Eelgrass (*Zostera marina*) ecosystems in eastern Canada and their importance to migratory waterfowl

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Abstract

Seagrasses are marine flowering plants that create some of the most productive coastal habitats globally and play a key role in the functioning of nearshore ecosystems. The most common seagrass genus in Canada is Zostera and the species Zostera marina (eelgrass) is the predominant seagrass in intertidal and subtidal shoreline zones along the Atlantic, Pacific, and eastern James Bay coasts. Eelgrass has specific habitat requirements, with growth and productivity optimized within particular ranges of salinity, temperature, light availability, and nutrient concentrations. Large eelgrass meadows can impact nearshore environments by filtering the water column, stabilizing sediment, buffering shorelines, and providing habitat for various marine and coastal species, including commercially important species like Atlantic cod (Gadus morhua) and lobster (Homarus americanus). Eelgrass is also a vital food resource for migratory waterfowl, notably Canada Geese (Branta canadensis), Pacific Black Brant (Branta bernicla nigricans), and Atlantic Brant (Branta bernicla hrota). Despite their ecological importance, seagrasses are among the most vulnerable coastal ecosystems on the planet. The global loss of seagrass has been linked to a variety of human activities, including pollution, invasive species, and catchment modifications. There is an urgent need to improve monitoring of seagrass responses to environmental change, better document the importance of seagrass meadows to species reliant on them for food and habitat, and advance effective management and conservation of seagrass ecosystems. In this thesis, I investigated the spatiotemporal dynamics of eelgrass meadows in eastern Canada and the importance of eelgrass as a food source for migratory waterfowl, using remote sensing data, longterm monitoring data (biomass, density, and cover), and field observations. In Chapter 3, I used a novel cost-efficient approach for satellite imaging time-series to examine changes in eelgrass distribution and abundance from 1984 to 2017 in a wetland of international importance in northeastern New Brunswick. With minimal ground truth data, the novel time-series approach revealed a slow and steady decline in eelgrass abundance in some areas of the estuary. In contrast, other areas were characterized by highly dynamic shifts in eelgrass cover over time. I demonstrated how time-series analysis can be used to identify potential drivers of seagrass change and the benefits of including time-series analysis in seagrass monitoring programs. In Chapter 4, I contributed to advancing knowledge of migratory waterfowl stopover behaviour by examining the influence of eelgrass and human activities on Canada Geese habitat selection. Combining field observations of Canada Geese and the eelgrass distribution maps produced in Chapter 3, I found that Canada Geese selected areas with high eelgrass availability during periods of low human disturbance, which emphasized the importance of eelgrass as a food source during the fall migration. However, higher levels of human disturbance led to a redistribution of geese away from dense eelgrass meadows. In Chapter 5, I presented new insights into the recent and current state of eelgrass along the eastern coast of James Bay after a drastic and large-scale decline in the late 1990s. By aggregating, synthesizing, and analyzing long-term monitoring data and current surveys, spanning 1982 – 2020, I provided the first quantitative evidence that changes in eelgrass biomass in northeastern James Bay may reflect synergistic impacts of climate change and altered freshwater discharge regimes. Overall, this thesis advances understanding of how temperate and subarctic Zostera marina ecosystems and associated fauna respond to coastal development and climate change.

Résumé

Les herbiers marins sont des plantes marines à fleurs qui créent certains des habitats côtiers les plus productifs au monde et jouent un rôle clé dans le fonctionnement des écosystèmes littoraux. Zostera est le genre d'herbes marines le plus commun au Canada et Zostera marina (zostère marine) représente l'espèce prédominante dans les zones littorales intertidales et subtidales le long des côtes de l'Atlantique, du Pacifique et de l'est de la baie James. La zostère a des besoins spécifiques en matière d'habitat, sa croissance et sa productivité étant optimisées dans des plages particulières de salinité, de température, de disponibilité de la lumière et de concentrations en nutriments. Les grands herbiers de zostère peuvent avoir un impact sur les environnements littoraux en filtrant la colonne d'eau, en stabilisant les sédiments, en protégeant les rivages et en fournissant un habitat à diverses espèces marines et côtières, y compris des espèces importantes sur le plan commercial comme la morue de l'Atlantique (Gadus morhua) et le homard (Homarus americanus). La zostère est également une ressource alimentaire vitale pour certaines espèces d'oiseaux migrateurs, notamment la bernache du Canada (Branta canadensis), ainsi que la bernache cravant du Pacifique (Branta bernicla nigricans) et de l'Atlantique (Branta bernicla hrota). Malgré leur importance écologique, les herbiers marins font partie des écosystèmes côtiers les plus vulnérables de la planète. La disparition globale des herbiers marins a été liée à diverses activités humaines, notamment la pollution, les espèces envahissantes et les modifications des bassins versants. Il est urgent d'améliorer la surveillance des réponses des herbiers aux changements environnementaux, de mieux documenter l'importance des herbiers pour les espèces dont l'habitat et la nourriture en dépendent et de faire progresser la gestion et la conservation efficaces des zostéraies. Dans cette thèse, j'ai étudié la dynamique spatio-temporelle des zostéraies dans l'est du Canada et l'importance de la zostère marine comme source de nourriture pour la sauvagine migratrice, en utilisant des données de télédétection et historiques (biomasse, densité et couverture), ainsi que des observations sur le terrain. Dans le Chapitre 3, j'ai utilisé une nouvelle approche efficace et économique exploitant des séries chronologiques d'imagerie satellitaire afin d'examiner les changements dans la distribution et l'abondance des zostéraies de 1984 à 2017 dans une zone humide d'importance internationale dans le nord-est du Nouveau-Brunswick. Avec un minimum de données validées sur le terrain, la nouvelle approche utilisant des séries chronologiques a révélé un déclin lent et régulier de l'abondance de la zostère dans certaines zones de l'estuaire. En revanche, d'autres zones étaient caractérisées par des changements très dynamiques de la couverture de zostères au fil du temps. J'ai démontré comment l'analyse des séries chronologiques peut être utilisée pour identifier les facteurs potentiels de changement des herbiers marins et souligné les avantages d'inclure l'analyse des séries chronologiques dans les programmes de surveillance des herbiers marins. Dans le Chapitre 4, j'ai contribué à faire progresser les connaissances sur le comportement de la sauvagine migratrice en examinant l'influence de la zostère et des activités humaines sur la sélection de l'habitat de la bernache du Canada. En combinant les observations des bernaches du Canada sur le terrain et les cartes de distribution des zostères produites au Chapitre 3, j'ai constaté que les bernaches du Canada choisissaient les zones où les zostéraies étaient abondantes pendant les périodes de faibles perturbations humaines, ce qui souligne l'importance des zostères en tant que source de nourriture pendant la migration d'automne. Cependant, des niveaux plus élevés de perturbations humaines ont entraîné une redistribution des bernaches loin des herbiers de zostères denses. Dans le Chapitre 5, j'ai présenté de nouvelles données sur l'état récent et actuel de la zostère le long de la côte est de la baie James après un déclin drastique et à grande échelle à la fin des années 1990. En regroupant,

synthétisant et analysant les données de surveillance à long terme et les relevés actuels, couvrant la période 1982 - 2020, j'ai fourni les premières preuves quantitatives que les changements dans la biomasse de la zostère dans le nord-est de la baie James peuvent refléter les impacts synergiques des changements climatiques et des régimes altérés de décharge d'eau douce. Dans l'ensemble, cette thèse permet de mieux comprendre comment les écosystèmes de zostères tempérés et subarctiques et la faune associée répondent au développement côtier et aux changements climatiques.

Land Acknowledgement

McGill University is situated on the traditional and unceded territory of the Kanien'kehà:ka. The Kanien'kehà:ka territory has long served as a site of meeting and exchange amongst nations, including the Handenosaunee and Anishinabeg nations. The McGill community acknowledges and respects the Kanien'kehà:ka as the traditional custodians of the lands and waters of the area on which the university is situated.

The data for the chapters 2 and 3 were collected on the traditional and unceded territory of the Esgenoôpetiji Mi'kmaq First Nation. The Tabusintac watershed is one of the largest watersheds in eastern New Brunswick, Canada, with a portion of the watershed part of the Esgenoôpetiji Mi'kmaq First Nation (33 km²) territory. The Esgenoôpetiji Mi'kmaq First Nation continues to rely on the Tabusintac River for resources, particularly Atlantic salmon (*Salmo salar*).

The data for Chapter 4 were collected within the Eeyou Istchee Cree territory of northern Québec, Canada, which covers an area of approximately 400,000 km². Eeyou Istchee Cree territory is comprised of eleven Cree communities (5 of which are coastal communities), has over 300 traplines (which are traditional family hunting and trapping grounds), and is home to 18, 000 people (source from the Grand Council of the Crees: <u>www.cngov.ca/community-culture/communities/</u>).

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During the early stages of my Ph.D., I worked with members of the Migratory Habitats Task Force MHTF, a non-profit organization comprised of Cree Land Users committed to the conservation of coastal wildlife habitats in Eeyou Istchee (eastern James Bay, Québec, Canada). I thank the MHTF members George Lameboy, Rodrique Pachano, and Louie Kanatewat for this opportunity.

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Contribution to Original Knowledge

Throughout this thesis, I contribute to our understanding of the spatiotemporal dynamics of eelgrass (*Zostera marina*) habitats and the importance of eelgrass to migratory waterfowl in eastern Canada. In doing so, I believe this thesis has made several unique contributions to knowledge by:

- Evaluating the potential of a novel and cost-effective algorithm applied to a time-series of remote sensing images to provide information about seagrass's spatial and temporal dynamics,
- Demonstrating the potential of freely available Landsat imagery to map seagrass habitats in Atlantic Canada,
- Highlighting the advantages of including satellite time-series in seagrass monitoring programs to investigate seagrass long-term trends,
- Underscoring the interactive effects of human disturbance and eelgrass abundance in driving the stopover behaviour of Canada Geese during the fall migration in eastern Canada,
- Synthesising and analyzing historical and current observations of eelgrass abundance along the eastern James Bay coast,
- 6. Providing the first quantitative evidence that changes in eelgrass meadows in northeastern James Bay could result from climate change-related factors acting synergistically with the seasonal freshwater discharge from a regulated river.

Seagrasses are essential components of coastal ecosystems. The global loss of seagrasses has sparked a worldwide effort among scientists and resource managers to increase research efforts and improve monitoring strategies. Understanding how and why seagrasses are changing are critical steps required to implement mitigation and restoration efforts. As a result, access to cost-effective seagrass monitoring tools is emerging as a priority for resource managers and conservation organizations. Even though Landsat time-series is one of the most cost-effective options for monitoring landscapes, the use of Landsat images to monitor seagrasses is limited due to various factors, including difficulties obtaining accurate ground-truth data and perceived limitations in mapping nearshore marine ecosystems. In Chapter 3, I demonstrated the value of freely available Landsat imagery for evaluating changes of eelgrass Zostera marina, the most widely distributed seagrass species in Canada. I also tested a novel cost-efficient approach for classifying multitemporal satellite imagery (automatic adaptive signature generalization, AASG) that requires minimal ground truth data and has yet to be used to assess seagrass changes at large spatial scales. In doing so, I demonstrated the feasibility of using the AASG to map seagrass and the advantages of including satellite time series in monitoring programs to investigate seagrass dynamics and long-term trends and identify potential drivers of change.

Many animal species rely on seagrass for food or habitat and understanding these reciprocal links is fundamental to seagrass management and conservation. While most Canada Geese populations traveling across the continental interior use agricultural habitats as stopover areas, populations migrating along coastal routes continue to rely on natural coastal habitats such as salt marshes and seagrass meadows. However, given the increasing anthropogenic impact on coastal ecosystems, geese traveling along coastal zones may find it more challenging to find good stopover sites where food is abundant, and disturbance is low. Chapter 4 examined the

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influence of eelgrass abundance and human disturbance on Canada Geese foraging site selection and its impact on flock size in the Tabusintac Estuary in New Brunswick, Canada. I demonstrated Canada Geese selected locations with high eelgrass abundance, highlighting the importance of eelgrass as a food source for migratory waterfowl in eastern Canada. I also showed Canada Geese altered their distribution and flock size in response to human disturbance.

In the 1970s, the eelgrass meadows along the eastern coast of James Bay, Québec, Canada, were considered among the most extensive in North America. This area remained largely undeveloped until the early 1970s when the first phase of hydroelectric production on the La Grande River began. The large-scale network of diversions prompted the establishment of the most extensive eelgrass monitoring program in eastern Canada in 1982. An unprecedented drastic decline of eelgrass was observed by the Cree First Nations of Eeyou Istchee in the late 1990s. Although several hypotheses have been proposed over the years, the cause of the decline has yet to be established. In Chapter 5, I aggregated, synthesized, and analyzed long-term monitoring data and current surveys to examine the temporal and spatial trends of eelgrass in eastern James Bay, emphasizing northeast James Bay where biomass and density monitoring began in 1982. This analysis yields new insights into the temporal and spatial dynamic of eelgrass abundance over 30 years and the current state of eelgrass along the entire coastline. I also provided the first quantitative evidence that changes in eelgrass biomass in northeastern James Bay could result from climate change-related factors acting synergistically with the seasonal freshwater discharge of a regulated river. This research contributes to our understanding of the vulnerability of subarctic and Arctic coastal systems to coastal development and climate change.

Contribution of Authors

This thesis has a manuscript-based structure and follows the guidelines of *Global Change Biology*. All chapters were conceived and written by myself, and they are largely the results of my research efforts. Dr. Murray M. Humphries, my primary supervisor, provided guidance in developing thesis chapters and sampling designs, as well as analytical and editorial assistance for all chapters.

Chapter 3 (published in the Canadian Journal of Remote Sensing):

Chapter 3 is co-authored with A. Larocque, B. Leblon, A. Hanson, and M. M. Humphries and has been published in the *Canadian Journal of Remote Sensing*. I conceived the idea to conduct a retrospective analysis of eelgrass (*Zostera marina*) cover using Landsat imagery, designed the methodology, collected the data with the assistance of field technicians, completed all the analysis, and wrote the manuscript. M.M. Humphries provided statistical and editorial assistance. B. Leblon and A. Larocque helped with the remote sensing analysis and provided editorial assistance. A. Hanson provided ideas and comments on the draft.

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Chapter 4 (submitted to Ocean and Coastal Management journal):

Chapter 4 is co-authored with A. Hanson, B. Leblon, A. Larocque, and M. M. Humphries. The idea to evaluate the influence of eelgrass and human disturbance on Canada Geese habitat selection in a fall stopover arose from discussions between A. Hanson, M.M. Humphries and myself. I designed the methodology, collected the data with the assistance of field technicians, conducted the analysis, and wrote the manuscript. M.M. Humphries provided statistical and editorial assistance. A. Hanson provided ideas and editorial assistance. B. Leblon and A. Larocque provided feedback and comments on the draft.

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Chapter 5 (in preparation for Global Change Biology journal):

Chapter 5 is co-authored with Mary I. O'Connor, Z. Kuzyk, F. Noisette, K. Davis, L. Richer, E. Rabbitskin, L.-L, Sam, J.-P. Gilbert, D. Babb, J. Ehn, B. Leblon, and M. M. Humphries. I conceived the idea to aggregate the monitoring data, conducted all the analysis, and wrote the manuscript. The 2019 data were collected by M.L. Leblanc, M. I. O'Connor, F. Noisette, K. Davis, and L. Richer, whereas the 2020 data were collected by E. Rabbitskin and L.L. Sam. M.M. Humphries, M. I. O'Connor, Z. Kuzyk, and Fanny Noisette provided statistical and editorial assistance. K. Davis, B. Leblon, and J.-P. Gilbert provided ideas and comments on the draft. D. Babb provided the ice break-up dates for James Bay, while J. Ehn provided the sea surface temperatures for eastern James Bay, and both provided information on how these were generated.

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Chapter 1: Introduction

Seagrasses are marine angiosperms that form vast and highly productive meadows in shallow coastal waters (Hartog & Kuo, 2006). Their global spatial distribution is estimated to be between 177, 000 – 600, 000 km², which is higher than mangrove, salt marsh, and kelp habitats but lower than coral reefs (Mcleod et al., 2011; McKenzie et al., 2020). Like grasslands, prairies, and savannas, seagrasses support a great variety of animals. Recognition of their contribution to carbon storage, coastal geological processes, and food security has gained momentum in the scientific literature in recent decades (Unsworth et al., 2015; Nordlund et al., 2018). Their essential role in nearshore marine environments has prompted the establishment of the World Seagrass Conference & International Seagrass Biology Workshop, the World Seagrass Association, and, more recently, the establishment of global seagrass monitoring programs (Short et al., 2006; Duffy et al., 2015). Despite the recent monitoring and research efforts, seagrass ecosystems have been deteriorating globally at an unprecedented pace since the mid-1990s (Waycott et al., 2009), with approximately 14% of all seagrass species considered at risk of extinction (Short et al., 2011), due to primarily anthropogenic factors (Grech et al., 2012; Murphy et al., 2019). There is an urgent need to improve monitoring of seagrass responses to environmental change, better document the importance of seagrass meadows to species reliant on them for food and habitat, and advance effective management and conservation of seagrass ecosystems.

The overarching goal of this thesis was to contribute to a better understanding of eelgrass (*Zostera marina*) ecosystems in eastern Canada by assessing the temporal and spatial dynamics of eelgrass, demonstrating the importance of eelgrass to migratory waterfowl, and investigating potential drivers of eelgrass change in subarctic Canada. In Chapter 2, I provide a brief review of

existing literature on seagrass taxonomy, distribution, and ecology with a particular emphasis on eelgrass, the most widespread species in eastern Canada. The study presented in Chapter 3 aimed to assess the potential of the AASG (Automatic Adaptive Signature Generalization) algorithm, a novel cost-efficient approach for satellite imagery time-series, to generate eelgrass maps from Landsat imagery. These maps were then used to assess change in eelgrass coverage from 1984 to 2017 in the Tabusintac Estuary, located in northeastern New Brunswick, Canada. Using the eelgrass maps generated in Chapter 3 and field observations, the research objective of Chapter 4 was to assess the influence of eelgrass availability and disturbance on Canada Geese (Branta canadensis) foraging site selection in a fall stopover site (Tabusintac Estuary, New Brunswick). Using long-term monitoring data and supplementary information about river freshwater discharge and climate, the research study presented in Chapter 5 aimed to assess the spatiotemporal patterns of eelgrass along the eastern coast of James Bay (Québec, Canada), evaluate the current state of eelgrass meadows following a drastic decline in the late 1990s and investigate possible drivers of eelgrass change. In Chapter 6, I summarize the key findings from chapters 3, 4, and 5, as well as outline major knowledge gaps in eelgrass research. I also provide suggestions for directions of future eelgrass research and monitoring in Canada. Finally in Chapter 7, I present concluding remarks about the importance of eelgrass research and monitoring in changing coastal environments.

Chapter 2: Literature Review

In this chapter, I will provide a brief overview of the published literature discussing seagrass taxonomy and distribution. I will then discuss the importance of eelgrass (*Zostera marina*) to coastal ecosystem function and migratory waterfowl. In addition, I will discuss the major threats to this species and the various methods used to monitor eelgrass, and how monitoring connects with community partnered research.

2.1 Seagrass taxonomy and distribution

Like terrestrial plants, seagrasses have above and below-ground parts. Morphological and physiological traits that distinguish seagrasses from terrestrial plants include an adaptation to saline environments, growing when wholly submerged, using rhizomes and roots as an anchoring system, and a hydrophilous pollination mechanism (Hartog & Kuo, 2006). Seagrasses are all classified within the superorder Alismatiflorae (Monocotyledonae) and are grouped in four families. Three out of four families consist exclusively of seagrasses: the Zosteraceae, the Cymodoceaceae, and the Posidoniaceae. The fourth family, the Hydrocharitaceae, contains genera adapted to saltwater and freshwater environments (Hartog & Kuo, 2006).

Since all seagrasses need light for photosynthesis, seagrass meadows are commonly found in shallow near-shore waters on all continents' coasts, except for Antarctica (**Figure 2.1**). Compared to terrestrial plants, the global diversity of seagrass is relatively low (< 60 species) (Short et al., 2007). The highest seagrass diversity is found in the south-eastern hemisphere, notably in the tropical Indo-Pacific region. In contrast, the northern hemisphere has less seagrass diversity (Short et al., 2007).

