seaward facing fyke nets at both sampling sites with the green crabs at the Kingsport site included.

SUMMARY

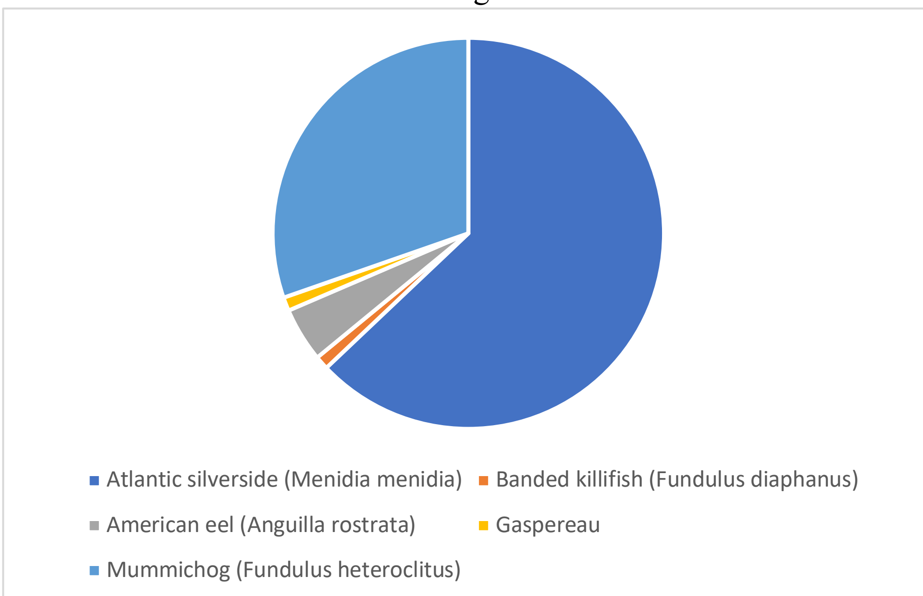
Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	4	134	33.5	992.333333
Column 2	4	90	22.5	683.666667

ANOVA

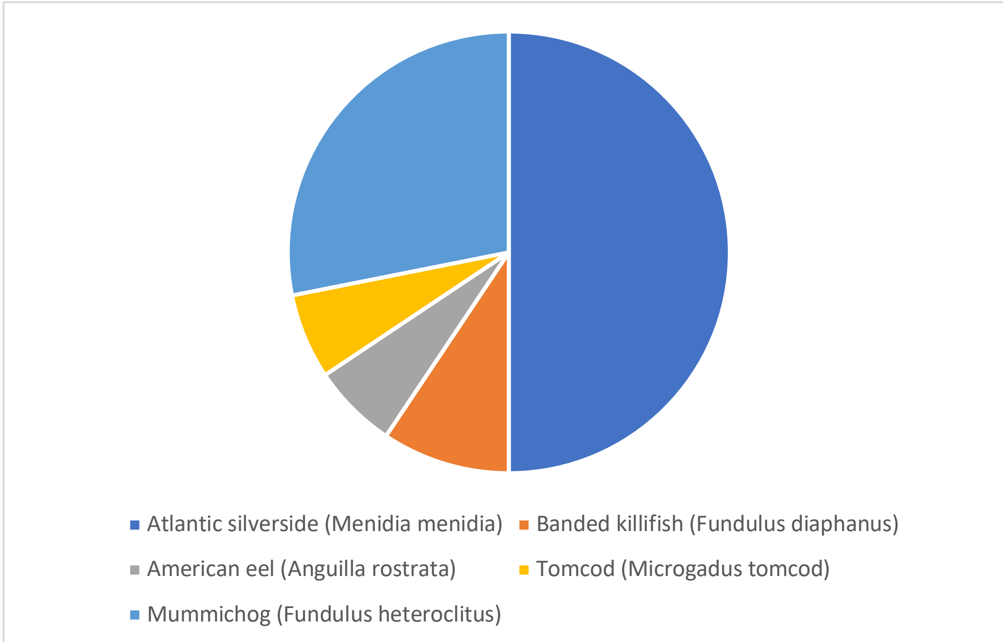
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	242	1	242	0.28878282	0.6103367	5.98737761
Within Groups	5028	6	838			
Total	5270	7				