Eelgrass (*Zostera marina* Linnaeus, family Zosteraceae) is the most widely distributed seagrass species in the northern temperate hemisphere (Green & Short, 2003). It is the most

abundant seagrass species in Canada, occurring in shallow coastal waters along the Atlantic, Pacific, and eastern James Bay coasts (Murphy et al., 2021). According to genetic studies, eelgrass originated in the Pacific Ocean between 8 and 20 million years ago. It spread to the Atlantic through the Arctic Ocean via a then-available link between the Pacific and Arctic Oceans (Olsen et al., 2004). Because of repeated long-distance dispersal events, the eelgrass populations along the Pacific and Atlantic coasts are not genetically distinct (Olsen et al., 2004; Olsen et al., 2016). Brackish widgeon grass (*Ruppia maritima*) is sometimes found in eelgrass meadows in eastern Canada, while widgeon grass and *Zostera japonica* (a non-native seagrass species) sometimes co-occur with eelgrass on the north-east Pacific coast (Short et al., 2008; Wong et al., 2013).



Figure 2.1 A) The diversity and distribution of seagrasses around the world. Green shading denotes the number of species recorded in the area; points denote confirmed reports of seagrass occurrence (figure from Short et al., 2007), B) Schematic of a *Zostera marina* eelgrass shoot showing the whole plant structure (figure produced by M.L. Leblanc).

2.2 Eelgrass Zostera marina L.

2.2.1 Environmental requirements

Key environmental drivers that influence eelgrass include substrate type, depth, temperature, salinity, light availability in the water column, nutrient concentrations, and wave regime (Moore & Short, 2006). Unconsolidated soft-sediment bottom habitats (mud to cobble or mixed) are critical for establishing eelgrass shoots because soft-sediment bottom habitats allow for the extension and proliferation of rhizomes and roots (Hemminga & Duarte, 2008). Ammonium (NH4⁺) concentrations in sediments are a vital nitrogen supply to the plant (Short, 1983), and, when depleted, can limit plant growth (Touchette et al., 2003). Eelgrass has a high minimum light requirement (Moore & Short, 2006; Lee et al., 2007), with 10 to 20% surface light being the minimum limit for survival (Short et al., 1995). Eelgrass shoots maximize light absorption by adjusting chlorophyll-a and nutrient concentrations in leaves (Staehr & Borum, 2011) and increasing shoot length in deeper waters (Boström et al., 2014). Temperate eelgrass populations can survive in low light environments under sea ice cover during the winter and maintain metabolic activity by utilizing carbohydrates stored in rhizomes over the summer (McRoy, 1970). Eelgrass can be found in a wide temperature range (~ 5 to 25 °C, mean summer (June to August) air temperature, Olesen et al., 2015). While low water temperatures do not limit eelgrass productivity (Biebl & McRoy, 1971; Lalumière et al., 1994; Olesen et al., 2015), mortality rates increase at water temperatures above ~ 25 °C (Nejrup & Pedersen, 2008). Eelgrass can tolerate a wide range of salinities (from 5 to 35), but the optimum salinity for growth, photosynthesis, and germination is usually > 15 (Lee et al., 2007; Xu et al., 2016).

Eelgrass occurs across a wide range of environmental conditions, including high intertidal to subtidal areas, in protected sites or exposed sites (Fonseca et al., 1983; Wong et al.,

2013), but is generally found in areas where the water current velocity is below 50 cm s⁻¹ (Lalumière et al., 1994). As current velocity increases, eelgrass shoots will invest more in the belowground biomass to enhance their anchoring capacity (Fonseca et al., 1983).

Most temperate eelgrass populations are perennial and grow by rhizome extension (Olesen & Sand-Jensen, 1994). Flowering frequency in temperate eelgrass populations is about 10% in the summer (Lalumière et al., 1994; Olesen, 1999), but it can vary in response to local disturbances (Lalumière et al., 1994) or summer temperatures (Olesen et al., 2015; Blok et al., 2018). Annual eelgrass populations, which typically occur in highly disturbed environments (e.g., ice-scour, high summer temperatures), rely on sexual reproduction to produce seeds to recover quickly (Keddy & Patriquin, 1978; Santamara-Gallegos et al., 2000). Eelgrass seed germination is influenced by many factors, including light, salinity, and water temperature (Phillips et al., 1983; Xu et al., 2016).

2.2.2 Ecological function

Eelgrass meadows provide essential ecosystems services. Dense eelgrass meadows attenuate wave energy and substantially reduce current velocity (Grizzle et al., 1996; McMahon et al., 2014), which can, on a larger scale, buffer shorelines from wave action, reducing shoreline erosion (DFO, 2009a). Due to the reduced water current velocity in seagrass meadows, sediment particles in the water column fall out of suspension and settle to the seafloor, increasing nearshore water clarity (Fonseca et al., 1983; Fonseca & Cahalan, 1992) and stabilizing coastal sediments (Marin-Diaz et al., 2020).

The structure of the eelgrass food webs will vary according to density, distribution, and locations of eelgrass meadows (Schmidt et al., 2017; Murphy et al., 2021). In general, the base of

the eelgrass meadows where nonliving leaf debris accumulates is occupied by invertebrates, microorganisms, and fish that consume the detritus (**Figure 2.2**, Murphy et al., 2021). Eelgrass shoots provide support for epiphytic micro-and macro-algae (e.g., diatoms, seaweeds). The epiphytic layer on eelgrass shoots accumulates on the leaves as they grow, and if too thick, can reduce the amount of light required for photosynthesis (Sand-Jensen, 1977). However, epiphyte accumulation on leaves is generally kept in check by mesograzers (e.g., crustaceans, gastropods, amphipods, copepods) that consume primarily epiphytic algae and rarely consume eelgrass directly (Valentine & Duffy, 2006). Mesograzers are consumed by many small and juvenile fish that dwell in seagrass meadows that also feed on algae and detritus (Valentine & Duffy, 2006). In Canada, fish species that live in eelgrass meadows all year long include sculpins and gunnels (Robinson et al., 2011; Iacarella et al., 2018), whereas salmon and cod are fish species that use eelgrass during parts of their life cycle (Gorman et al., 2009; Kennedy et al., 2018).

Temperate eelgrass is an important habitat and food source for many migratory waterfowl species. Some species such as the great blue heron (*Ardea Herodias*) will forage for small fish or invertebrates in eelgrass meadows (Huang et al., 2015). Other species such as Canada Goose (*Branta canadensis*), Atlantic Brant (*Branta bernicla hrota*), Black Brant (*Branta bernicla nigricans*) and dabbling ducks (e.g. *Anas americana*) use eelgrass as a food source (Ganter, 2000; Kollars et al., 2017). Birds that consume seagrass rely on the physical maceration of the leaves in their gizzards to make accessible the nutrients and sugars in the cells for digestion (Thayer et al., 1984).

Waterfowl species that rely on eelgrass as a food source will closely track eelgrass distribution and abundance, resulting in waterfowl-eelgrass dependent species and eelgrass to covary in space and time (Kollars et al., 2017). Atlantic Brant heavily relies on eelgrass during

migration, and the importance of eelgrass to this species was first observed in the 1930s when a large-scale eelgrass die-off along the Atlantic coast coincided with a drastic decline of the Atlantic Brant (Cottam et al., 1944; Ganter, 2000). A decline of Canada Geese and Goldeneyes (*Bucephala clangula*) in a coastal lagoon in Nova Scotia, Canada, in 2000 was attributed to a decline in eelgrass (Seymour et al., 2002). Similarly, a decline of the Pacific Brant at their overwintering bay in Mexico in 1998 was also attributed to an eelgrass decline (Sedinger et al., 2006).



Figure 2.2 Example of a species assemblage found within temperate eelgrass meadows, including assemblages found in the below and above ground eelgrass biomass (figure from Murphy et al., 2021).

2.3 Anthropogenic and natural threats to seagrasses

Many eelgrass habitats in temperate zones are near human settlements, making them vulnerable to coastal development that impacts water quality (Orth et al., 2006; Waycott et al., 2009; Murphy et al., 2019). Agriculture runoff, industrial development, urban centers, septic

systems, and aquaculture activities near coastlines can impact water quality by increasing the organic nutrient loading in coastal waters. Increase nutrient loading in the water column can stimulate the growth of competitive algae, decrease light availability for eelgrass, and consequently lower eelgrass growth and survival (Coll et al., 2011; Schmidt et al., 2012; Schmidt et al., 2017; Coffin et al., 2018; van den Heuvel et al., 2019). Approximately 64% of eelgrass meadows in the Maritime Provinces are currently threatened by anthropogenic nitrogen loading (Murphy et al., 2019).

Invasive species represent another threat to eelgrass habitats on the Pacific and Atlantic coasts (Williams, 2007). Invertebrates such as cnidarians (sea anemones), ascidians (tunicates), mollusks, polychaetes (ragworms, lugworms), and crustaceans make up most of the invasive species in eelgrass habitats in Canada (Williams, 2007; Carmen & Grunden, 2010). Fouling by colonial tunicates, such as the violet tunicate (*Botrylloides violaceus*), can decrease eelgrass growth by reducing light reaching the plant and by breaking leaves and shoots (Wong et al., 2021). The European green crab (*Carcinus maenas*) is a widespread invasive non-native species that can reduce eelgrass biomass by burrowing for shelter or foraging for food in eelgrass meadows (Howard et al., 2019), resulting in sudden massive eelgrass declines (Garbary et al., 2014).

Rising sea temperatures and sea level associated with climate change are projected to impact marine and coastal ecosystems, particularly seagrass habitats (Short & Neckles, 1999). High summer temperatures can directly impact seagrass by causing important die-offs (Carr et al., 2010) and indirectly impact seagrass by accelerating algae proliferation (Short & Neckles, 1999) or triggering eelgrass wasting disease outbreaks caused by a marine slime-mold-like protist (*Labyrinthula zosterae*) (Muehlstein et al., 1991; Sullivan et al., 2013; Dawkins et al.,

2018). Changes in precipitation patterns and timing of snow and ice melts are expected to reduce salinity levels, which could reduce eelgrass density and reproduction (Pan et al., 2011; Salo & Pedersen, 2014; Xu et al., 2016). Increase in storms frequency and intensity due to climate change may increase nearshore turbidity and, as a result, temporally reduce light availability to seagrasses (Short & Neckles, 1999).

River and catchment modifications for hydroelectric and industrial development represent another threat to seagrass but have received less attention than the previously described threats. Typically, hydroelectric development requires diverting rivers to create vast water reservoirs from which water is released into downstream rivers to generate electricity. Most of Canada's hydroelectric megaprojects are in sub-arctic regions, such as the La Grande River complex in Northern Québec and the Churchill River power project in Northern Manitoba. North-temperate rivers in their natural state have significant floods in the spring due to snowmelts, followed by decreased freshwater discharges in the summer and winter (Rosenberg et al., 1997). Rivers downstream of reservoirs, on the other hand, have an inversed water flow regime, with increased water flows occurring during the winter to accommodate high energy demands in southern regions. Flow alterations related to hydroelectric development have affected the physicochemical environments of coastal lagoons and estuaries (Rosenberg et al., 1997; Bernard et al., 2005), wildlife (Foster & Rahs, 1985; Zhong & Power, 1996; Mahoney & Schaefer, 2002), and traditional subsistence fishing and hunting of northern Indigenous communities (Berkes, 1981; Berkes, 1982).

2.4 Seagrass monitoring and management

With increasing anthropogenic pressure on coastal zones, the need to monitor and better understand seagrass habitats has taken on greater significance. Monitoring seagrass distribution

is essential to assess the direction of change and, if declining, investigate possible drivers of these changes (Moore & Short, 2006). Methods for monitoring range from coarse-grain assessments such as presence/absence observations or remotely sensed meadow extent estimates to fine-grain assessments such as the percent seafloor covered by seagrass (cover), above ground biomass weight per m², number of shoots per m² (density), and chemical constituents (i.e. isotopic signals for C, N, and S) (Neckles et al., 2012; Marbà et al., 2013). Most monitoring programs rely on shoot density, cover, and above ground biomass to assess change (Duarte et al., 2006; Short et al., 2006b). Eelgrass monitoring is generally conducted during the growing season or when shoots have attained their maximum annual biomass. Deep-water seagrass is primarily regulated by light, making it a stronger indication of changes in water clarity than shallow-water seagrass, which is more vulnerable to physical disturbances, winds, and wave movement, as well as ice scouring (Lalumière et al., 1994; Krause-Jensen et al., 2004).

With the growing availability of freely available remotely sensing data and open-source processing tools (e.g. Google Earth Engine), seagrass maps generated from remotely sensed data are increasingly being used to research and monitor changes in seagrasses (Hossain et al., 2015). Remote sensing is defined as any measurement made from an object without physical contact and includes sensors in airplanes, drones, satellites, and visual observations from aircraft and boats (Phinn et al., 2018). Remote sensing data can be used to measure the extent and percent cover of seagrass meadows (Phinn et al., 2018). Remote sensed data with high spatial resolution can be used to assess the size and shape of meadows in highly fragmented seagrass landscapes, while high spectral resolution imagery can be used to detect multiple seagrass species occurring within the same regions (Hossain et al., 2015). However, because seagrasses are immersed in water, the concentrations of suspended material and chlorophyll-a in the water column can

reduce seagrass detection, thereby decreasing mapping accuracy (Blakey et al., 2015; Hossain et al., 2015).

Although eelgrass is recognized as an ecologically significant species (DFO, 2009a) and is protected from harmful disturbances (DFO, 2012), there is no nationwide standardized eelgrass monitoring program in Canada (Murphy et al., 2021). Eelgrass habitats are however being included in future marine protected areas (DFO, 2007; DFO, 2009a). Given how coastal conditions and anthropogenic factors differ across coastal landscapes, eelgrass monitoring programs in Canada should be adapted to local and regional conditions (Murphy et al., 2021). Also, given the scarcity of baseline data in many coastal regions, well-developed collaborative partnerships between scientists, First Nations, local stakeholders, and non-profit environmental organizations could facilitate *i*) identifying potential drivers of change, *ii*) understanding seagrass past and present status, and *iii*) co-developing locally relevant coastal management and conservation strategies (Berkes et al., 2000; Loch et al., 2021; Murphy et al., 2021).

2.5 Coastal Partner Researched: Coastal Habitat Comprehensive Research Program

The Coastal Habitat Comprehensive Research Program (CHCRP) is a large-scale community-partnered research project that was initiated in 2017 in response to concerns by Coastal Cree Land Users over the current state of eelgrass along the eastern coast of James Bay (Eeyou Istchee). The CHCRP aims to bring together Cree Traditional Knowledge and scientific research to gain a detailed and holistic understanding of the coastal ecology of Eeyou Istchee (see **Figure 2.3**) and the study presented in Chapter 5 is part of this project. The research is overseen by a Steering Committee that is comprised of representatives from four Cree coastal communities (Waskaganish, Eastmain, Wemindji, and Chisasibi), regional Cree organizations, Hydro-Québec, and the Canadian Wildlife Service, among other organizations. Cree coastal communities along the eastern coast of James Bay have a detailed and indepth understanding of coastal ecosystems and actively monitor coastal resources through land use (Berkes et al., 1995; Berkes, 2009; Royer and Herrmann, 2013). Until the mid 1990s, the eelgrass meadows in eastern James Bay were among the most extensive eelgrass meadows in North America (Lalumière et al., 1994) and considered as critical habitats for coastal wildlife (Curtis, 1974-1975). Rodrique Pachano, former Chief of the Cree Nation of Chisasibi, has described the link between coastal ecosystems and the Cree culture as follows:

"From different perspectives—public health, nutrition, and our desire to protect our own culture and traditions—we consider the coastal ecosystem to be something that will play a key role in our survival as communities and as a people...These beds [eelgrass, Zostera marina] are a key element in a coastal ecosystem. They serve as feeding grounds and nurseries for coastal fish species— whitefish, cisco, and trout—and shellfish. And they are grazed by brant, Canada geese, and ducks." (Rodrique Pachano, SCFOE, 2008).

Eastern James Bay, however, like many northern regions in Canada, is changing at a fast pace. During the last few decades, coastal Cree Land Users have seen changes in weather patterns and the distribution and abundance of flora and animals (Dickey, 2015). One significant environmental change observed and recorded along the east coast of James Bay is the decline in the extent of eelgrass in the late 1990s (Dickey, 2015). Concomitant with this decline, coastal Cree hunters have noted a dramatic decrease in Canada Geese and Atlantic Brant abundance along the coast (Short, 2008; Dickey, 2015). Drastic changes in environments can have a
substantial impact on access to the land and resources, impacting livelihoods, culture, and food security (Whiteman, 2004; Berkes, 2009). The Cree Land Users have described these changes as follows:

"The community has seen sharp declines in waterfowl numbers along the coast in recent years and a corresponding decline in hunting success. There are also concerns about fish stocks and the rest of the food chain along the coast because of the changed flows and the loss of the eelgrass beds and the fish habitat they provide" (Rodrique Pachano, SCFOE, 2008).

"I think since Hydro-Québec made the reservoirs, the geese changed their patterns. If you look at the maps all the way to Eastmain River, there is a lot of water, just like James Bay. That's why I think that's one thing that they follow. And along the Bay, there used to be grass... We call it in Cree sishkabash [eelgrass, Zostera marina]. Over 10 years now, there used to be lot of sishkabash ... there is just a little bit of that now...." (Cree Land User from Wemindji, Peloquin & Berkes, 2009).

"This year and last year, we had an early spring, early open water. The ice went really fast, so there is less geese. Because the snow is really going fast, and there is hardly any water in the swampy areas, the geese don't land and (they) don't stick around." (Cree Land User from Wemindji, Peloquin & Berkes, 2009).

The CHCRP regards the knowledge exchange between Cree Land Users and researchers as pivotal for assessing the current state of eelgrass and how it compares to the past. The findings of this study are expected to improve research collaboration by mutually enriching knowledge exchange between local knowledge experts, the research team, and other stakeholders. Furthermore, the findings of the CHCRP will contribute to a better understanding of how the environment, food systems, and traditional land use are connected and change, therefore enhancing and improving Cree involvement in future research and monitoring of their coastal ecosystems.



Figure 2.3 Outreach pamphlet of the Coastal Habitat Comprehensive Research Program describing the importance of eelgrass to the coastal ecosystems of James Bay. Content and text by M.L. Leblanc and graphics by ALGN Illustration.

Connecting Statement

In Chapter 2, I provided a brief overview of the existing literature on the significance of eelgrass *Zostera marina* to coastal ecosystems, the major threats to this species, and the many methods used to monitor eelgrass. In Chapter 3, I evaluated a novel cost-efficient approach for satellite imagery time-series to assess changes of distribution and abundance of eelgrass over the last three decades in a coastal estuary in northeastern New Brunswick.

Chapter 3: Using Landsat time-series to monitor and inform seagrass dynamics: a case study in the Tabusintac Estuary, New Brunswick, Canada.

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3.0 Abstract

The recent worldwide loss of seagrasses, which are critical components of coastal ecosystems, has ignited an effort among scientists and resource managers to develop effective monitoring tools. Although Landsat time-series is considered one of the most cost-effective options for monitoring landscapes, its application of monitoring seagrasses remains scarce due to many factors including difficulties obtaining accurate ground-truth data and perceived limitations in mapping nearshore marine ecosystems. Here, we report on the use of archived Landsat multispectral imagery and the automatic adaptive signature generalization (AASG) to evaluate eelgrass (Zostera marina) distribution and abundance between 1984 to 2017, in an estuary located in northeastern New Brunswick, Canada. The AASG algorithm, a novel cost-efficient approach for satellite imagery time-series analysis that requires limited ground truth data, was used to produce fourteen maps, four of which had accuracies ranging from 75% to 85%. The results indicated that eelgrass meadows near the barrier beach were highly dynamic, exhibiting high abundance fluctuations between years and conversion of dense eelgrass to medium-low eelgrass near the main coastline. This study demonstrates the feasibility of using the AASG algorithm to map seagrass and the advantages of including satellite time series in monitoring programs to investigate seagrass dynamics and long-term trends.

3.1 Introduction

Described as a foundation species, seagrasses are considered to be key primary producers in coastal ecosystems that create habitat for other species (Bell et al., 2001; Bruno et al., 2003; Boström et al., 2006; Micheli et al., 2008; Warren et al., 2010; Lilley & Unsworth, 2014), safeguard coastal food security (Nordlund et al., 2018; Unsworth et al., 2019b) and mitigate climate change by carbon sequestration (Fourgurean et al., 2012). Given their importance to coastal ecosystems, the recent and widespread decline of seagrasses around the world has initiated a global effort among scientists and resource managers to improve seagrass monitoring strategies (Duarte, 2002; Orth et al., 2006; Duffy et al., 2019). However, monitoring dynamic ecosystems such as seagrasses is challenging because changes can occur over small to large spatial scales, either abruptly or gradually, depending on the disturbance's origin, magnitude and duration (Vandermeulen et al., 2012; Unsworth et al., 2015, Murphy et al., 2019). In temperate regions, ice movement, high wave-energy events and waterfowl grazing can create year-to-year fluctuations of seagrass abundance (Fonseca et al., 1983; Robertson& Mann, 1984; Kollars et al., 2017). In contrast, anthropogenic stressors such as climate change, invasive species such as the green crab (*Carcinus maenas*), or coastal pollution generally affect seagrass ecosystems at much larger spatial and temporal scales (Garbary et al., 2014; O'Brien et al., 2018). Measurements that enable the disentangling of long-term trends from natural fluctuations underpins effective monitoring, but can only be achieved if monitoring is conducted across adequate spatial and temporal scales and resolutions (Kennedy et al., 2014). Significant changes operating at large scales (e.g. bay, estuary) may go undetected if monitoring is limited at the meadow scale, while low temporal resolution monitoring may lead to drawing incorrect inferences about how the ecosystem is changing (e.g. gradual, threshold response, cyclical).

Long-term monitoring, consisting of repeated measurements spanning at least ten years (Lindenmayer & Likens, 2010), provides highly valuable information, including generating baseline data (Fourqurean et al., 2012), evaluating ecosystem degradation or recovery (Kirkman & Kirkman, 2000), and assessing conservation efforts (Sherwood et al., 2016). However, many long-term seagrass monitoring programs restrict their monitoring activities to one or two sites surveyed at least once throughout the year. While useful for understanding biological processes, these types of assessments may not necessarily reflect changes that are occurring at a larger scale, where most management and conservation efforts are directed (Cardinale et al., 2012). Faced with ever-changing environmental conditions, there is a pressing need to invest time and effort to develop tools capable of assessing changes in seagrass ecosystems over large areas at low costs that are easy to implement (Neckles et al., 2012; Unsworth et al., 2019a).

Free archives of multispectral Landsat imagery with 30 m resolution is considered one of the most cost-effective options for monitoring ecosystem changes due to their accessibility, large area coverage, long archive period, and repeated observations (Pasquarella et al., 2016) and are one of the most widely used imagery products to map seagrasses (Hossain et al., 2015). Studies that have used Landsat TM, - ETM+ and -OLI imageries to map seagrass habitats within 3 to 5 classes using a pixel-based approach have done so with moderate to high success, with overall accuracies ranging from 46% to 87%, depending on water clarity, benthic spatial complexity and seagrass substrate type (Wabnitz et al., 2008; Pu et al., 2012; Blakey et al., 2015). But despite the recent progress in seagrass mapping using satellite imagery, the use of Landsat time-series to monitor seagrass ecosystems remains scarce due to many factors including difficulties obtaining accurate *in-situ* multi-date ground-truth data (Barrell et al., 2015), time-consuming processing (Dannenberg et al., 2016) and concerns over the potential accuracy of low-resolution imagery.

In an effort to overcome these challenges, a variety of mapping methods have been developed, including object-based classification (Lyons et al., 2013; Roelfsema et al., 2013, 2014) and the development of spectral signatures (Fyfe, 2003). Although these techniques are useful and practical, they generally require specialized equipment and software, as well as expert knowledge to conduct the mapping. Blakey et al. (2015) developed a cost-effective approach specifically designed for time-series, which consisted of creating pixel-based spectral classes from three recent Landsat images, which were then used to classify a series of older images. This generalized pixel-based classifier is simple in its application and practical, but spectral signatures transferability across images may be limited if inter-image variability persists even after atmospheric correction is applied (Gray & Song, 2013). The automatic adaptive signature generalization (AASG) algorithm is a novel approach to imagery time-series that requires few ground truth data and is adaptive to different atmospheric, radiometric and phenological characteristics between images, while maintaining semantic consistency in class definitions across time-series (Gray & Song, 2013; Dannenberg et al., 2016; Dannenberg et al., 2018). The AASG uses a simple single band-differencing procedure to identify stable sites (no-change) between two satellite images acquired at different dates. Class-specific signatures are extracted from stable locations and used to identify a new image, making this approach suitable for timeseries satellite image analysis. The AASG algorithm has been successfully combined with Landsat imagery to describe land cover change in many different landscapes including rural (Qiu et al., 2017), forest (Kim et al., 2014), and urban (Stow et al., 2014) areas, but its potential to assess how seagrass ecosystem change over time has yet to be tested.

Eelgrass (*Zostera marina* L.) is the most widely distributed seagrass species of the northern hemisphere and is the dominant species in Atlantic Canada (Murphy et al., 2019).

Eelgrass can form vast and continuous subtidal or intertidal meadows in shallow coastal estuaries, lagoons, and areas. In Atlantic Canada, eelgrass has been designated as an Ecologically Significant Species by the Department of Fisheries and Ocean (DFO) as eelgrass meadows support marine food webs, provide critical habitats to a wide variety of animals, and contribute to maintaining ecosystem function and structure (DFO, 2009a). While eelgrass can tolerate a broad range of environmental and oceanographic conditions, its ecological performance is optimized within specific salinity, surface light irradiance, and temperature ranges (Murphy et al. 2021). However, seagrass ecosystems have been deteriorating globally at an accelerated rate over the past few decades due to anthropogenic factors that impact water quality (Waycott et al., 2009). Although the information on eelgrass distribution in eastern Canada is scarce, important eelgrass declines have been reported in a few locations in the Maritime Provinces, with inter-annual declines ranging between 30% to 95% (Hanson, 2004; DFO, 2009a).

The overall aim of this study was to assess the potential of the AASG algorithm to generate eelgrass maps, which were then used to assess change in eelgrass coverage in the Tabusintac Estuary, located in northeastern New Brunswick, Canada. We chose the AASG algorithm because it is a low-cost, easy-to-implement approach to produce reliable reference data for the training and accuracy evaluation of seagrass distribution maps. The Tabusintac Estuary is an excellent candidate location to test the potential of the AASG algorithm using Landsat imagery, as it is relatively shallow and harbours vast eelgrass meadows (Forsey et al., 2020). First, we determined the eelgrass abundance and distribution with the 2017 image, which was then used as a reference image to assess the spatiotemporal dynamics of eelgrass between 1984 to 2017. We discuss the advantages of integrating a Landsat time-series in seagrass monitoring strategies and challenges of the AASG approach in seagrass mapping, as well as proposed

potential local factors that may account for the observed spatiotemporal trends of eelgrass in Tabusintac.

3.2 Methods

3.2.1 Study Area

The Tabusintac Estuary (47°20'N, 64°56'W) is located on the east coast of New Brunswick, Canada (Figure 3.1). The estuary covers an area of approximately 4900 ha and is protected from the Gulf of St. Lawrence's wave action by a 15 km long natural barrier beach separated by channels and gullies (Figure 3.1). Water circulating outside the estuary along the barrier beach transports sand southward causing channels to close and re-open elsewhere over time (CBCL, 2014). The water depth within the estuary is a maximum of 2 to 3 m and the tides are mixed diurnal and semidiurnal in character (Leys and Lehmann, 2016). The estuary harbours large, continuous perennial eelgrass meadows (Friolet et al., 2008; Vandermeulen, 2014; Webster et al., 2016; Forsey et al., 2020). The eelgrass meadows in Tabusintac are subtidal. The Tabusintac River is the main source of fresh water in the estuary. The coastal development near the estuary is low and the surrounding habitats consist mostly of estuarine flats, shoreline black spruce (*Picea mariana*), and jack pine (*Pinus banksiana*) forests (Friolet et al., 2008). Because of its importance to waterfowl and shorebirds, the Tabusintac Estuary is a Wetland of International Importance (RAMSAR, 2017) and an Important Bird Area (IBA Canada, 2017). New navigation channels were dredged between June 29th and July 16th, 2014, to improve boating safety and access (Leys & Lehmann, 2016). After dredging, Secchi disc measurements in the study area showed that the water clarity was high, as the disc was visible throughout the entire water

column (Stantec, 2014). Surveys and studies from the past two decades indicated a low level of eutrophication in the Tabusintac River and estuary (Friolet et al., 2008; Schmidt et al., 2012; McIver et al., 2019). Commercial activities in the estuary consist mostly of small-scale fisheries of American eel (*Anguilla rostrata*), oyster (*Crassostrea virginica*) aquaculture and peat moss harvesting near the coastline (Friolet et al., 2008). The estuary borders a few rural communities including Brantville and Tabusintac. The nearest urban centre is Tracadie-Sheila (population of 16,000; Canadian Census, 2011), located 20 km north of Tabusintac.



Figure 3.1 A) Map showing the location of the study area on RGB true composite of the Landsat 2017 image, Tabusintac Estuary, in northeastern New Brunswick (NB), Canada, B) underwater photo of eelgrass in the Tabusintac Estuary, and schematic illustration of eelgrass showing the above- and belowground biomass.

3.2.2 Data

3.2.2.1 Field data

Field data for image training and validation were obtained from various projects with similar data collection methods. Field surveys were conducted in the late summer when eelgrass has reached its maximum biomass (Olesen & Sand-Jensen, 1994). All field survey points across years consisted of georeferenced underwater images acquired using a downward-looking underwater camera or video, from which eelgrass percentage coverage was estimated. The eelgrass percentage cover of ground truth points within Landsat pixels was averaged.

In 2017 and 2016, field data were collected along transects perpendicular to the shore, between August 1 and September 30. Eighteen transects were sampled in 2017, while 10 transects were surveyed in 2016. In both years, at every 200 m along the transects, percent cover of eelgrass was estimated in five to six 0.50 m^2 quadrats that were haphazardly located distanced 5 m apart. On September 24, 2014, field data were collected on haphazardly selected sampling points within a hexagonal grid and eelgrass percent cover at each site was estimated in three to four randomly located 0.50 m² quadrats (Stantec, 2014). Due to the small number of ground-truth points with low and moderate cover in the 2014 data set, field observations were complemented with data from an eelgrass classification generated from high-resolution imagery (see Wabnitz et al., 2008). In this instance, we identified locations with eelgrass cover < 60% based on an eelgrass distribution map generated from a 2-m resolution multispectral satellite image (WorldView-2, WV2) acquired on September 24, 2014, and classified by the consulting company Stantec (Stantec, 2014). Image processing and atmospheric correction of the image were performed in TerrSet (IDRISI), and a supervised classification was conducted using a Maximum Likelihood classifier and field data collected in 2014, with an overall classification

accuracy of 70%. In 2008, field data were collected along 16 transects perpendicular to the shore using a differential GPS positioned Towfish holding side-scan sonar and a downward-looking video camera (Vandermeulen, 2014). Eelgrass percent cover was estimated at intervals every 10 seconds.

Ancillary data were used to generate ground truth data points for sand flats that were near the barrier beach because this area is not accessible by boat due to its shallowness. To generate sand flat ground truth points - for the 2017 and 2016 images, we used a WV2 image acquired July 12, 2016 (ESRI base map, 2016 WV2 Imagery from Digital Globe), - for the 2014 image, it was a WV2 image acquired September 24, 2014 (Stantec, 2014); and - for the 2008 image, it was an eelgrass presence map produced in 2008 by aerial photo interpretation (Mahoney & Hanson, 2008) and Landsat 5 TM 2008 visual interpretation.

3.2.2.1 Landsat Imagery

We searched the U.S. Geological Survey (USGS) archive for Landsat 5-Thematic Mapper (TM), Landsat 7- Enhanced Thematic Mapper Plus (ETM+), and Landsat 8-Operational Land Imager (OLI) Level-1 images captured between July and September (peak eelgrass biomass, Olesen & Sand-Jensen, 1994) to allow a maximum opportunity to obtain cloud and haze-free images between 1984 to 2017. This time window typically yielded 4-6 images per year, given the 16-day acquisition schedule. The prevalence of cloud and haze along this coastal region caused 92% of images to be excluded due to low visibility. Thus, despite the assessment of multiple images per year, adequate quality images were available for only 14 out of 33 years (**Table 3.1**). However, years with available images were well-distributed through the time series, such that this did not create an over-representation of specific phases within the time series. The two Landsat 7 ETM+ SLC-off images had minimal gaps over the study area. The 2016 image had a small cloud in the northern portion of the study area, while all other images were cloud-

free.

Landsat sensor	Image ID	Date	Cloud cover [#] (%)	Path/row	Sun elevation (°)	Sun azimuth (°)	Tide level [±]	Reference data
	LC80090272017256LGN00	2017/09/13	6.94	9/27	43.78	156.43	mid	Yes
	LC80090272016206LGN00	2016/07/24	8.02	9/27	58.02	143.55	mid	Yes
8-OLI	LC80090272015235LGN00	2015/08/23	23.22	9/27	50.70	150.39	high	No
	LC801002272014271LLG01	2014/09/28	0.00	10/27	38.57	160.00	high	Yes
	LC80090272013213LGN00	2013/09/18	0.26	9/27	56.73	145.62	low	No
7 ETM	LE70090272010261ASN00	2010/09/18	0.00	9/27	41.59	155.01	low	No
/-E.I.WI	LE70090272008240EDC00	2008/08/27	0.00	9/27	48.26	147.64	low	Yes
	LT50090272005239GNC01	2005/08/27	0.00	9/27	48.35	147.44	mid	No
	LT50090271997233PAC00	1997/08/21	5.17	9/27	48.45	140.07	high	No
	LT50100271996238PAC00	1996/08/25	1.00	10/27	45.70	136.76	low	No
5-TM	LT50090271992220PAC00	1992/08/07	0.00	9/27	50.81	133.01	high	No
	LT50090271990230PAC00	1990/08/18	13.91	9/27	47.99	135.26	low	No
	LT50090271987190PAC00	1987/07/09	19.89	9/27	56.38	128.44	mid	No
	LT500900271984262PAC04	1984/09/18	0.00	9/27	39.67	148.09	low	No

Table 3.1 Characteristics of the Landsat images used for this study.

[#] Percentage cloud cover for the entire image

[±] Tide level based on the closest location with historical tide data, Lower Escuminac (47°5'0"N, 64°53'0"W) (Fisheries and Oceans Canada, 2018)

3.2.3 Pre-classification processing

All pre-classification processing of the Landsat images was completed using ENVI 5.1

image processing software and included three steps, which were (1) radiometric calibration and

atmospheric correction, (2) masking land, navigation channels, cloud and gaps, and (3)

correcting the water column effect (Lyzenga, 1978, 1981) (Figure 3.2).



Figure 3.2 Flowchart for eelgrass classification of Landsat imagery using the automatic adaptive signature generalization (AASG) algorithm.

Prior to conducting an atmospheric correction, a radiometric calibration in ENVI 5.1 image processing software was used to convert the digital number of the selected images into spectral radiance using ENVI's built-in calibration coefficients for each Landsat sensor. The calibrated images were then converted to at-ground reflectance using the Fast Line-of-Sight Atmospheric Analysis of Spectral Hypercubes (ENVI FLAASH Module, 2009), an atmospheric correction module implemented in ENVI. The FLAASH module incorporates the MODTRAN 4 radiation transfer code for all MODTRAN atmosphere and aerosol types. The atmosphere model was mid-latitude summer using a maritime aerosol model.

Land and navigation channel masking. The land area surrounding the Tabusintac Estuary, navigational channels, cloud, and Landsat ETM+ gaps were masked out in order to limit the analysis to the shallow water between the main coast and the barrier beach and to ensure the time-series analysis was conducted over the same surface area. The land masking process was conducted using the near-infrared (NIR) band of the 2017 image, which is known to provide an accurate delineation between land and water (Phinn et al., 2005; Roelfsema et al., 2013). The channel mask was extracted from the topographic-bathymetric map (Webster et al., 2014; Collins et al., 2016).

Water Column Correction. Light attenuation, a process by which light intensity decreases as water depth increases, can have a profound impact on the mapping accuracy of seagrass meadows. The attenuation in the water column varies according to the wavelength of electromagnetic radiation, with infra-red light attenuating very rapidly compared to the shorter wavelengths in the green or blue portions of the visible spectrum. Therefore, at a depth of 1 m, the spectral signature of seagrass could be different from that of 4 m. The effect of the water column should be reduced prior to classification because variable water depths can cause considerable uncertainty between class spectral signatures.

Lyzenga's (1981) water column corrections method is the most used to correct for variable water despth due to its ease of use and efficiency (Hossain et al., 2015). Application of this standard correction factor in time-series, however, assumes relative stability of the water clarity over time. Longer-term sampling, showing constancy in the bay's water clarity from 1990 to recent (Friolet et al., 2008; Schmidt et al., 2012; Stantec, 2014; McIver et al., 2019), indicates that the Lyzenga's (1981) water column corrections are suitable for the Tabusintac Estuary. While it is possible day-to-day or within-season variation in organic matter, phytoplankton, or inorganic matter to add noise to our classification, it should not introduce directional change across the time series.

Lyzenga's (1981) water column correction method consists of creating three different Depth Invariant Index bands (DII) using the visible bands. The first step entailed linearizing the

relationship between reflectance values and depth by applying a natural logarithm (ln) on the visible bands. The second step required calculating the ratio of attenuation coefficients for three band pairs (green-blue bands, blue-red bands, and green-red bands). This was done by selecting pixels of the same substrate at varying depths, plotting linearized pixel (*ln*) values of Band_i and Band_j, and computing the slope that, according to Lyzenga (1981), represents the ratio of attenuation coefficients between Bands_{ij}. The ratio of attenuation (k_i/k_j) was then used to minimize the water column effect from paired bands_{ij} using the following equation:

$Depth-Invariant \ Index \ Band_{ij} = ln(Band_i) - [(k_i/k_j) \ ln(Band_j)]$ (1)

which resulted in a Depth-Invariant Index band for each pair of bands. For this study, sandy mud bottom was selected at various depths (0.5 m to 3 m) using the topographic-bathymetric map (Webster et al., 2014; Collins et al., 2016) and field data from the corresponding year, if available, and visual interpretation of the image of the corresponding year. Three Depth-Invariant Index bands were computed for each image, thereby reducing the influence of different tidal conditions between the images. DII bands were used in the AASG processing and the classification.

3.2.4 Image classification

We used the automatic adaptive signature generalization (AASG) algorithm to generate class-specific signatures adapted to 13 images. To generate training sites for 13 images, the AASG method requires three data inputs, a reference image (I_R), a reference map generated from the reference image, and a target image (I_T - image to be classified). The first step consists in locating stable sites between I_R and I_T. Stable sites, defined as core areas that remain unchanged between images acquired at different dates, were located using a simple band difference histogram:

$$\Delta I_n = I_R - I_T \tag{2}$$

where I_T was one of the DII bands from a target image, while I_R is a DII band from the 2017 reference image. Stable sites should be found within the interval

$$u_{\Delta I} \pm C_K \times \sigma_{\Delta I} \tag{3}$$

where $\mu_{\Delta I}$ is the mean, $\sigma_{\Delta I}$ is the standard deviation of ΔI , and C_K is a class-specific threshold parameter for each class *k*. C_K corresponds to the number of standard deviations from the mean of the image difference histogram considered as stable (Dannenberg et al., 2016). Stable sites were then subjected to a class-specific spatial erode filter to reduce errors due to image misregistration. The final step entailed generating training data for the I_T by extracting classspecific signatures from the I_T and coupling these with their respective class labels via a reference map. See Gray & Song (2013) and Dannenberg et al. (2016) for the full detailed methodology of the AASG algorithm.

3.2.5 AASG Reference map

In this study, we used the 2017 image to generate the reference map. Considering the disparity in the spatial resolution between the Landsat pixels (30 m x 30 m) and ground truth data (0.5 x 0.5 m), single pixels were used for training units instead of the neighbourhood average (Blakey et al., 2015). The classification scheme used in this study is similar to what has been used in other studies using Landsat to generate seagrass distribution maps (e.g. Wabnitz et al., 2008; Pu et al., 2012; Blakey et al., 2015). Four cover classes were defined for classification: i dense and continuous eelgrass ($\geq 60\%$ eelgrass cover), ii medium and discontinuous eelgrass

(between 11% and 59% eelgrass cover), *iii*) low eelgrass (patchy eelgrass cover, between $\geq 1\%$ to $\leq 10\%$ eelgrass cover) and *iv*) sand flats. The spectral separability of the different cover classes was examined prior to the mapping being conducted using the Jeffries–Matusita (JM) distance (Richards, 1999) with the 2017 training points. The JM distance creates an index between 0 to 2 for given pairs of classes, with values leaning towards 2 indicating a good separability between classes. Five pairs (dense/ low eelgrass cover, dense eelgrass cover/ sand, medium/ low eelgrass cover, medium eelgrass cover/ sand and low eelgrass cover/ sand) had J-M distances higher then 1.9, and one pair of classes (dense/ medium eelgrass cover) had a J-M distance of 1.6, indicating a good separability between all classes (Table 3.2).