Appendix C
Species composition

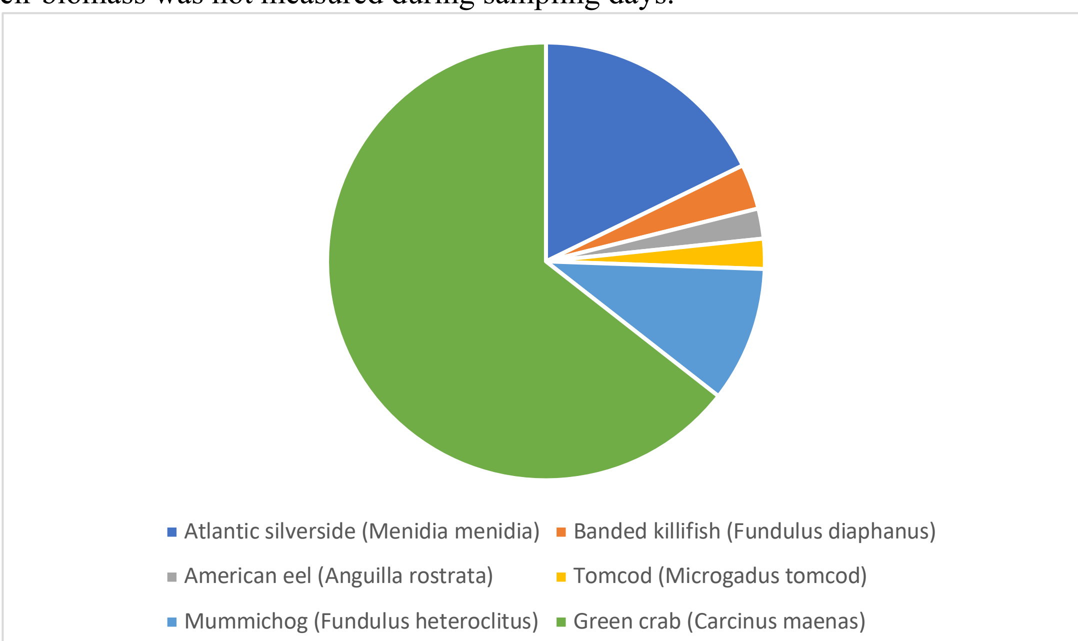
Appendix C1. Pie chart demonstrating species composition caught in the landward facing net from all samples. Atlantic silversides were the most abundant species comprising 63% of the catch in for this net. Banded killifish and gaspereau were the least abundant species each making up 1.1% of the total catch in the landward facing net.



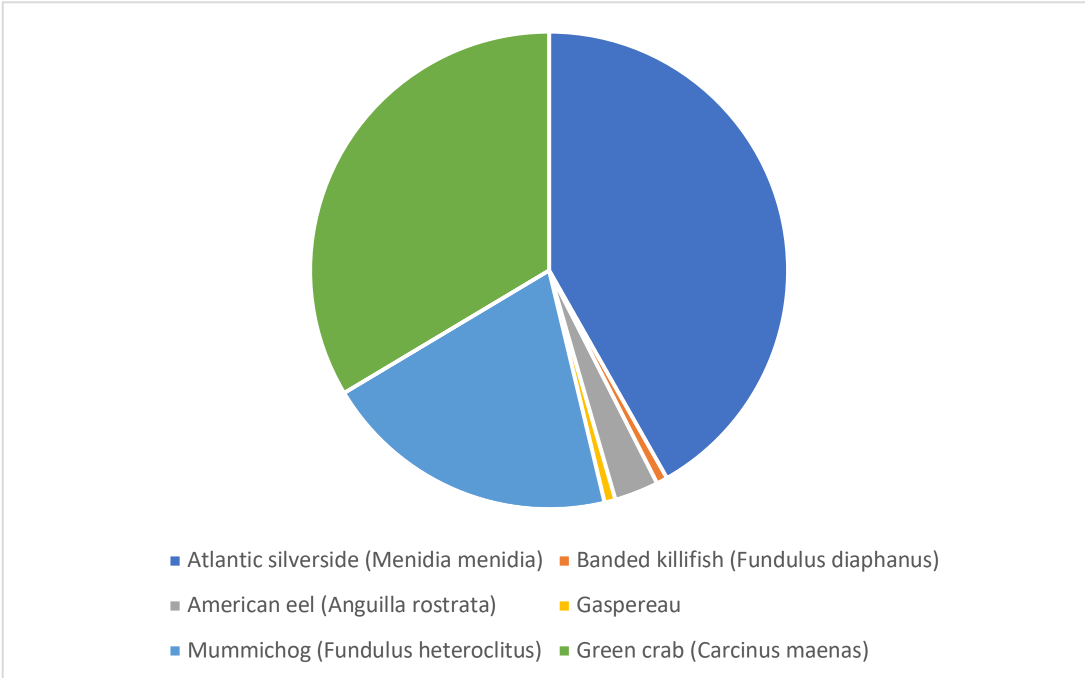
Appendix C2. Pie chart demonstrating species composition caught in the seaward facing net from all sampling days. Atlantic silversides were also the most dominant species comprising 50% of the total catch in for this net. Tomcod and American eels were the least abundant species in the seaward facing net each making up 6.3% of the total catch.



Appendix C3. Pie chart showing species composition including green crabs from the seaward facing fyke net. Green crabs were the most abundant species in the seaward facing fyke net comprising 64% of the total catch. They were only present at the Kingsport, NS sampling site and their biomass was not measured during sampling days.



Appendix C4. Pie chart showing species composition including green crabs from the landward facing fyke net. Green crabs were the second most abundant species in the landward facing fyke net comprising 34% of the total catch. They were second only to Atlantic silversides that comprised 42% of the total catch in the landward facing net. They were only present at the Kingsport, NS sampling site and their biomass was not measured during sampling days.



Appendix D
Pilot study methodology

Appendix D1. Schematic showing the way in which fyke nets were set at both sites during sampling days. Fyke net wings were set on the marsh platform while the main net basket sat flush with the bottom of a salt marsh creek that branched off of a main salt marsh channel. The landward facing fyke net caught fish leaving on the ebbing tide while the seaward facing fyke net caught fish coming into the salt marsh with the flooding tide.