Table 3.2 Jeffries-Matusita (JM) distances for all pair-wise class comparisons for the 2017 reference image.

Class	Medium	Low	Sand
Dense	1.58	1.97	2.00
Medium		1.91	2.00
Low			1.97

The 2017 reference map was generated by applying ENVI's Maximum Likelihood classifier to the three depth-invariant bands of the 2017 reference image, with no probability threshold and a data scale factor of 1, using 50% of the 2017 ground truth data (**Table 3.3**). The Maximum Likelihood classifier is a supervised classification method based on the Bayes theorem, that uses training data to estimate a class mean vector and covariance matrix which serve as input to a discriminant function to assign pixels to the class with the highest likelihood (Ahmad & Quegan, 2012).

2.2.6 AASG algorithm

Once the 2017 reference map was generated, it was used to identify stable sites through image differentiation using a single depth-invariant band between the I_{R-2017} and I_{Tn}. This process was repeated for 13 target images. Based on prior testing, we used the green-blue depth invariant band for the AASG analysis for images between 2016 and 2005 and the green-red depth invariant band for images between 1997 to 1984. Changes in the depth-invariant band could be due to different radiometric resolutions between sensors or, perhaps, to changes in the water chemistry (e.g. salinity, pH, dissolved organic carbon – see Hirtle & Rencz, 2003; Schroeter & Gläber, 2011; Lagomasino et al., 2014). Once stable sites were located, class spectral signatures were - extracted from the target image, -labeled to their respective classes using the reference map and - used as input into a Maximum Likelihood classifier, as well as the three depth-invariant bands, to classify the target image. Class-specific signature extraction and target image classification were conducted in the software R, v.3.3.1 (R Core Team, 2017) using the AASG, raster, and rgdal packages (Dannenberg et al., 2017; Bivand et al., 2018; Hijmans, 2020).

3.2.7 Accuracy assessments

Fifty percent of the 2017 ground-truth points were randomly selected and reserved as validation points for the reference map, while the entire ground truth datasets of 2016, 2014, and 2008 were used as validation points only for classification generated by the AASG algorithm (**Table 3.3**). The 2017, 2016, 2014, and 2008 classified images and corresponding validation points were compiled into standard confusion matrices and used to calculate overall accuracies, User's accuracies, Producer's accuracies, and Kappa coefficients (Congalton, 1991).

Class	Training	Validation					
	2017	2017	2016	2014	2008		
Dense (≥60%)	45	41	32	59	84		
Medium (between 11% and 59%)	25	30	15	60	16		
Low between ($\geq 1\%$ to $\leq 10\%$)	20	20	19	20	35		
Sand	20	21	20	19	17		

Table 3.3 Number of pixels used for training and validation sites per class and per year.

3.2.8 *Time-series analyses*

The percentage of the surface area (hectare) was calculated for each class type and a standard linear regression was used to estimate the approximate trend in surface area over time with a significance level set at $\alpha = 0.05$. To assess spatial trends and variability in eelgrass cover, we opted for a flexible approach to time-series analysis that would allow us to adequately quantify eelgrass change and describe the type of change that was similarly used by Lyons et al. (2013). We converted each eelgrass cover vector data into a raster format at a spatial resolution of 30 m, assigned each pixel an ordinal scale value reflecting eelgrass cover (e.g. 1=sand, 2=low eelgrass, 3=medium eelgrass, and 4= dense eelgrass), and created a raster stack comprised of 14 rasters. This allowed us to calculate, for each pixel, a coefficient of variation (CV = SD / \overline{X}) to estimate eelgrass cover variation and a linear regression slope to estimate the direction of change. High CV in the class variability summary map indicated high eelgrass cover variability over time. Negative slopes in the class trends summary map indicated an eelgrass cover loss, positive slopes indicated eelgrass cover gain over time, while near-zero slopes indicated constancy or bidirectional change (gain followed by loss, or loss followed by gain). Statistical analysis was conducted in the software R, v.3.3.1 (R Core Team, 2017) using the raster package (Hijmans, 2020). The maps were created using ArcGIS 10.5.1 software (Esri, 2016) projected in UTM (Universal Transverse Mercator) Zone 19 or 20 using the WGS 84 (1984

World Geodetic System) datum and contain information licensed under the GeoNB (2006) Open Data License.

3.3 Results

3.3.1 Accuracy of eelgrass percentage cover maps

When compared to the GPS validation sites, the overall accuracy of the 2017 reference classified image was 75% (Table 3.4, Figure 3.3), while those of 2016, 2014, and 2008 maps generated using the AASG algorithm were 76.7%, 81.76%, and 76.31%, respectively (Table 3.5, Figure 3.4). Dense eelgrass cover and sand classes were mapped consistently in all years, with a User's accuracy for both classes above 80% in 2017, 2016, 2014, and 2008 (Tables 3.4 and 3.5). The User's accuracy of the classes of medium and low eelgrass cover varied between years and averaged between 54% for medium and 68% for low. The Producer's accuracies varied across years for all eelgrass density classes, except sand, which had a value of 100% across all years (Tables 3.4 and 3.5). For dense and low eelgrass cover classes, Producer's accuracies averaged 77% and 82%, respectively, and both were 90% in 2014. For the medium eelgrass cover class, Producer's accuracies averaged 59% across all years, with a maximum of 86% in 2016 and a minimum of 23%, in 2008. Due to the high confusion between the medium and low classes in the 2008 classification, both classes were merged into one 'medium-low' class for all the images. The subsequent analyses were thus conducted on three different cover types, which were dense eelgrass ($\geq 60\%$, continuous eelgrass meadows), medium-low eelgrass cover (between $\geq 1\%$ to \leq 59%, discontinuous eelgrass meadows), and sand.

Table 3.4 Confusion matrix and associated accuracies when comparing the GPS validation points with the classified image the 2017 reference classified image. The bold numbers represent the number of correctly classified pixels in each class.

		Reference							
	Class	Dense	Medium	Low	Sand	Total	User's	Error of	
						Total	accuracy (%)	commission (%)	
Classified	Dense	27	5	0	0	32	84.38	15.63	
	Medium	14	23	7	0	44	52.27	47.73	
	Low	0	2	13	0	15	86.67	13.33	
	Sand	0	0	0	21	21	100.00	0.00	
	Total	41	30	20	21	112			
	Producer's	65.95	76.67	65.00	100.00	Ove	rall accuracy	75.00	
	accuracy (%)	05.85	/0.0/	05.00	100.00	(%)		73.00	
	Error of omission (%)	34.15	23.33	35.00	0.00	Kapı	oa coefficient	0.66	



Figure 3.3 A) RGB true composite of the Landsat 2017 reference image with an overlay of the ground truth data; B) 2017 eelgrass reference classification with an overlay of the validation points.

Table 3.5 Confusion matrix and associated accuracies when comparing the GPS validation points with the AASG classified image of A) 2016, B) 2014, and C) 2008. The bold numbers represent the number of correctly classified pixels in each class.

		Reference Class									
A) 2016	Class	Dense	Medium	lium Low		Sand	Total	ac	User's ccuracy (%)	Error of commission (%)	
	Dense	20	1	0		0	21		95.24	4.76	
	Medium	11	13	5		0	29		44.83	55.17	
_	Low	1	1	13		0	15		86.67	13.33	
fied	Sand	0	0	1		20	21		95.24	4.76	
Classi	Total	32	15	19		20	86				
	Producer's accuracy (%)	62.50	86.67	68.42	10	00.00 Overa		all accuracy (%)		76.74	
	Error of omission (%)	37.50	13.33	31.58	(0.00	Kap	pa co	pefficient	0.69	
			Reference Class								
B) 2014	Class	Dense	Medium	Low		Sand	То	tal	User's accuracy (%)	Error of commission (%)	
	Dense	52	12	1		0	6	5	80.00	20.00	
	Medium	7	41	1		0	4	9	83.67	16.33	
	Low	1	7	18		0	2	6	69.23	30.77	
ssified	Sand	0	0	0		19	1	9	100.00	0.00	
	Total	60	60	20		19	15	59			
Cla	Producer's accuracy (%)	86.67	68.33	90.00	00.00) Ove	Overall accuracy (%)		81.76	
	Error of omission (%)	13.33	31.67	10.00		0.00	Ka	appa	coefficient	0.73	
	Class	Reference Class									
C) 2008		Dense	Medium	Low		Sand	To	Total User's (%)		Error of commission (%)	
	Dense	75	8	1		0	84	4	89.29	10.71	
	Medium	9	6	1		0	10	5	37.50	62.50	
Classified	Low	5	12	18		0	3:	5	51.43	48.57	
	Sand	0	0	0		17	1'	7	100.00	0.00	
	Total	89	26	20		17	15	2			
	Producer's accuracy (%)	84.27	23.08	90.00		100.00) Ove	Overall accuracy (%)		76.32	
	Error of omission (%)	15.73	76.92	10.00		0.00	Ka	Kappa coefficient		0.61	



Figure 3.4 Classifications produced using the AASG algorithm and corresponding validation points for A) 2016, B) 2014, and C) 2008.

3.3.2 Temporal and spatial trends

Medium-low eelgrass cover showed a significant increasing trend (Y = -21667 + 11.32(x), adj. $R^2 = 0.34$, P = 0.01), whereas sand cover showed a significant decreasing trend from 1984 to 2017 (Y = 7072.90 -3.39(x), adj. $R^2 = 0.33$, P = 0.02) (Figure 3.5). The total eelgrass cover and dense eelgrass cover did not show any significant temporal trends (adj. $R^2 = 0.17$, P = 0.08 for total eelgrass cover; adj. $R^2 = 0.17$, P = 0.08 for dense eelgrass). However,

total eelgrass cover showed a slight increasing trend, while dense eelgrass cover showed a slight decreasing trend.



Figure 3.5 Class cover surface areas (ha) from 1984 to 2017. Standard linear regression lines indicate the approximate trend in areas of cover classes over time. Breaks on the *x*-axis indicate a temporal gap in the time series.

Eelgrass cover variability from 1984 to 2017 was highest in shallow waters near the barrier beach (Areas C1 and C2 in **Figure 3.6 A**), moderate near the main coastline (Area C3 in **Figure 3.6 A**), and low in deeper waters, particularly in the southern portion of the estuary (Area C4 in **Figure 3.6 A**). Eelgrass cover declined most near the main coastline, particularly in the northern portion of the study area (Areas C1, C2, and C4 in **Figure 3.6 B**), where visual interpretation of few selected classified images (1984, 1990, 1996, 2005, 2010 and 2017, **Figure 3.6 C**) indicates dense eelgrass gradually transitioned to medium-low eelgrass (Areas C1, C3 and C4 in **Figure 3.6 C**). Long-term changes in shallow water near the barrier beach seem more stochastic, where both gain and loss of eelgrass have occurred (**Figure 3.6 A**, **Figure 3.6 B**, and areas C1 and C2 of **Figure 3.6 C**). Eelgrass meadows located in deeper water sections of the

estuary, south of the main channels, either maintained or increased in eelgrass cover (Figure 3.6





Figure 3.6 A) Eelgrass cover variability map, where colour gradient represents pixels with low (red) to high (yellow) coefficient of variation values from 1984 to 2017; B) Eelgrass cover trends map, where the colour gradient represents pixels with negative slopes associated with eelgrass cover loss (red) and pixels with positive slopes associated with eelgrass cover gain (green) from 1984 to 2017. C) Selected areas are shown on classified images (C1-C4).

3.4 Discussion

3.4.1 Seagrass image classification with Landsat

This study evaluated the potential of the AASG algorithm applied to a time series of 14

Landsat images to provide information about the spatial and temporal dynamics of eelgrass

change in a coastal estuary. The results from the time series indicated that eelgrass meadows near

the barrier beach were highly dynamic, exhibiting high abundance fluctuations between years

and conversion of dense eelgrass to medium-low eelgrass near the main coastline. This study demonstrates the feasibility of using the AASG algorithm to map seagrass and the advantages of including satellite time series in monitoring programs to investigate seagrass dynamics and longterm trends.

The overall accuracies of the reference classification (2017) and classifications generated using the AASG algorithm (2016, 2014, and 2008) are within the range of those reported in studies that used Landsat imagery to classify seagrass meadows (Wabnitz et al., 2008; Pu et al., 2012; Blakey et al., 2015). Most misclassification occurred in fragmented eelgrass meadows near the main coastline and near the meadow edges, between the low-medium and dense eelgrass classes. High shoot density variability near the patch margins due to the impacts of hydrodynamics (Fonseca et al., 1983; Olesen & Sand-Jensen, 1994) could increase the discrepancies between Landsat spatial resolution and ground truth data if ground truth data does not adequately characterize eelgrass cover within the 30 m pixel. To ensure consistency between ground validation points and imagery with low to moderate spatial resolution, increased sampling may be needed in patchy areas. The high overall accuracies for the 2014 classified image could be attributed in part to a better pixel characterization yield from high-resolution imagery in 2014.

Using images from different Landsat sensors (5 TM, 7 ETM+, and 8 OLI) to extend the length of time series involves a trade-off between time span and mapping precision. Landsat OLI imagery classifications (2017, 2016, and 2014) had higher accuracy in the low eelgrass cover class compared to the Landsat ETM+ classification (2008), which is, perhaps, due to Landsat OLI's higher radiometric resolution (12-bit) compared to Landsat ETM+ (8-bit) (Verde et al., 2018; Topouzelis et al., 2018). Similar findings have been shown in other studies using Landsat TM or ETM+ to map seagrass, with a high misclassification occurring between low cover seagrass (approximately 1-25 percent) and medium cover seagrass (approximately 26-60 percent) (Pu et al., 2012; Blakey et al., 2015). However, to maximize the length of the time series, the classifications were reduced to two eelgrass cover classes (low-medium and dense), at the cost of a loss of information about the extent of eelgrass change. High-resolution imagery such as SPOT 6/7 (6 m pixel, see Wilson et al., 2019), Quick Bird (2.4 m pixel), and Worldview-3 (2 m pixel) could be used to obtain more detailed classifications but involve higher image acquisition costs and shorter duration archives. On the other hand, freely available Sentinel-2 (10 m spatial resolution, 5-day revisit frequency), available since 2015, have been shown to produce accurate seagrass maps (Kovacs et al., 2018; Traganos & Reinartz, 2018) and represent a viable alternative to Landsat imagery for recent time periods or to map short-term seasonal time-series.

3.4.2 Considerations and limitations of the AASG for seagrass time-series

This study establishes the feasibility of mapping eelgrass meadows in eastern Canada using the AASG algorithm. However, a few aspects about the AASG algorithm need to be specified. A major limitation of this study is the accuracy uncertainty of 11 maps included in this study's time series for which we do not have validation data. One could assume that the accuracies of all other classifications generated from the AASG will most likely be similar to that of the reference map. The accuracies of the 2016, 2014, and 2008 classifications, which were either similar or slightly above those of the reference classification, appear to give weight to this assumption.

Second, because AASG works under the assumption that, over very large landscapes, the conversion from one cover class to another is fairly rare; the majority of the landscape should remain stable between two images acquired at different dates (Dannenberg et al., 2016) and it is

under that assumption that stable sites are located. Although this was the case for the Tabusintac Estuary, sudden and drastic changes of seagrass density and abundance over very large spatial scales have been reported in many areas, including Chesapeake Bay (Virginia, USA) (Johnson et al., 2020), eastern James Bay (Krause-Jensen et al., 2020) and in the Antigonish estuary, Nova-Scotia (Garbary et al., 2014). If two images acquired at different dates become too different due to the sudden and abrupt changes across the landscape and seagrass meadows become highly fragmented, the process of identifying stable sites between images through image differentiation might be compromised because of low overlap between similar benthic features. Under those circumstances, a more sophisticated approach other than a simple band differentiation technique may be required to generate training sites.

3.4.3 Landsat time-series to inform seagrass dynamics and trends

The temporal variability and trends analysis showing that the total eelgrass coverage in Tabusintac Estuary slightly increased from 1984 to 2017 corroborate with the previous finding that eelgrass extent expanded between 2008 and 2014, based on interpretation of aerial photographs taken in 2008 and the classification of a WV-2 image acquired in 2014 (Forsey et al., 2020). It is also important to note that although there was a slight increase in the overall cover of eelgrass there was a gradual transition from high density to low-density meadows. This result highlights that monitoring the total seagrass area of seagrass presence/absence may be insufficient, as important changes in density or abundance may go undetected.

The class variability summary map revealed that eelgrass cover varied most overtime in shallow waters near the barrier beach (**Figure 3.6 A**). The dynamic cover change in that location could, in part, be attributed to hydrodynamic processes occurring at this habitat edge, where

small channels form and close over time, impacting water action, sedimentation, and ice action. However, a few sand flats adjacent to the barrier beach have remained stable over the past decades. Some of the most stable eelgrass patches occurred in deeper water in the southern portion of the estuary.

Finally, this study suggests a gradual decline of dense eelgrass meadows near the main coastline (**Figure 3.6 B** and **C**), possibly due to the presence of persistent and ongoing environmental stressors in that area. This has significant ramifications for eelgrass ecology, monitoring, and management. As dense eelgrass meadows disappear in Tabusintac, so do the valuable ecosystem services that eelgrass provides. Dense seagrass meadows harbour a greater diversity and higher abundance of fauna compared to low seagrass cover (Gorman et al., 2009; McCloskey & Unsworth, 2015), are the preferred feeding and foraging grounds for a wide variety of birds (Butler, 1993; Moore & Black, 2006) and have a greater capacity to stabilize sediments and increase water clarity (Carr et al., 2010; van Katwijk et al., 2010). While eelgrass extent is an important indicator of the state of seagrass ecosystems, mapping specific eelgrass cover may be a better choice if conservation and management goals include monitoring long-term changes of function, structure, and resilience of seagrass meadows.

3.4.4 Landsat time-series to inform seagrass monitoring and research

Responding to a need to improve seagrass monitoring methods and research, Neckles et al. (2012) proposed a three-tier of monitoring that is integrated across spatial scales and sampling intensities. Tier 1 monitoring consists of monitoring large spatial scales through the use of airborne or remote sensing methods, Tier 2 monitoring consists of evaluating seagrass attributes (e.g. canopy height or percent cover) at the meadow scale through the use of a ground-based

approach, and Tier 3 monitoring consists of evaluating eelgrass condition or productivity at specific locations. Integrating time-series analysis derived from the AASG to the three-tier framework would offer many advantages. Results from time series could be used to provide insights on the potential causes of these changes based on the location and magnitude of the changes observed, providing insights regarding seagrass decline and persistence at the onset of monitoring, which in turn can facilitate site selection for process-based investigations at smaller scales (Tier 2 and Tier 3).

In the case of Tabusintac, future intensive field-based investigations should prioritize areas along the main coastline, where eelgrass loss was the greatest. The observed transition from dense eelgrass to medium-low eelgrass near the main coastline, particularly in the northern section, could be linked to high water temperatures during the summer. Compared to the southern portion, the northern portion of Tabusintac is shallower and the water residence time is greater due to the low water flushing rates in that area (CBCL, 2014). Therefore, the northern portion of Tabusintac towards the main coast is more susceptible to reach high temperatures (> 20 ° C) during the summer, which could have a negative impact on eelgrass growth and productivity (Lee et al., 2007).

Oyster aquaculture, which was identified as an important threat to eelgrass meadows in Tabusintac by Murphy et al. (2019), could be an additional factor contributing to the decline of dense eelgrass along the main coastline. Aquaculture leases border the main coastline, overlapping eelgrass meadows from the mid-northern section down towards the southern section of the estuary. Mechanisms related to aquaculture known to negatively impact seagrass include a decrease in light availability near aquaculture equipment (Skinner et al., 2013), organic loading at the lease scale (Booth & Heck, 2009), and physical damage (Tallis et al., 2009). Other factors potentially affecting eelgrass near the main coastline include peat moss operations occurring near the coastline. Because eelgrass meadows in Tabusintac are subtidal, desiccation is not likely to be a major driver of eelgrass decline, and ongoing and past surveys do not show any signs of wasting disease outbreak, caused by *Labyrinthula zosterae*. Parallel to the decline of dense eelgrass, the extent of medium-low eelgrass increased, while that of sand flats decreased. Eelgrass cover expansion could be attributed in part to channel dynamic processes that could have impacted water height near the barrier beach , thereby facilitating eelgrass expansion over time.

3.5 Conclusions

Understanding how and why coastal ecosystems, including seagrass, are changing is a vital and necessary step prior to implementing the proper mitigating and restoration projects. Therefore, access to effective seagrass cost-effective monitoring tools that are easy to implement and require little ground truth data will become increasingly important to resource managers and conservation agencies. Although we used ENVI® software for atmospheric correction, Level 2 Landsat imagery could be used in the AASG algorithm, which would enable an entirely free, open-source processing chain in qGIS and R, thereby creating opportunities to increase the monitoring capacity of seagrass ecosystems at little cost.

The use of the AASG algorithm using Landsat imagery will work well where seagrass meadows are dense and continuous and where the coastal waters are relatively clear. But many seagrass meadows in Atlantic Canada have, over the past few decades, undergone significant changes mostly due to high nitrogen loading (van den Heuvel et al., 2019) and to the activity of an invasive green crab (Garbary et al., 2014). Under both conditions, eelgrass meadows tend to become highly fragmented. Although the AASG algorithm offers many advantages for seagrass mapping and monitoring, the unexpected shift in seagrass ecosystems over relatively large scales in terms of density and cover could compromise the AASG's ability to locate stable sites. Future work regarding Landsat seagrass time-series using the AASG should therefore focus on improving the detectability of seagrass cover change in highly variable environments and establish guidelines to assist resources managers in determining if the AASG is applicable in their region.

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Connecting Statement

In Chapter 3, I used a novel cost-efficient approach for satellite imaging time-series to examine changes in eelgrass distribution and abundance from 1984 to 2017 in the Tabusintac Estuary, New Brunswick. With minimal ground truth data, the novel time-series approach revealed a slow and steady decline in eelgrass abundance in some areas of the estuary. In contrast, other areas were characterized by highly dynamic shifts in eelgrass cover over time. The findings in Chapter 3 emphasize the importance of using proper temporal and spatial scales to distinguish long-term trends from short-term variations. In Chapter 4, I assessed the influence of eelgrass availability and human disturbance on Canada Geese foraging site selection in a fall stopover site (Tabusintac Estuary, New Brunswick), using field observations and eelgrass distribution maps generated in Chapter 3. As a secondary objective, I evaluated the influence of disturbance on Canada Geese flock size during the fall migration.

Chapter 4: Influence of disturbance and eelgrass (*Zostera marina*) on foraging site selection by Canada Geese (*Branta canadensis*) at a fall migration stopover site.

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4.0 Abstract

Canada Geese (Branta canadensis) migrating along coastal flyways remain reliant on natural coastal habitats. Within these natural coastal habitats, eelgrass (Zostera marina), the most common and widespread seagrass species in North America, is known to be an important food resource to migrating birds. But given the growing anthropogenic pressure on coastal ecosystems, geese migrating along coastal regions may find it increasingly difficult to access suitable stopover sites where food is abundant, and disturbance is low. In this study, we assessed the influence of eelgrass availability and disturbance on Canada Geese foraging site selection in the Tabusintac Estuary, a fall stopover site in New Brunswick, Canada. We fitted binomial generalized linear mixed-effects models in three different hunting periods to examine the distribution of geese in relation to hunting and boat activity, the distribution of dense eelgrass meadows, water depth, tidal conditions, and wind fetch. Canada Geese selected areas with high eelgrass availability early in the season, when rates of disturbance were low, emphasizing the importance of eelgrass as a food source during the fall migration in that region. However, later in the season, when boat traffic and hunting activity had increased, geese shifted their distribution to areas farther offshore and away from dense eelgrass meadows. Thus, our results highlight the interactive effects of human disturbance and eelgrass abundance in driving the stopover behaviour of Canada Geese during the fall migration in eastern Canada.

4.1 Introduction

A critical component of most long-distance migrations is brief stops or stopovers when migrants rest and replenish their energy reserves by eating high-energy foods before continuing their migration (Kaiser, 1999; Delingat, 2006; Schaub et al., 2008). Stopover studies have shown these stops to have potential impacts on survival (Weber et al., 1999; Sheehy et al., 2011; Halupka et al., 2017) and reproductive success (Sandberg & Moore, 1996; Bêty et al., 2003; Inger et al., 2008b) and thereby play a critical role in the annual cycle of migratory bird populations. While most Canada Geese (*Branta canadensis*) populations migrating through the continental interior use agricultural habitats as stopover sites (Fox & Abraham, 2017), some goose populations migrating along coastal routes continue to depend on natural coastal habitats such as salt marshes and seagrass meadows (Reed et al., 1996). Coastal habitats, however, are under growing pressure worldwide as a result of coastal development and climate change (Lee et al., 2006) that have compromised the integrity of coastal ecosystems, especially seagrass meadows (Waycott et al., 2009, Murphy et al., 2019).

Eelgrass (*Zostera marina*) is the most widespread seagrass species in North America and has long been considered an important food source for many waterfowl species (Ganter, 2000; Kollars et al., 2017). Eelgrass typically grows in shallow or intertidal areas where tidal cycles influence its accessibility to foraging birds (Fox, 1996). Herbivorous waterfowl usually feed on eelgrass by upending, with maximum feeding depth determined by bird size, eelgrass length, and water depth (Clausen, 2000). At high tide, birds tend to forage in shallower areas where eelgrass remains more accessible (Moore & Black, 2006). Eelgrass-reliant waterfowl populations tend to closely track the abundance of this resource during migration and abrupt changes in eelgrass

availability have been known to significantly alter the timing and location of their stopover behaviour (Kollars et al., 2017).

Waterfowl populations known to feed exclusively on eelgrass include Black Brant (*Branta nigricans*) on the west coast (Moore et al., 2004) and Atlantic Brant (*Branta bernicla hrota*) on the east coast (Ladin et al., 2011). Although migrating Canada Geese (*Branta canadensis*) have a more diverse diet compared to Brant, their reliance on eelgrass during migration tends to increase when no alternative natural or agricultural resources are available in relatively large quantities (Rivers & Short, 2007). In such cases, the reliance of Canada Geese on eelgrass has been described to be similar to that of Brant (Seymour et al., 2002), with evidence of starvation observed on the Atlantic coast of Nova Scotia, Canada, following an eelgrass decline during the early 2000s (Hanson, 2004).

Because of the proximity of coastal environments to human settlements, migratory waterfowl using coastal habitats must also cope with disturbance from human activities including hunting, fishing, and boating (Davidson & Rothwell, 1993). Waterfowl hunting, which is widespread and common in coastal wetlands in both Europe and North America, is regarded as one of the most significant causes of disturbance during the autumn and winter seasons, impacting geese directly through killing and indirectly through disturbance (Madsen, 1995; Madsen & Fox, 1995). Studies have shown hunting disturbance to temporally affect the diurnal behaviour of numerous waterfowl species by causing a temporary displacement (Béchet et al., 2004) and increasing the escape flight distance (Adam et al., 2016). Birds tend to avoid hunting disturbance by foraging in legally designated refuges, migratory bird sanctuaries, or alternative habitats where hunting is prohibited or low (Madsen, 1998; Mori et al., 2001; Evans & Day, 2002; Casazza et al., 2012) or by aggregating in large flocks (Rosin et al., 2012; Laursen et al., 2016).

Studies on migratory bird foraging site selection indicate that birds tend to select areas where resource availability is high (Hedenström & Alerstam, 1997) and where energy expenditure is low (Goss-Custard & Charman,1976; Davidson & Rothwell, 1993). Disturbance can cause birds to move temporarily (or permanently) from preferred habitats, representing a form of habitat loss. The capacity of birds to compensate for this loss depends on whether they can find alternative feeding areas of comparable quality so as not to reduce intake during the stopover. However, waterfowl species that depend heavily on intertidal or subtidal resources, such as seagrasses, which can be restricted by tidal conditions, may struggle to find alternative habitats (Madsen & Fox, 1995). Understanding the impact of eelgrass availability and hunting activity on migratory waterfowl habitat use is therefore critical for developing coastal waterfowl conservation and management plans. However, information on the use of eelgrass by Canada Geese during the fall season is limited (Seymour et al., 2002).

In this study, we assessed the influence of eelgrass availability and disturbance on Canada Geese foraging site selection in a stopover site in the Tabusintac Estuary in New Brunswick, Canada during the fall migration. The Tabusintac Estuary was designated as a wetland of international importance under the Ramsar Convention in 1993 due in part to the eelgrass meadows and use by migrating Canada Geese (RAMSAR, 2017). Special hunting regulations were established for the Tabusintac Estuary, with no hunting in the river area (Migratory Bird Regulations CRC, c. 1035) and hunting being prohibited in the estuary after 13h00 (Government of New Brunswick, 2020). We evaluated alternative hypotheses on foraging site selection by Canada Geese based on human disturbance, eelgrass availability, and environmental attributes including tide height (**Table 4.1**). As a secondary objective, we evaluated the influence of disturbance on Canada Geese flock size during the fall migration. By simultaneously examining the influence of eelgrass and disturbance on Canada Geese habitat use, this study advances knowledge of stopover behaviour and habitat selection that informs the harvest management of migratory waterfowl and the protection of eelgrass-rich estuaries.

Table 4.1 Proposed hypotheses relating foraging site selection patterns of migrating Canada Geese to eelgrass availability and human disturbance at Tabusintac, New Brunswick, Canada. See **Table 4.2** for environmental variables description.

Attribute	Hypothesis	Prediction: Probability of occurrence of Canada Geese will:				
Eelgrass availability						
Dense eelgrass extent	Canada Geese select sites to maximize nutrient intake- thereby geese should select areas with high food availability (Percival et al., 1996; Clausen, 1998).	positively coincide with the distribution of dense eelgrass.				
Water depth	Water depth is an important limiting factor of herbivorous birds that forage on subtidal eelgrass-thereby water depth should influence their spatial distribution (Moore and Black, 2006).	be highest where dense eelgrass coincides with shallow water depth.				
Tide level	Receding or rising tides will affect eelgrass availability - thereby tide levels should influence the temporal distribution of Canada Geese (Moore and Black, 2006).	reflect the distribution of dense eelgrass and tide-specific water depth.				
Fetch	Longer fetches that result in large wind- generated waves will increase energy demands to swim and forage - thereby longer fetch will reduce the foraging efficiency of Canada Geese (Michot et al., 1994).	reflect the distribution of dense eelgrass, tide-specific water depth, and fetch- and wind-dependent wave action.				
Disturbance avoidance						
Time (as a proxy for hunting disturbance; AM – hunting is allowed / PM – hunting is prohibited)	Hunting disturbance can cause temporary disruption and displace Canada Geese at a local scale (Dieter et al., 2010) – thereby, Canada geese will avoid Tabusintac when hunting activity is high.	increase when hunting activities decrease or cease.				
Distance to the mainland coastline	Canada Geese avoid human disturbance near the mainland coastline (i.e. boating, aquaculture) – thereby Canada Geese will select areas that are the farthest from the human presence (Rosin et al., 2012).	increase with increasing distance from locations of disturbance.				
Interaction						
Eelgrass selection and disturbance avoidance	The distribution of Canada Geese will be affected by both food resources and disturbance avoidance	increase with increasing availability of eelgrass when disturbance is low				

4.2 Methods

4.2.1 Study area

We conducted surveys in the Tabusintac Estuary (47 21'00" N, 64 54'24" W) located on the east coast of New Brunswick, Canada (Figure 4.1). The estuary covers an area of approximately 4900 ha and is protected from the Gulf of St. Lawrence by a 15 km long system of barrier beaches and dunes (Friolet et al., 2008; Leys & Lehmann, 2016). The estuary contains extensive subtidal meadows of eelgrass (Forsey et al., 2020; Leblanc et al., 2021). Dense eelgrass meadows (eelgrass cover > 60 %) are mostly found along the barrier beach, in the mid and southern portions of the estuary (Figure 4.2). Temperate eelgrass populations typically reach their maximum annual biomass in late summer, between August to September (Sand-Jensen, 1975). The tides are mixed diurnal and semidiurnal and rarely exceed two meters (Friolet et al., 2008). The average annual precipitation in rain is 812 mm, most of which falls during the summer and fall (Friolet et al., 2008). The mean air temperatures in September and October are 15 °C and 13 °C, respectively (Environment Canada, 2020). Predominant winds during the late summer and fall are from the north or north-east and are stronger in the afternoons (Environment Canada, 2020). The estuary freezes at the end of December and ice break-up normally occurs at the end of April (Friolet et al., 2008).

The natural surrounding habitats of the study area consist of sand flats, dunes, small salt marshes (average size 4 ha), bogs, shoreline black spruce (*Picea mariana*), and jack pine (*Pinus banksiana*) (Friolet et al., 2008). A Natural Protected Area (108 ha) located on the southern shoreline of the Tabusintac Estuary is protected under the New Brunswick Protected Natural Areas Act and prohibits hunting, fishing, trapping, or any other type of commercial activity (i.e., forestry, agricultural, mining).



Figure 4.1 Study area is the Tabusintac Estuary, located in north-eastern New Brunswick, Canada. A - Image from Google Earth (2021), B - Canada Geese were surveyed in areas (1-6) from mid-September to late October in 2016 and 2017. The abundance of Canada Geese and environmental variables were summarised at a grid resolution of 375 m \times 375 m. Map contains information licensed under the GeoNB Open Data License.



Figure 4.2 Distribution of the percentage of dense eelgrass extent (DEE) within 375 m \times 375 m cells in the Tabusintac Estuary, New Brunswick, Canada, in 2016 and 2017. Map contains information licensed under the GeoNB Open Data License.

Commercial activities in the area during the fall period include oyster (*Crassostrea virginica*) aquaculture, lobster (*Homarus americanus*) fishing, peat extraction, and commercial blueberry (*Vaccinium* section *Cyanococcus*) harvest in the Tabusintac River's watershed. Aquaculture leases border the mainland coastline, overlapping eelgrass meadows from the midnorthern section down towards the southern section of the estuary. The estuary borders a few rural communities including Brantville and Tabusintac, and the nearest urban center is Tracadie-Sheila, with a population of 16,000, located 20 km north of Tabusintac. Boats from several wharves transit through the Tabusintac lagoon to and from the Gulf of St. Lawrence and navigational channels are maintained through periodic dredging (Leys & Lehmann, 2016).

The area is considered to be an important fall stopover site for the North Atlantic Population (NAP) of Canada Geese (*Branta canadensis canadensis*) (Hanson, 2004). NAP Canada Geese breed in Labrador, Newfoundland, eastern Québec, and winters in estuaries and lagoons along the Atlantic coast between Nova Scotia (Canada) to North Carolina (US) (Atlantic Flyway Canada Goose Committee, 2008). Canada Geese migrating to their wintering grounds stage in the aera for several weeks from late September to late October.

The migratory bird hunting season in Tabusintac is from September 8 to September 22 and from October 1 to December 18. The early September hunting season is scheduled to allow for the hunting of Atlantic Flyway Resident Breeding population of Canada Geese prior to the arrival of NAP Canada Geese. Peak hunting season typically occur during the first two weeks of October. Hunters hunt near the barrier beach in boats, onshore, or in sink boxes, with the occasional use of decoys along the barrier beach coastline (Friolet et al., 2008). The New Brunswick Ministry of Energy and Resource Development regulations prohibit migratory birds hunting in the Tabusintac Estuary between 13h00 and one half-hour before sunrise the following day, but this restriction does not extend to land outside of the Tabusintac Estuary (Government of New Brunswick, 2020). This regulation is not reinforced by local or provincial governments.

4.2.2 Data collection

Fall staging Canada Geese were surveyed from September 18 to October 24 in 2016 and from September 19 to October 26 in 2017 in six survey areas covering the entire Tabusintac Estuary (Figure 4.1). Observers used a spotting scope to observe Canada Geese at a survey station within a particular survey area. Every day, two different survey areas were visited, rotating between survey areas located south, north, and in the center of the estuary, and each survey area was visited at least twice a week, once in the morning (8h00 to 12h00) and once in the afternoon (13h00 to 16h00). Surveys were not conducted during high rain or fog when light conditions were poor. When a goose flock was located, the number of birds and behaviour (average flock activity (> 50%) feeding, resting, swimming) were noted. The flock position was determined by recording its distance from the mainland coast or barrier beach, taking a bearing with a compass, and using the Global Positioning System (GPS) location of the survey station. During each survey, hunting activity (gunshots from hunters and, when possible, if gunshots were within or outside of the estuary and the distance from station were noted) and the distance of passing boats (whether used for hunting, fishing, aquaculture, and recreational activities) were recorded. Observers seldom encountered hunters since they were normally near the barrier beach. Aircrafts passing over the Tabusintac Estuary flew at very high altitudes and were not considered a significant source of disturbances. The southern end of the Tabusintac Estuary was not visible from the station six and could not be surveyed (Figure 4.1). Similarly, the area behind Brant Island (island near the barrier beach in survey area 4) could not be surveyed due to the lack of visibility (Figure 4.1). Both areas were excluded in the analysis.

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4.2.3 Environmental explanatory variables

Spatial and temporal explanatory variables expected to influence fall staging Canada Goose habitat use in Tabusintac are listed and described in Table 4.2. Variables related to eelgrass availability for goose foraging included water depth (WD, m), dense eelgrass extent (DEE, ha), tide height (m) and fetch (km). Flock distance from the mainland coastline (DMC, km) and time (morning [8h00-12h00] vs afternoon [13h00-16h00]) were used as indicators for geese response to human disturbance. Maps corresponding to water depth, dense eelgrass extent, fetch and distance from the mainland coastline were calculated using ArcGIS 10.5.1 software (Esri, 2016). The tide height data was obtained from the nearest weather station located in Neguac, New Brunswick (Lower Neguac (#2020); https://www.waterlevels.gc.ca/eng), whereas the wind speed data was obtained from Environment Canada (https://weather.gc.ca/). Water depth was determined using a topographic-bathymetric map (Webster et al., 2014b; Collins et al., 2016) and tide height. Dense eelgrass extent for 2016 and 2017 was estimated from two eelgrass distribution maps generated from Landsat 8-OLI imagery (Leblanc et al., 2021). Fetch, which corresponds to the distance the wind travels across open water was calculated using the prevailing wind directions at the time of the survey (Tang et al., 2020). The abundance of geese and environmental variables were summarised at a grid resolution of 375 x 375 m, allowing us to capture the spatiotemporal response of Canada Geese to hunting activity while acknowledging the uncertainty in bird locations (Austin et al., 2017).

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Variable	Description	Range	Median (IQR)
Survey Area	Code for the area within the estuary surveyed	1-6	
Dense eelgrass extent	% of dense eelgrass cover (> 60 % cover) within 375 x 375 m cell	0-14.07	0.97(0-5.36)
Water depth	Mean water depth (m) within each cell	0-1.75	0.18(0-0.50)
Tide level ^a	Tide level (m) during surveys	0.45-1.27	0.79(0.67-0.87)
Fetch	Mean estimated fetch (km) within the cell	0-0.53	0.50(0.45-0.51)
Time	Indicator of hunting activity is coded AM for hunting and PM for no hunting	0/1	
Distance from the mainland coastline	The cell's shortest distance from the mainland coastline (km)	0-2.69	0.91(0.35-1.49)
Wind speed	Mean wind speed (km/h) from September to October	0-31	13(7-18)
areas I among randing a	I D		

Table 4.2 Environmental variables considered in the foraging site selection analysis of Canada Geese in the Tabusintac Estuary, New Brunswick, Canada, 2016-2017. The values are median and range, with interquartile range [IQR] in parentheses.

^aFrom Lower Escuminac, New Brunswick

4.2.4 Statistical data analysis

All statistical analyses were conducted in R version 4.0.3 (R Core Team, 2019). To assess the behavioural response of Canada Geese to hunting activity, the survey period was divided into three distinct hunting periods, each indicating a different hunting intensity: 1- prehunting season (September 19 to 30), 2- high hunting (October 1 to 11) and 3- low hunting (October 12 to 29). The pre-hunting period includes days when migratory bird hunting was open (September 18 to 22). However, hunting activity in September is generally very low and most surveys in September were conducted when hunting season was closed (September 23 to September 30). In this study, hunting activity was defined as the number of gunshots per hour. We evaluated the temporal patterns of hunting activity in two separate steps. First, we tested for differences in gunshots per hour between the three hunting periods (pre-hunting season, high hunting, and low hunting) using generalized linear mixed-effects models (GLMMs; glmer function from 'lme4' package, Bates et al., 2019) fitted with a Poisson distribution, with year as a random effect. Using the same approach, we then evaluated the difference in gunshots per hour between the morning (8h00-12h00) and afternoon (13h00-16h00) for the high hunting period. The spatial pattern of hunting activity was assessed by evaluating the difference of gunshots per hour between the six stations in the morning and afternoon surveys for the high hunting activity period, using a GLMM fitted with a Poisson distribution, with year as a random effect. We determined the temporal trends of boat traffic by evaluating the difference of boat counts per hour between the hunting periods for each time frame (morning and afternoon) separately using a GLMM fitted with a Poisson distribution, with year as a random effect. We also assessed the difference of boat counts per hour between the morning and afternoon surveys only, using a GLMM fitted with a Poisson distribution, with period and year as random effects. We did not determine the spatial patterns of boat traffic in the estuary because many boats moved across the estuary from one oyster lease to another.

We investigated staging Canada Geese habitat use in each hunting period separately using GLMMs fitted to survey presence (≥ 1 observation) and absence (no observations) data with a binomially error distribution and logistic-link function. For each presence (occupied 375 m x 375 m cells), we randomly selected 3 cells with no observations within the survey area where the presence was observed, for a presence/absence ratio of 1:3. Prior to model fitting, collinearity among variables was examined using Pearson's correlation to ensure that all variables in models had *r* values < 0.5. Also, the continuous explanatory variables were mediancentered to reduce remnant multi-collinearity (Aiken and West, 1991). For this analysis, we did not include geese flocks outside the estuary, resting on the barrier beach.

We used a stepwise backward-selection approach to select the best model for each hunting period. The full binomial GLMM for each hunting period included all single covariates listed in **Table 4.2** as fixed effects, as well as two interaction terms that relate to eelgrass

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availability, which are dense eelgrass extent \times water depth and fetch \times water depth \times wind speed. The full model also included year and survey sites as random effects. The full models for each hunting period were simplified by sequentially eliminating the least important covariate according to effect size based on the absolute value of $\hat{\beta}/SE$ (Pagano and Arnold, 2009), except we retained week linear effects if included in an interaction term. If a simplified model led to a reduction in Bayesian Information Criterion (BIC), the full model was eliminated from the model set. We stopped removing variables from the model when the remaining effect size was > 1(Austin et al., 2017). For each final model, we calculated the variance inflation factors (VIFs) to assess collinearity between the remaining covariates (Belsley et al., 2005). The final models were also checked for the spatial autocorrelation in residuals by plotting Moran's I correlograms (Legendre & Legendre, 2012). The predictive performance of all three models was evaluated by generating the receiver operating characteristic (ROC) and calculating the area under curve (AUC) statistic using the *pROC* package in R (Robin et al., 2011). The spatial distribution of the predicted probability of occurrence of Canada Geese was mapped for each hunting period using the kriging interpolation method in ArcGIS 10.5.1 software (Esri, 2016).

We assessed the influence of hunting activity on flock size and the surface area occupied in survey areas using GLMMs. Canada Geese flock size in this study was defined as the number of geese within a 375 m x 375 m cell, while the surface area occupied corresponded to the mean cells occupied within each survey area in percentage. GLMM models for flock size and percentage of surface area occupied included time (morning vs afternoon), hunting periods (prehunting, high hunting, and low hunting), and their interaction as fixed effects and year and survey areas as random effects, with a Gaussian distribution for flock size and binomial distribution for the percentage of surface area occupied. For all GLMMs in this study, we used

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the *Anova* function from the '*car*' package in R (Fox & Weisberg, 2011) to obtain the X^2 and *p*-values. We then performed posthoc pairwise comparisons (with Holm-Bonferroni adjustment) using the *emmeans* function from the 'emmeans' package in R (Lenth et al., 2019).

4.3 Results

Canada Geese surveys resulted in 10657 geese observations in 2016 and 8250 geese observations in 2017. The hunting activity (gunshots/hr) ranged from 0 to 15 but was mostly between 0 to 5 (see **Figure S.1.1** in Supplementary Materials), with almost all the activity occurring within the estuary near the barrier beach. Hunting activity (gunshots/hr) was significantly different between the hunting periods ($X^2 = 125.32$, p < 0.000), with the highest hunting activity recorded during the first two weeks of October (**Figure 4.4 A**). During the first two weeks of October, hunting activity was significantly higher during the morning (8h00 to 12h00) compared to the afternoon ($X^2 = 33.16$, p < 0.000) (**Figure 4.4 B**). Hunting activity during the morning was significantly different between stations ($X^2 = 16.08$, p = 0.007), with the highest hunting activity reported in station 6, in the southern part of the estuary, and the lowest hunting activity reported in station 1, in the northern part of the estuary (**Figure 4.4 C**). Hunting activity in the afternoon did not statistically differ among stations ($X^2 = 1.28$, p = 0.94).



Figure 4.3 Counts of fall staging Canada Geese in the Tabusintac Estuary, New Brunswick, Canada, in 2016 and 2017. Vertical dashed lines indicate the different hunting periods.



Figure 4.4 Hunting activity (mean number of gunshots heard per hour \pm SE) over the entire Tabusintac Estuary, New Brunswick, Canada in 2016 and 2017 A) as a function of the three different periods: pre-hunting season, high hunting period, and low hunting period, B) as a function of the time of the day: morning (8h00 – 12h00) and afternoon (13h00 – 16h00) for the high hunting period, and C) as a function of the station in the morning and afternoon during the high hunting period. Letters indicating significance at **p**-values ≤ 0.005 .

Daily boat traffic in Tabusintac consisted mostly of boats traveling between 500 to 600 m from the mainland coastline, near the oyster leases. The boat counts (boats/hr) ranged from 0 to 4 and did not differ in the morning (X^2 = 1.34, p = 0.51) and afternoon (X^2 = 0.37, p = 0.83) between hunting periods (**Figure 4.5**). Also, boat counts did not differ between the morning and afternoon throughout the survey period (X^2 = 1.84, p = 0.18).



Figure 4.5 Mean number of boats per hour (\pm SE) passing through each survey area for each hunting period A) in the morning (8h00-13h00) and B) afternoon (13h00 -16h00) in the Tabusintac Estuary, New Brunswick, Canada, in 2016 and 2017.

The final binomial GLMM model for the pre-hunting season period included dense eelgrass extent, distance to the mainland coastline, water depth, and tide level, with a BIC 16 % (293) smaller compared to the full model's BIC. The probability of occurrence of geese throughout the estuary increased with increasing dense eelgrass extent and distance to the mainland coast ($\hat{\beta}$ dense eelgrass extent = 0.18 [0.10, 0.26], distance to the mainland coast = 0.59 [0.020, 0.044]; **Table 4.3**). In contrast, the probability of occurrence of Canada Geese decreased with increasing water depth ($\hat{\beta}$ water depth = -3.16 [1.18, 5.34]). When keeping other independent variables stable at their median values, the probability of occurrence of geese

For the high hunting period, the final binomial GLMM model included distance to the mainland coast and water depth and had a BIC that was 21 % (186) smaller compared to the full model's BIC. The probability of occurrence of geese increased from 0.06 to 0.47 with increasing distance from the mainland coast and decreased from 0.25 to 0 with increasing water depth ($\hat{\beta}$ distance to the mainland coastline = 0.18 [0.10, 0.26], $\hat{\beta}$ water depth = -1.62 [0.04, 3.22], **Table 4.3**, **Figure 4.6**). There was no statistical relationship between the probability of occurrence with dense eelgrass extent.

The final binomial GLMM model for the low hunting period included distance to the mainland coast and the interaction term fetch × water depth, with a BIC that was 9% (169) smaller than the full model's BIC. The probability of occurrence of geese increased from 0.02 to 0.75 with increasing distance from the mainland coast ($\hat{\beta}$ distance to the mainland coast = 1.68 [0.66, 2.7], **Table 4.3**, **Figure 4.6**). The fetch × water depth interaction indicated an influence on the presence of Canada Geese ($\hat{\beta}$ fetch × water depth = -1.40 [0.38, 2.42], **Table 4.3**). The probability of Canada Geese presence declined with increasing water depth when fetch was mid

and high, while the probability of Canada Geese increased with increasing water depth when fetch was low (**Figure 4.6**).

Canada Goose flock size was influenced by the time × hunting period interaction (X^{2} = 231.43, p < 0.001). Post-hoc pairwise comparisons are reported in **Table S.1.1**. The morning and afternoon flock sizes in the pre-hunting season were not significantly different but were significantly different for the high and low hunting periods (**Figure 4.7 A**). During the high hunting period, the flock size was lower in the morning, compared to the afternoon. During the later period in October, when seasonal hunting pressure was lower the flock size was higher in the morning than in the afternoon. Contrary to flock size, the percentage of cells occupied by flocks in survey areas was not influenced by the time × hunting period interaction (X^{2} = 0.03, p = 0.98) (**Figure 4.7 B**). However, a visual inspection of the figure suggests that geese occupied less area in the area during the high and low hunting periods.

The ROC curve of the three final models indicated high predictive power (AUC of 0.87 for the prior to hunting season model; - 0.87 for the high hunting activity model, and 0.90 for the low hunting activity model). VIF values for all final models were < 2, revealing little collinearity between variables. In most cases, the Moran's I coefficient did not exceed 0.05 and there was no pattern in the residual semivariogram at distances relevant within the study area.

Table 4.3 Logistic regression coefficients of binomial GLM models for the different hunting periods linking habitat attributes to the relative probability of fall migrating Canada Geese presence within areas of the Tabusintac Estuary, New Brunswick, Canada, 2016-2017. Variables that had insignificant coefficients were dropped from the final models. Values are statistically significant if *p*-values are ≤ 0.05 ; bolded values are significant.

	Pre-hunting season $(n = 314)$			High hunting period $(n = 182)$			Low hunting period $(n = 198)$					
Model coefficient	β	$SE(\hat{\beta})$	Ζ	P(Z)	β	$SE(\hat{\beta})$	Ζ	P(Z)	β	$SE(\hat{\beta})$	Ζ	P(Z)
Intercept	-2.01	0.23	-8.91	<0.001	-1.50	0.24	-6.17	<0.001	-1.86	0.39	-4.79	<0.001
Dense eelgrass extent	0.18	0.04	4.83	<0.001								
Distance to the mainland coastline	0.59	0.25	2.36	0.018	1.05	0.32	3.28	0.001	1.68	0.51	3.31	0.001
Water Depth	-3.26	1.04	-3.14	0.002	-1.62	0.79	-2.03	0.042	0.17	1.07	0.15	0.878
Tide level	2.19	1.16	1.88	0.059								
Fetch									0.24	0.15	1.64	0.101
Fetch x Water depth									-1.40	0.51	-2.70	0.006



Figure 4.6 Partial effects plot showing the influence of several habitat attributes on the probability of occurrence of Canada Geese in the Tabusintac Estuary (New Brunswick, Canada) as a function of the hunting period. Effects were estimated from $\hat{\beta}$ coefficients in generalized linear mixed-effects binomial models. Shaded areas are the confidence intervals. Partial effects were estimated while other variables were held at their means, except for the partial effect of water depth, which was estimated at low (10th percentile), median, and high fetch (90th percentile). DEE: dense eelgrass extent, DMC: distance to the mainland coastline.



Figure 4.7 A) Canada Geese mean flock size (\pm SE) and B) area occupied in survey areas in percentage (\pm SE) by Canada Geese in the morning (8h00 – 12h00) and afternoon (13h00 – 16h00) as a function of the hunting period in the Tabusintac Estuary, New Brunswick, Canada. * Indicating the morning and afternoon are statistically significant at a *p*-values are ≤ 0.005 .


Figure 4.8 Averaged probability of occurrence of Canada Geese in the Tabusintac Estuary based on binomial GLMM for the pre-hunting season, high hunting period, and low hunting period. The gradient goes from dark blue (probability 0) to yellow (probability 1). The black areas represent areas that were not surveyed due to the lack of visibility. Map contains information licensed under the GeoNB Open Data License.

4.4 Discussion

We tested whether eelgrass availability and human disturbance influence Canada Geese diurnal foraging site selection during the fall migration in a coastal estuary located in northeastern New Brunswick, Canada. Our findings suggest that Canada Geese selected areas with high eelgrass availability prior to the hunting season, consistent with the importance of eelgrass as a food source for migratory waterfowl in Tabusintac. However, during both the high and low hunting periods, Canada Geese shifted their distribution farther offshore and away from the densest eelgrass meadows. This habitat selection response during the hunting season is consistent with interactive effects of resource selection and disturbance avoidance by migrating waterfowl using natural coastal habitats as stopover sites.

The daily counts of Canada Geese showed that they continued to use the Tabusintac Estuary throughout the hunting season. The fluctuations in Canada Geese daily counts, ranging from 0 to 730 in 2016 and from 0 to 503 in 2017, are most likely due to different areas of the estuary surveyed each day, as well as birds transiting through Tabusintac to go to nearby estuaries. The highest daily Canada Geese counts were recorded during the pre-hunting season in 2016 and during the low hunting period in 2017. The hunting disturbance frequency during the high hunting period was 2.0 shots/hr, which is slightly lower than the 2.5 shots/hr classified as high disturbance by Bélanger & Bédard (1990) but much higher than the 0.06 shots/hr classified as low disturbance by Ward et al. (1994). Hunting was more prevalent in the southern section of the estuary, which is deeper than the northern section and thereby more accessible to boat-based hunters. Frequencies of boating, which ranged between 0 to 1.2/hr, were mostly concentrated along the mainland coastline and were consistent during the entire September – October period. Given the consistency of boating activity and the marked differences in hunting activity over

time, we believe that disturbance from hunting activity had more of an influence than commercial boat activity on the distribution of Canada Geese.

The pre-hunting season model supported hypotheses associated with eelgrass availability and human disturbance avoidance, as Canada Geese selected dense eelgrass in shallow areas and the probability of occurrence increased with increasing distance from the mainland coast. The highest probability of occurrence of Canada Geese during this period was found in the northern portion of the estuary and along the barrier beach south of station 3 (**Figure 4.8**). Geese are perhaps drawn to the northern portion of the estuary because the eelgrass is more accessible due to the area's shallowness in comparison to the southern portion. The shallowness of the northern portion could also explain why the tidal conditions had little influence on the temporal patterns of habitat use by Canada Geese. The spatial distribution of Canada Geese in the northern portion of the estuary may also be attributed to lower boat traffic in that area, whereas the spatial distribution of Canada Geese near the barrier beach in the middle of the estuary may be attributed to the presence of boat traffic near the mainland coastline.

The high hunting period model indicated the primary importance of human disturbance as Canada Geese selected shallow areas that were farthest from the mainland coastline. Compared to the pre-hunting season, the highest probability of occurrence of Canada Geese during the high hunting period was found closer to the barrier beach and extended in the southern portion of the estuary (**Figure 4.8**). The lack of support for the dense eelgrass hypothesis in this model may be attributed in part to Canada Geese moving from the center of the eelgrass meadows to the outer edge as they distance themselves from the mainland coastline. Foraging in areas near the barrier beach during the high hunting period would allow for early detection of approaching hunters in boats. Stopover studies have shown that birds typically prefer to forage in sites with good visibility, with birds in agricultural landscapes foraging in larger fields (e.g. spring-staging Pinkfooted Geese *Anser brachyrhynchus*, Chudzińska et al., 2015), while avoiding foraging in low elevation sites (e.g. spring-staging Pink-footed Geese, Jensen et al., 2008) or near forest edges (e.g. White-fronted Geese *Anser albifrons*, Bean Geese *Anser fabalis*, and Greylag Geese *Anser anser*, Rosin et al., 2012). During the high hunting period, the distribution of shifting towards the barrier beach away from the eelgrass meadows could be the outcome of a possible trade-off between foraging efficiency and predator avoidance; a well-documented response to disturbance in many bird species including House Sparrows (*Passer domesticus*) (Grubb and Greenwald, 1982), Black-capped Chickadee (*Parus atricapillus*) (Lima, 1985), Common Teal (*Anas crecca*) and Tufted Duck (*Aythya fuligula*) (Zimmer et al., 2011).

Within the hunting season, the distribution of geese did not change markedly between morning, when hunting is allowed in the estuary, and afternoon, when hunting is prohibited. However, flock size was smaller in the morning $(71 \pm 42 \text{ SE})$, when hunting disturbance was 2.0 shots/hr, compared to the afternoon $(212 \pm 42 \text{ SE})$, when hunting disturbance was 0.4 shots/hr. Given that percentage of area occupied by geese was comparable in the morning and afternoon, the smaller flock size in the morning is indicative of fewer birds present throughout the estuary during the high disturbance period. Then, coinciding with the afternoon hunting closure, it appears that additional Canada Geese joined these small flocks, thereby increasing flock size and the total number of geese in the estuary. These large aggregations occurring in the afternoon, when hunting is closed within the estuary but remains open outside the estuary, and during the Oct 1-11 peak hunting period, are consistent with the general trend of forming larger groups in response to disturbance, as observed in other waterfowl species (Inglis & Lazarus, 1981; Schmitt, 1990), and other birds (Cresswell, 1994; Williams et al., 2003), as well as mammals

(Hass & Valenzuela, 2002) and insects (Burger & Gochfeld, 2001). Forming larger groups in response to disturbance is also a key behavioural characteristic of non-breeding waterfowl (Inglis & Lazarus, 1981; Schmitt, 1990). The benefits of foraging in larger groups include a lower rate of being killed or captured because of the uncertainty and dilution effect of larger groups (Lind & Cresswell, 2005) and increased vigilance due to more individuals scanning the environment (Morelli et al., 2019).

Although hunting is not permitted within the Tabusintac Estuary after 13h00, gunshots were heard after 13h00 during the high hunting period especially from survey stations 4-6 in the southern part of the estuary, but these may have originated from outside the estuary. Gunshots heard in the afternoon were at a lower rate than in the morning and because the 13h00 hunting restrictions do not apply to areas outside of the estuary. This could explain, in part, why Canada Geese returned to the estuary after 13h00. In that case, the Tabusintac Estuary may act as a refuge for migratory Canada Geese, allowing geese to feed and rest during migration. By comparing bird distribution before and after the establishment of refuges (Madsen, 1998; Madsen et al., 1998) or monitoring bird movement between habitats (Béchet et al., 2003; Si et al., 2011), studies have shown that birds appear to congregate in low-disturbance habitats in response to hunting. Bélanger & Bedard (1990) suggested that hunting disturbance frequencies above 2.0/hr decreased the energy balance for Snow Geese (*Chen caerulescens atlantica*). Thus, keeping the hunting disturbance frequencies below 2.0/hr in Tabusintac after 13h00 would ensure that it continues to act as a refuge for Canada Geese during migration.

Alternatively, Canada Geese could be returning to the estuary because the adjacent habitats are perceived as less suitable for foraging and staging. Scattered within the Tabusintac watershed are small agricultural fields, bogs, and salt marshes. Most agricultural fields are near

commercial blueberry fields, where noisemakers (devices that release loud sounds, similar to gunshots, at fixed time intervals) are used as wildlife deterrents during the fall. These sounds could act as a deterrent for Canada Geese as well. Salt marshes also occur inland but are typically restricted to small, discreet patches surrounded by forest that may be less desirable to fall staging geese.

The low hunting period model supported the hypothesis associated with avoiding human disturbance, as Canada Geese selected areas farthest from the mainland coastline. Similar to the Canada Geese spatial distribution in the pre-hunting season, Canada Geese's probability of occurrence was highest in the northern portion of the estuary closer to the barrier beach (Fig. 8). Contrarily to what was detected in the pre-hunting season, Canada Geese's probability of occurrence increased with increasing water depth, but only where fetch was low – as the energy used to forage in deeper waters at higher fetch would probably exceed the energy gained by foraging. Although hunting activity was low (0.07 shots/hr), Canada Geese during the low hunting period aggregated in large groups (170 ± 23 SE). Given that hunting activity generates a strong response relative to other types of disturbances (Madsen & Fox, 1995), low frequencies of hunting have been shown to prompt a strong and prolonged response from birds (Ward et al., 1997).

The high abundance of food sources in Tabusintac relative to neighbouring habitats may be one of the factors that make the Tabusintac Estuary an important fall staging site for migrating Canada Geese. However, a recent retrospective analysis using Landsat imagery showed a loss of dense eelgrass meadows along the Tabusintac Estuary's mainland coastline (Leblanc et al., 2021). Although the impact of herbivorous birds on seagrasses can be substantial and overgrazing by resident Canada Geese has been observed (Rivers & Short, 2007), in most

situations grazing is compatible with eelgrass persistence and health (Vermaat & Verhagen, 1996; Hughes & Stachowicz, 2004). Overgrazing by migrating Canada Geese is unlikely to be the cause of these declines in Tabusintac, as the geese in this study avoided the mainland coastline, where a decline of eelgrass was detected from time-series analysis (Leblanc et al., 2021). Instead, climate change and oyster aquaculture have been identified as potential threats to eelgrass meadows in Tabusintac (Murphy et al., 2019; Leblanc et al., 2021). While Tabusintac is designated as a wetland of international importance, the RAMSAR convention offers no specific protection. However, according to Article 3.2 of the Ramsar Convention, each contracting party shall inform the Secretariat if the ecological character of designated wetland, is changing or is likely to change as the result of technological developments, pollution, or other human interference. It would be beneficial to propose the protection of the Tabusintac Estuary through federal or provincial protected area legislation to ensure proper management and protection of the area and the eelgrass ecosystem it harbours.

4.5 Conclusions

This study is among the very few to have looked how disturbance and eelgrass availability influence Canada Geese habitat use at a fall stop over site. Results suggest that more geese aggregated in the estuary during the afternoon hunting closure than in the morning when hunter disturbance is higher. This study has also shown how hunting disturbance can reduce the grazing intensity of geese on eelgrass meadows by shifting their distribution farther from the coast and away from areas with the highest eelgrass abundance. Compared to the Atlantic and Pacific Brant, Canada Geese herbivory on eelgrass has received less attention (Martel, 1969; Newman-Smith, 1983; Seymour et al., 2002). While this study does provide some insights about the influence of eelgrass on Canada Geese foraging site selection, much about the Canada Geese-eelgrass interaction remains unknown. Future studies might investigate Canada Geese feeding site selection in eelgrass meadows at multiple spatial scales to better understand its habitat use in relation to eelgrass quality (protein content), density, biomass, and spatial extent.

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Connecting Statement

In Chapter 4, I assessed the influence of eelgrass availability and disturbance on Canada Geese foraging site selection and flock size in a fall stopover site. I found that Canada Geese selected areas with high eelgrass availability during periods of low human disturbance, which emphasized the importance of eelgrass as a food source during the fall migration. However, higher levels of human disturbance led to a redistribution of geese away from dense eelgrass meadows. In Chapter 5, I used eelgrass monitoring data spanning a period of 38 years (1982 – 2020) to assess the spatio-temporal trends of eelgrass abundance along the eastern coast of James Bay. I also investigated if the changes in eelgrass abundance were collorated to possible enviromental drivers, including river freshwater discharge, air temperatures, sea surface temperature, accumulated growing degree days, ice breakup dates. This study is part of the Coastal Habitat Comprehensive Research Program.

Chapter 5: Large-scale regional decline and post-decline status of subarctic *Zostera marina* L. eelgrass along the eastern coast of James Bay, Canada

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5.0 Abstract

Capable of withstanding a wide range of conditions and fluctuations on a daily and seasonal basis, seagrasses are well adapted to dynamic coastal systems. Nevertheless, seagrass ecosystems have been deteriorating globally at an accelerated rate during recent decades. In 1999, a decline of eelgrass (Zostera marina) was reported by the Cree First Nations of Eeyou Istchee along the eastern coast of James Bay at the southern end of Hudson Bay. We used three decades of eelgrass biomass monitoring data collected in northeast James Bay since 1982 to detect change and assess possible environmental drivers. Eelgrass habitats in northeastern James Bay are within the influence of a regulated river freshwater plume, so we considered freshwater discharge as a potential driver of change in eelgrass, together with accumulated growing degree days, air temperatures, sea surface temperatures and ice breakup dates. We detected a decline in eelgrass biomass in northeastern James Bay between 1995 and 1999 relative to historic levels and found that low biomass was associated with local warming and higher summer freshwater discharge. Eelgrass cover estimates collected since 1999 indicated that the eelgrass decline encompassed the entire east coast of James Bay and that post-decline recovery is limited, e.g., low eelgrass cover (<25%), low above ground biomass, smaller shoots, and marginally low densities persisted at most sites in 2019 and 2020. Our study showed a 40% loss of dense eelgrass meadows in eastern James Bay since 1996, representing the largest scale eelgrass decline documented in eastern Canada. However, the lack of control sites, limited baseline data and the absence of water quality measurements prevent drawing any cause-effect relationships from the patterns we observed. Nevertheless, the results caution against assuming subarctic seagrass ecosystems have avoided recent global declines or will benefit from ongoing climate warming.

5.1 Introduction

Capable of withstanding a wide array of different conditions and fluctuations on a daily and seasonal basis, seagrasses are well adapted to dynamic coastal systems. Seagrass resistance to perturbation has been attributed to many factors including phenotypic plasticity (Maxwell et al., 2014), genetic diversity (Hughes & Stachowicz, 2004), and feedback mechanisms that increase light availability and indirectly reduce epiphyte accumulation on leaves (Maxwell et al., 2017). However, as anthropogenic pressures increase, the seagrasses' capacity to absorb repeated disturbances declines, decreasing the likelihood of a full recovery after a perturbation (Unsworth et al., 2015). As a result of accelerated environmental change in coastal zones, seagrass ecosystems have been deteriorating globally during the past few decades (Orth et al., 2006) at an annual rate estimated between 1.4% (Short et al., 2010) and 9% (Waycott et al., 2009).

Given the importance of seagrass meadows to coastal ecosystems, monitoring these meadows is critical to better understand important drivers of change. Methods used to monitor seagrasses range from coarse-grain assessments, such as presence/absence observations or meadow extent estimates based on remotely sensed observations, to fine-grain assessments, such as the percent seafloor covered by seagrass (cover), weight per m² (biomass), number of shoots per m² (density) and chemical constituents (e.g., isotopic signals for C, N, and S) (Neckles et al., 2011; Marbà et al., 2013). Biomass monitoring is typically conducted during the growing season or when shoots have reached their maximum annual biomass. Deep-water seagrass is mostly regulated by light, making it a better indicator for changes in water clarity than shallow-water seagrass, which is more susceptible to physical disturbances caused by wind and wave action and ice scouring (Krause-Jensen et al., 2004). Long-term monitoring data can be used to distinguish trends from natural fluctuations (Leblanc et al., 2021) and, when combined with appropriate environmental data can be used to identify drivers of changes (O'Connor et al., 2015).

Eelgrass (Zostera marina) is the most commonly distributed seagrass species in the northern hemisphere, occurring in the arctic, subarctic, temperate, and subtropical coastal regions (Short et al., 2007). Due to their proximity to coastal human settlement or agricultural areas, eelgrass habitats are also among the most monitored seagrass species (Larkum et al., 2006), with surveys conducted in Europe (Boström et al., 2014; Moksnes et al., 2017), North America (Rivers & Short, 2007; Garbary et al., 2014), and Asia (Whanpetch et al., 2010). Eelgrass meadows play a key role in nearshore marine habitats as they support marine food webs (Plummer et al., 2013; Thormar et al., 2016), provide valuable ecosystem services (Schmidt et al., 2011; Schmidt et al., 2012; Namba et al., 2018) and help maintain coastal biodiversity (Whippo et al., 2018; Stark et al., 2020). Over time, eelgrass meadows can be spatially dynamic, with natural variation in covers up to 50% between decades (Frederiksen et al., 2004a), or they can be remarkably stable (Ward et al., 1997; Orth et al., 2006a), depending in part on the local tidal regime, exposure to waves and wind, and level of embayment (Fonseca et al., 1983; Meysick et al., 2019). Sensitive to changes in light availability, as well as in the salinity, temperature, and nutrient regimes, eelgrass abundance generally reflects changes in water quality (Echavarria-Heras et al., 2006; Krause-Jensen et al., 2008; Salo & Pedersen, 2014). Eelgrass habitat response to climate change is predicted to vary depending on biogeographic region, with temperate eelgrass populations at the southern limit of their distribution range expected to experience important declines (Wilson & Lotze, 2019), whereas northern populations are expected to expand poleward (Beca-Carretero et al., 2018).

For Cree from the Eeyou Istchee region of eastern James Bay, extensive, healthy eelgrass meadows have served as a foundation species that support livelihoods, culture, and food security. Eeyou Istchee Cree rely on hunting and fishing, and many of these activities are ecologically supported by and organized in relation to eelgrass (SCFOE, 2008). This fundamental connection between Cree and their territorial lands, waters, and wildlife is foundational within the James Bay Northern Québec Agreement and subsequent agreements with provincial and federal governments associated with the hydroelectric development in the region. In the Cree's experience, James Bay eelgrass has gone through considerable changes over the past decades. The vast majority of Cree Land Users agree that a massive and unprecedented eelgrass decline occurred in the spring of 1999 (Lemieux et al., 2000; Dickey, 2014). Cree also reported that since the 1999 decline, recovery of the eelgrass has been very slow, and the eelgrass currently observed in some areas seems unhealthy (e.g. shorter, less dense, discoloured) (Dickey, 2014).

Since the 1970s, and throughout the 1990s and 2000s, concurrent with the reported eelgrass decline, several changes have unfolded in the local climate and hydrology in eastern James Bay. Hydroelectric development in the eastern James Bay watershed, which began in the 1970s, has entailed diverting water from different rivers into the La Grande River watershed that drains into northeast James Bay. This large-scale network of diversions prompted the 1982 initiation of what has become the largest and longest-term eelgrass monitoring program in eastern Canada. The eelgrass monitoring was led by the James Bay Energy Corporation (S.E.B.J.) from 1982 to 1995, then by Hydro-Québec, the Québec government corporation that leads the hydroelectric development, from 1999 to 2019. Beginning in 2018, eelgrass meadows were also monitored as part of a multi-disciplinary large-scale project, the Coastal Habitat Comprehensive Research Project (CHCRP). Although some of the early phase monitoring

activities have been reported previously (see Lalumière et al., 1994), the collective results of the monitoring efforts undertaken from 1982 to 2020 have not been aggregated, synthesized, analyzed, or published in a manner that enables reconstruction of a time series and statistical analysis of James Bay eelgrass meadows across this period of change. Thus, three general questions remain unaddressed in the published literature: 1) did systematic monitoring of eelgrass meadows reflect Cree knowledge of eelgrass decline in the late 1990s, 2) if a decline was detected, has monitoring indicated recovery of eelgrass following the decline, and 3) is it possible to attribute changes in eelgrass meadows detected by systematic monitoring to environmental drivers?

Here, we aimed to answer these three questions using eelgrass monitoring data spanning a period of 38 years (1982 – 2020) combined with river freshwater discharge and climate variables (air temperatures, sea surface temperature, accumulated growing degree days, ice breakup dates) covering the same period. To test for a quantitative decline in eastern James Bay eelgrass meadows and to include observations from as many times and locations as possible, we analyzed temporal trends in four measures of eelgrass abundance over time: shoot density, eelgrass above ground biomass, eelgrass percent cover, and shoot length. These four measures are derived from different original data sources and observations. Density, biomass, and shoot length estimates are derived from samples collected on SCUBA, while percent cover estimates are derived from underwater videos. To compare observations among different years with minimal uncertainties due to how variables were estimated, we obtained raw images and data, and we collated, re-processed, and analyzed data from multiple sets of monitoring surveys. Specifically, we ask the following questions: (i) Has eelgrass abundance in monitoring sites changed over the observation period beginning in 1982?, (ii) If a change is detected, does it

depend on location or depth?, iii) Was there a temporal change in potential drivers of eelgrass declines such as regional or local environmental drivers (air temperature, sea surface temperature, ice breakup, accumulated growing degree days and regulated river freshwater discharge) and iv) Can changes in eelgrass be attributed to any of these potential drivers, and v) What is the current status of eelgrass in eastern James Bay.

5.2 Methods

5.2.1 Study area

Hudson Bay is the largest embayment of the northern Canadian Arctic region and is comprised of two nested bays. James Bay is a smaller, strongly river-influenced, southern extension of Hudson Bay (**Figure 5.1**). Both Hudson Bay and James Bay receive Arctic marine waters from Foxe Basin and Hudson Strait, together with freshwater runoffs from a continentwide fluvial drainage system (Martini, 1986). A near-continuous sea-ice cover forms and melts annually. The temperature and salinity patterns throughout the system's surface waters are influenced by the seasonal cycles of freshwater inputs, the sea-ice cover, and air-sea heat fluxes (Prinsenberg, 1986b). Hudson Bay and James Bay both have been getting progressively warmer during recent decades and evidence of climate change is reflected in the decrease in sea ice extent in eastern Hudson Bay (Cavalieri & Parkinson, 2012; Kowal et al., 2017) and warming of sea surface temperatures (Galbraith & Larouche, 2011; Brand et al., 2014).



Figure 5.1 A) Location of the eastern coast of James Bay, Québec, Canada, with the Eeyou Istchee territory shown in gray, B) Locations of eelgrass monitoring sites, cover monitoring sites and biomass sampling sites, C-1 to C-4) Locations of eelgrass monitoring sites from 1982 to 2020.

Eastern James Bay is ice-covered between December and early June each year, although the date of fast ice breakup has occurred progressively earlier since 1980 (Galbraith & Larouche, 2011; Andrew et al., 2018; Taha et al., 2019). The tides in eastern James Bay are semidiurnal with amplitudes that range from 1.5 m at neap tide to 2.4 m at spring tide. The geomorphology of the northeastern coast of James Bay is complex, characterized by numerous bays, points, and peninsulas and dotted with islands and reefs, while the southeastern coast is less complex, characterized by large open embayments (Dignard et al., 1991). All along the eastern coast, the relief is low and the land surface is undergoing isostatic rebound, uplifting between 1.0 to 1.5 cm year⁻¹ as a residual effect of the Laurentide Ice Sheet, which retreated from the area approximately 8000 years ago (Martini, 1986; Pendea et al., 2010; Izaguire et al., 2018). The main river discharging into the study area is the La Grande River, which produces a plume that extends and spreads mostly northward along the coast due to the bay's general cyclonic (anticlockwise) water circulation pattern (Prinsenberg, 1986a). Additional rivers flowing into eastern James Bay include the Castor, Maquatua, Old Factory, Eastmain, and Rupert River south of La Grande and the Roggan River north of La Grande.

There are four coastal Cree communities along the eastern coast of James Bay---Chisasibi, Wemindji, Eastmain, and Waskaganish --- with populations (mostly Cree First Nations) ranging from about 900 people in Eastmain to nearly 5000 people in Chisasibi. Except for the hydroelectric development initiated in the early 1970s, there is little coastal development in the region. The James Bay hydroelectric project, considered to be amongst the largest power generation projects in North America, was constructed in multiple phases from 1979 to 2009 (Ma et al., 2005). It altered the natural flow regime of the Eastmain River and La Grande River starting in 1979, the Caniapiscau River, which naturally flows into Ungava Bay, in 1982, and the Rupert River in 2009. The Eastmain River annual freshwater flows were reduced by 85% with flow diverted north into the La Grande River watershed to create large water reservoirs (Roy & Messier, 1989). The water in the reservoirs is released into the La Grande River (LGR) for hydroelectric production, with the highest freshwater discharge occurring in winter to meet peak energy demands in southern Québec (Déry et al., 2016). The increase of freshwater discharge of the LGR caused the winter 15 surface isohaline to expand 55 km northward and 37 km southward from the La Grande River mouth (Messier, 2002). The summer 15 surface isohaline has also expanded, though to a considerably lesser extent than the winter plume, extending 15 km north and 10 km south of the LGR. However, the summer 15 surface isohaline is highly variable, and its expansion is influenced by climate, atmospheric pressure, and freshwater discharge (Messier, 2002).

The first map of eelgrass meadow distribution was produced in 1975, prior to hydroelectric development, and indicated the presence of eelgrass along the entire eastern coast, the absence of eelgrass near the LGR mouth, and the most extensive eelgrass meadows located in the northern sector of the coastline above Castor River (Curtis, 1974-1975). The eelgrass meadows are generally found in shallow lagoons, protected embayments, and estuaries where both the tidal flats and subtidal slopes are gentle (Lalumière et al., 1994). Surveys conducted in the late 1980s reported eastern James Bay eelgrass is mainly perennial, grows in oligotrophic water, and reaches peak shoot biomass in the summer (Lalumière, 1987a; Lalumière, 1988a).

5.2.2 Eelgrass monitoring data

The eelgrass monitoring data used in this study come from various sources including S.E.B.J., Hydro-Québec, and independent research groups working within the CHCRP. The majority of the compiled information consists of monitoring reports produced by consulting firms for the S.E.B.J. and Hydro-Québec, which were downloaded from the Hydro-Québec online library (www.cherloc.ca). Several different eelgrass monitoring strategies have been used over the last four decades (**Figure 5.2**); they may be summarized as follows:

- (i) *Eelgrass biomass monitoring*:
 - a. *Hydro-Québec*: In the early 1980s, the S.E.B.J. launched a coastal monitoring program to evaluate the possible impacts of hydroelectric production on various coastal components, including eelgrass in northeastern James Bay. Monitoring of eelgrass density and above ground biomass began in 1982 and ended in 2009. For this study, we compiled raw observations from 14 monitoring reports published between 1982 to 2009, and all information about sampling methods is also derived from these reports (see Table S.2.1 and Table S.2.2 in Supplementary Materials),
 - b. CCHRP: In 2019 and 2020, eelgrass density, above ground biomass, and shoot length were monitored by independent groups of researchers and coastal community members along the eastern coast of James Bay.

- (ii) *Eelgrass cover monitoring*:
 - a. *Hydro-Québec*: The eelgrass decline reported by the Cree in the spring of 1999 prompted Hydro-Québec to launch a new monitoring program that assessed eelgrass abundance qualitatively in 88 sites using underwater footage and photos spread along James Bay's entire eastern coast from 1999 to 2019 (see Table S.2.3 in Supplementary Materials),
 - b. *CCHRP*: Eelgrass cover was monitored along the eastern coast using underwater footage and photos in 61 sites in 2018 and 21 in sites in 2019.



Figure 5.2 A) Timeline showing the different eelgrass monitoring and surveys conducted between 1982 to 2020. Monitored by Hydro-Québec: from 1982 to 2009, eelgrass density and above ground biomass were monitored in 6 permanent sampling sites in August (in *red*); from 1999 to 2019, eelgrass cover was monitored in sites distributed along the eastern coast of James Bay (in *black*). Monitored by the Coastal Habitat Comprehensive Project (CHCRP): from 2018 and 2019, eelgrass cover (*in white*) was assessed in sites distributed all along the eastern coast; from 2019 to 2020, eelgrass density, above ground biomass and shoot length were estimated several sites along the eastern coast in August (in *green*). VF: video footage available at some sites; B) Schematic of a *Zostera marina* eelgrass shoot showing the whole plant structure.

5.2.3 Hydro-Québec eelgrass biomass monitoring in northeastern James Bay

The locations of eelgrass biomass permanent sampling sites were chosen based on two criteria: they were in estuaries that harboured dense and continuous eelgrass meadows, and these meadows were in the area expected most likely to be affected by the hydroelectric production in northeastern James Bay (Roche, 1982; Roche, 1985). Monitoring began in three sites in 1982, and three additional sites were established in 1988, for a total of six permanent sites sampled between 1988 and 2009 (**Figure 5.1 C**). A control site was set up 60 km south of the La Grand River but was only visited once in 1982 (Roche, 1982).

Eelgrass biomass monitoring was conducted during the first two weeks of August using similar sampling methods during the 13 years between 1982 and 2009 (but not every site was surveyed in each of the 13 years). Eelgrass was collected along transects perpendicular to the shore at depth increments of 0.5 m. From 1982 to 1986, the above- and below-ground biomasses were collected using a boat-based coring device with a surface area of 0.04 m², whereas from 1988 to 2009, above ground biomass was collected in 0.15 m² quadrats by SCUBA divers. The eelgrass abundance estimates reported included above ground biomass (g dry weight m⁻²), vegetative shoot density (number of vegetative shoots m⁻²), and reproductive shoot densities for each quadrat (number of reproductive shoots m⁻²). We calculated the percent of reproductive shoots for each quadrat. Above ground biomass was not available in 1982 because the above and below-ground biomass were not separated in core samples.

5.2.4 CCHRP eelgrass biomass monitoring

We compared estimates of eelgrass density and biomass from Hydro-Québec permanent sampling sites to new samples collected in August 2019 at 8 sites along James Bay's eastern coast by researchers part of the CHCRP (**Figures 5.1**). The sites were selected in June of 2019 in consultation with community members, as well as in consideration of standardizing water depth, level of exposure, and distance from other sites. Two sites were close to two Hydro-Québec permanent sampling sites (sites 5 and 6, **Figure 5.1 C4**). At each site, above ground eelgrass biomass was collected in three sets of 3 0.25 m² quadrats located 20 to 30 m apart (total of nine quadrats per site) at 1 to 1.5 m depth by SCUBA or SNUBA divers. Eelgrass vegetative shoots were counted for each quadrat. Once measured, eelgrass shoots were dried at 60°C for 48 hrs and weighed. All eelgrass measurements were converted to square meters.

In addition to time-series comparisons to detect changes, we used a two-point comparison of shoot length estimates between 2019 and 2020. The shoot length measurements were based on eelgrass shoots collected using an abbreviated sampling protocol, which consisted of collecting 5 to 15 eelgrass shoots at 43 sites in 2019 and in 24 sites in 2020 either by snorkeling, diving, or with a rake.

5.2.5 Hydro-Québec eelgrass cover monitoring

Responding to Cree observation of an eelgrass decline in the spring of 1999, Hydro-Québec developed a monitoring strategy to assess eelgrass abundance on a qualitative basis along the entire eastern coastline (**Figure 5.1**). The site locations were determined by using a map representing the eelgrass distribution in 1995-1996 (scale 1:125 000 km, Lalumière et al., 1996). The map showed eelgrass distribution along the eastern coast of James Bay in two cover classes, dense eelgrass meadows (eelgrass cover > 50%) and low-density eelgrass meadows (eelgrass cover < 50%). Sites selected from the map were 5 km apart, with 65% of the sites located in dense eelgrass meadows, while 35% of sites were in low-density eelgrass meadows. The sites selected from the 1995-96 eelgrass distribution map served as baseline data for eelgrass abundance status prior to 1999. The Hydro-Québec eelgrass cover monitoring sites were visited six times between 1999 to 2019.

An eelgrass cover monitoring site consisted of a single GPS position where SCUBA divers captured video footage of eelgrass at water depths ranging from 1.0 to 1.5 m (3 to 4 short videos of a duration of 25 to 50 s). In the Hydro-Québec reports, the eelgrass abundance, which was assessed using the video footage, was presented using a similar classification scheme as the 1996 eelgrass distribution map: (1) no eelgrass, (2) sparse eelgrass (eelgrass cover between 1% to 5%), (3) discontinuous eelgrass (eelgrass cover between 6% to 49%) and (4) continuous eelgrass (eelgrass cover between 50% to 100%) (see **Figure S.2.1** in Supplementary Materials for example for each class).

4.2.6 CCHRP eelgrass cover monitoring

In 2018, video footage was recorded (duration of approximately from 15 to 30 s) in 61 sites distributed along the eastern James Bay coast at water depths ranging between 0.5 to 1.0 m using a boat-based method, which consisted of a GoPro camera attached to an extension pole (see Anderson 2020 for a full description of the method).

Parallel to the Hydro-Québec eelgrass cover monitoring surveys conducted in 2019, eelgrass cover was surveyed in 21 sites along the coast where divers or snorkelers recorded video footage (video duration approximately of 40 s) or took photos of eelgrass at water depths ranging between 1.0 and 1.5 m.

5.2.7 Eelgrass cover assessment

Using the available video footage from Hydro-Québec and CHCRP cover monitoring sites, the cover of eelgrass (in %) was visually estimated in 10% increments but the minimum cover of eelgrass when present was set at 5% (0% when eelgrass was absent). The eelgrass cover was estimated on 5 to 7 randomly selected image stills on each video, resulting in 5 to 20 observations per site per year. We estimated eelgrass cover (%) for 12 sites for 2011, 11 sites for 2014, 61 sites for 2018, and 21 sites for 2019.

To detect change (or, to reject the hypothesis of change over time) in a categorical approach, we compared eelgrass cover between 1996, 1999, and 2019 at Hydro-Québec eelgrass cover monitoring sites. We extracted sites classified in 1999 (Lemieux et al., 1999) and pooled the three abundance classes with eelgrass cover < 50% (no eelgrass, sparse eelgrass, and discontinuous) into a single class termed 'low-density eelgrass' (eelgrass cover < 50%). In addition, we grouped the 2019 sites into the same two broad categories, dense eelgrass (cover > 50%) and low-density eelgrass (cover < 50%).
5.2.8 Environmental data

To assess potential environmental drivers of eelgrass abundance in northeastern James Bay, we selected covariates that represented potential regional and local drivers of eelgrass biomass, shoot density, and percent of reproductive shoots in the northeastern coast of James Bay (**Table 5.1**). The growing season for eelgrass in northeastern James Bay is from June to August, following ice-off (Lalumière et al., 1988a). Though conditions and events in the year prior can affect summertime eelgrass abundance, we restrict our analyses to conditions within the same growing season as the eelgrass observations.

Environmental variable	Unit	Range*	Source
Summer FD (June and July)	m ³ s ⁻¹	2127.75- 3408.74	From 1984 to 1987, Messier 2002; from 1988 to 2000 Lemieux and Lalumière 2000; 2009 - unpublished data, Hydro- Québec
Summer air temperature T (June and July)	°C, Celsius	10.52-14.74	Environment Canada weather information from the La Grande Rivière Airportmeteorological site (https://climate.weather.gc.ca/).
Summer sea surface temperature SST (June and July)	a surface e SST July)		High-Resolution Sea Surface Temperature (GHRSST)
Accumulated GDD	Accumulated number of days with temperatures above 5 °C from early March to late July	343-766	Derived from temperature records obtained from the Environment Canada La Grande Rivière Airport (https://climate.weather.gc.ca/).
Ice breakup date (IBU)	Day of Year	141-186	Canadian Ice Service ice charts (https://www.canada.ca/en/environment- climate-change/services/ice-forecasts- observations/latest-conditions.html)

Table 5.1 Environmental factors used as predictor variables in the generalized additive mixed models (GAMMs). FD: freshwater discharge, GDD: growing degree days

*from 1982 to 2019 for T, SST, and GDD, 1984 to 2019 for FD, and from 1985 to 2019 for ice-breakup.

We considered the following regional potential environmental drivers: summer air temperature (°C, mean, mean maximum, and mean minimum daily air temperature of June and July), summer sea surface temperature (°C, mean monthly sea surface temperature of June and July), accumulated growing degree days (GDD) and ice breakup dates (**Table 5.1**). We excluded August because eelgrass biomass was collected in the first two weeks of August. Due to the lack of water quality parameters, including water temperature, we used air temperatures as a proxy for local sea-water temperatures, which has been shown to follow water temperature patterns in shallow coastal estuaries and lagoons (Cabello-Pasini et al., 2003; Lee et al., 2007; Kim et al., 2016; Turner et al., 2017; Van Dam et al., 2021) and has been used in various seagrass studies when seawater temperature data are lacking (Clausen et al., 2014; Olesen et al., 2015; Blok et al., 2018). Growing degree days (GDD) is a measure of heat accumulation, which was developed to predict crop yield in agriculture and is increasingly applied in seagrass ecology (Infantes & Moksnes, 2018). Daily GDD was calculated as

$$GDD = \frac{Tmax + Tmin}{2} - T_{base} \tag{1}$$

where T_{max} and T_{min} are the maximum and minimum daily air temperatures, respectively and T_{base} is the minimum air temperature at which plant growth can start. We used 5°C as a T_{base} because eelgrass in colder regions can grow at relatively low temperatures (see Olesen et al., 2015). In this study, heat accumulation represented the cumulative sum of daily GDD from March 1st to the end of July, and higher accumulated GDD would suggest an early spring. Mean, maximum, and minimum summer air temperatures and accumulated GDD from 1982 to 2020 were calculated using hourly air temperatures recorded at the meteorological station of the La Grande Rivière Airport (53° 37' 31.00''N, 77°42'15.00''W), approximately 90 km east of the coastline. June and July air temperature measurements taken near La Grande River (2.9 km inland, La Grande-1 central) between 1990 and 1995 revealed that they were generally 1 to 4 degrees lower than those taken at the La Grande Rivière Airport but followed the same trends (Lalumière & Lemieux, 1995).

The sea surface temperature (SST) for James Bay was obtained from the Group for High-Resolution Sea Surface Temperature (GHRSST) product 'AVHRR_OI-NCEI-L4-GLOB-v2.1', which provides a continuous daily record of SST on a 0.25° spatial grid from 1982 to 2020 (Banzon et al., 2016). The product blends *in situ* and satellite observations, and uses optimum interpolation, to produce gap-free daily SST estimates. However, the principal data used is from the Advanced Very High-Resolution Radiometer (AVHRR) space-born infrared instruments (Banzon et al., 2016). Statistical analysis was conducted on monthly averages of the SST of the North-Eastern sector of James Bay (i.e., grid points falling within the area bounded by 53-55 °N and 79-80.7 °W).

The annual ice breakup date in James Bay was determined from regional ice charts produced by the Canadian Ice Service. Ice charts delineate different ice regimes with polygons that present sea ice concentration by stage of development using the World Meteorological Organizations egg code. Polygons are defined by expert manual interpretation of remotely sensed imagery and ship and airborne observations (Fequet, 2005; Tivy et al., 2011). The temporal frequency of ice charts has varied across seasons, with a historic emphasis on the summer shipping season, and across years. Focusing on the period of spring breakup, from 1985 to 2006 ice charts were produced biweekly during May and early June, and then weekly during late June and into July, from 2007 onwards ice charts have been produced weekly. From the ice charts, the total ice concentration of James Bay (sub-region 26 in Galbraith & Larouche, 2011) was calculated. The time series of total ice concentration was then interpolated to daily intervals, and the day on which total concentration fell below 50% was determined as the day of breakup (similar to the method used by Galbraith & Larouche, 2011).

We used the LGR's summer (mean June and July) freshwater discharge (m³ s⁻¹) as a proxy for water quality at the local scale. The monthly freshwater discharges between 1984 to 1987 were recorded at the Robert-Bourassa power generating site (formerly known as La Grande-2) located 110 km upstream from the river month (Messier, 2002), while the monthly freshwater discharges between 1988 to 2019 were obtained from the La Grande-1 power site, located 35 km upstream (1988 to 2000 from Lemieux & Lalumière, 2000; 2001 to 2019 from *unpublished data*, Hydro-Québec).

We compiled water quality data from 1999 to 2020 to determine temporal variation and inspect spatial patterns in salinity and surface temperature measured along James Bay's eastern coast. Available measurements of water quality extracted from Hydro-Québec reports included measurements of surface salinity and surface temperature (°C) at eelgrass cover monitoring sites from 1999 to 2019 (**Table S.2.3**). We also compiled measurements of surface salinity and surface temperature from eelgrass sites surveyed in 2018, 2019, and 2020.

5.2.9 Statistical analysis

All statistical analyses were conducted using the computing program R version 3.6.1 (R Core Team 2019). We performed five types of analyses on the eelgrass monitoring and biomass data and auxiliary climate and discharge data to assess: (i) temporal trends in vegetative shoot density, above ground biomass, and percent of reproductive shoots from eelgrass biomass monitoring sites, and to determine whether trends depended on depth or varied among sites, (ii) temporal trends in some possible drivers of change including summer air temperature, summer sea surface temperature, accumulated GDD, ice breakup, and summer LGR discharge, (iii) correlations between possible drivers and eelgrass vegetative shoot density, above ground biomass and percent of reproductive shoots, (iv) the differences in eelgrass cover (%) along the eastern coast of James Bay between 1996, 1999 and 2019, and (v) the difference in eelgrass shoot density, biomass and shoot length between historical and current estimates.

To explore how and if eelgrass vegetative shoot density, above ground biomass, and percent of reproductive shoots have changed as a function of year and depth, we used generalized additive mixed models (GAMMs) using R-package gamm4 (Wood & Scheipl, 2016). General additive models are non-parametric extensions of generalized linear models that apply non-parametric smoothers to each predictor and calculate the component response additively. GAMMs are ideal for detecting non-linear changes in seagrass meadows (Lefcheck et al., 2017; Shields et al., 2019). We included depth as a predictor using a categorical variable with two levels: "shallow" vs "deep". Shallow eelgrass was defined as eelgrass collected at 0.5 m, while deep eelgrass was defined as eelgrass collected at 1 to 2 m. Preliminary analyses showed no significant difference between eelgrass density and above ground biomass collected at depths between 1 and 2 m. GAMMs models assumed a Poisson distribution for densities, a Gaussian distribution for above ground biomass, and a binomial distribution for percent of reproductive shoots. The potential correlation between sampling times for each year was accounted for by using a splines function for years (Guest et al., 2016). The time series for sites 1 to 4 extended from 1984 to 2009. Because two 2019 sampling sites were in close proximity to the sites 5 and 6, the time series both sites extended from 1984 to 2019. GAMMs time-series were visually inspected to identify breakpoints in density, biomass, and percentage of reproductive shoots. The significance of the breakpoints was tested using the regression package segmented (Muggeo, 2008).

Prior to assessing the influence of the environmental variables on eelgrass shoot density, above ground biomass, and percent reproductive shoots, we used linear regressions to assess the temporal trends of summer air temperatures, sea surface temperatures, and accumulated GDD from 1982 to 2019 (37 years), ice breakup dates from 1985 to 2019 (34 years), and summer LGR freshwater discharges from 1984 to 2019 (35 years).

GAMMs were also used to test hypotheses listed in **Table 5.2**. Except for the null model (no variables), all models included site as a fixed effect and either a climate variable, a freshwater discharge variable or an interaction term (climate x freshwater discharge). The term included in model was fitted with a smoothing spline, with depth and year as random effects. GAMMs assumed a negative binomial distribution for shoot density and a Gamma distribution for above ground biomass. Analysis was conducted on sites visited at least 9 times between 1982 to 2009 (sites 1, 3, 5, and 6). Considering the high summer freshwater discharge that occurred in 1999, we conducted the analyses with and without the data collected in 1999. Collinearity among variables was examined using Pearson's correlation prior to model fitting to ensure that all variables in models had *r* values < 0.5 (**Table S.2.4**). GAMMs were compared using Akaike information criteria corrected for small sample size (AICc) to select the most parsimonious model (Burnham & Anderson, 2002).

Table 5.2 Proposed hypotheses and candidate models relating biomass (g DW m⁻²) in eelgrass biomass monitoring sites located in northeastern James Bay to four regional drivers (June and July monthly air temperature means (T), June and July monthly sea surface temperature means (SST), accumulated GDD (GDD) and ice breakup date (IBD)) and two local drivers (June and July monthly means freshwater discharge (FD) from the La Grande River) from 1982 to 1995. Interaction terms with Pearson's correlation coefficients > 0.50 excluded (see **Table S.2.4** in Supplementary Materials).

Environmental variable	Hypothesis	Prediction Eelgrass density
	ν 1	and biomass will:
La Grande River FD		
Summer FD	Increases in FD can change the abiotic and biotic coastal conditions (Ligon et al., 1995; Rosenberg et al., 1997; Nilson et al., 2005; Bernard et al., 2005). Increase FD during the growing season could affect eelgrass productivity.	decrease with increasing summer discharges.
T/SST	Water temperature plays a significant role in controlling the above ground biomass production of eelgrass and increasing temperatures in subarctic coastal zones will stimulate growth (Olesen et al., 2015; Wilson and Lotze, 2019).	increase with increasing summer temperatures/SST.
GDD	Higher GDDs suggest a warmer summer and early spring, which would influence eelgrass growth and productivity. Early ice break can lead can increase light availability for eelgrass.	increase with increasing GDD. increase with
IBD	which can stimulate growth early in spring.	decreasing IB.
Interactions		
Summer FD x summer T /SST/GDD	Changes in water quality associated with increased summer FD will outweigh the benefits associated with summer T and will have an adverse effect on eelgrass productivity. Warmer spring/summer temperatures combined with higher sea	decrease with increasing summer FD and increasing T. decrease with
SST x GDD	surface temperatures can alter the nutrient regime (Echavarria-Herras et al., 2006) and will have an adverse effect on eelgrass productivity.	increasing GDD and FD.
IBU x mean, min-max summer T	Early ice-break-up combined with warmer spring/summer temperatures could trigger phytoplankton production and decrease light availability for eelgrass during the growing season (Leblanc et al., 2019; Tedesco et al., 2019).	decrease with high summer temperatures and early ice break- up.

To assess the differences between shoot density and biomass between 1995 (prior to the decline) and 2019, we used generalized linear mixed models and linear mixed models from the Lme4 package (Bates et al., 2014). To assess the difference in shoot density between 1995 (n=6) and 2019 (n=8), we used a generalized mixed model with year as a fixed effect and site set as a random effect using a Poisson distribution. We used a linear mixed model to compare above ground biomass between 1995 and 2019 with year as a fixed effect and site set as a random effect. To compare shoot length estimates between recent years with historical data

(Lalumière et al., 1994), we used a linear mixed model with site and month set as random effects to evaluate the differences in shoot length between 2019 and 2020.

We compared the proportion of sites with dense eelgrass meadows and low-density eelgrass meadows using a Pearson Chi-Square test between the following paired years: [1996 -1999], [1999 - 2019] and [1996 - 2019]. We used a linear mixed model to compare eelgrass cover among years (2011, 2014, 2018, and 2019), with site set as a random effect. The water parameters measured at the single-point observations between 1999 to 2019 were tested for temporal trends using linear mixed models with year as a fixed effect and site set as a random effect. When a significant difference between years was observed, differences between means were compared using LSmeans multiple comparison tests from the LSmeans package (Lenth et al., 2017).

5.3 Results

5.3.1 Temporal trends of eelgrass abundance

In 1999, we detected a decline in vegetive shoot density and eelgrass above ground biomass ranging from 90% to 99% relative to pre-1995 levels in four of six sites in both shallow and deeper water (sites 1, 2, 3, and 6; Figure 5.3). Segmented regression analysis showed the existence of a breakpoint in 1995 for both density and above ground biomass in most stations in shallow and deep transects (Figure 5.3). Visual inspection of the time series for sites 1 and 2 suggested that the highest density and above ground biomass were observed in the 1980s and early 1990s, and the lowest density and above ground biomass occurred between 1999 to 2009. In site 3, the density and above ground biomass varied interannually but were generally highest between 1993 to 1995. Eelgrass density and above ground biomass increased between 1999 to 2009 but remained well below pre-decline levels. In site 6, prior to 1999, both density and above ground biomass in shallow transects gradually declined, whereas both eelgrass parameters remained relatively stable in deep transects. By 2019, vegetative densities and above ground biomass in site 6 increased but remained below pre-decline levels. Sites 4 and 5, which had low density and biomass prior to 1995, showed some declining trends but of lesser magnitudes. Contrary to temporal changes detected in shoot density and biomass, we detected no systematic changes in the percent of reproductive shoots (Table S.2.5; Figure S.2.2).



Figure 5.3 Mean ±SE A- shoot density (m⁻²) and B- biomass (g DW m⁻²) for each site from 1982 to 2009 for sites 1 to 4 and from 1982 to 2019 for sites 5 and 6. The fitted line is the predicted values based on the GAMMs time series (see Methods and table with GAMM stats), shaded areas are the 95% confidence intervals. Vertical lines show significant (p < 0.05) breakpoints in time series. Horizontal lines on above ground biomass indicating range measured prior to the hydroelectric development (100 to 400 g DW m⁻², Curtis, 1974-75).

5.3.2 Temporal trends in summer climate conditions and freshwater discharge

The mean daily summer temperatures (June and July) from the La Grande Airport from 1982 to 2019 showed a slight warming trend at a rate of (mean \pm SE) 0.04 \pm 0.02 °C yr⁻¹ (R² = 0.09, p = 0.04, N = 37 years, Figure 5.4), but not for mean maximum daily air temperatures (Figure 5.4, $R^2 = 0.07$, p = 0.06, N = 37 years) and mean minimum daily air temperatures (Figure 5.4, $R^2 = 0.08$, p = 0.05, N = 37 years). We did not detect a warming trend in mean summer sea surface temperature (June and July) (Figure 5.4, $R^2 = -0.01$, p = 0.47, N = 37 years) but summer sea surface temperatures were highly variable after 1998. Similarly, there was no temporal trend detected in the accumulated GDD (Figure 5.4, $R^2 = 0.35$, p = 0.13, N = 37 years) but the 1998 GDD stands out as a pronounced maximum. GDD over the following decade was highly variable until 2008, and there were more warm days (higher GDD) between 1998 and 2017 than between 1982 to 1994. James Bay ice breakup dates did not show any temporal trends over the study period (Figure 5.4, $R^2 = 0.04$, p = 0.13, N = 34 years), but the 1998 breakup occurred nearly a month earlier than the 1997 breakup. Mean monthly summer freshwater discharge (June and July) showed a significant increasing trend at a rate of (mean \pm SE) 25.64 \pm $6.399 \text{ m}^3 \text{ vr}^{-1}$ (R² = 0.30, p < 0.00, N = 35 years, Figure 5.4).



Figure 5.4 (A-C) Mean, maximum, and minimum summer air temperatures (°C). (D) Summer sea surface temperatures (°C), (E) accumulated GDD, (F) ice breakup date (DOY), and (G) summer freshwater discharge ($m^3 s^{-1}$) for eastern James Bay between 1984 to 2019. The dashed lines represent the increase of variables over time with the regression analysis. The coefficient of determination (R^2) and significance (p) of linear regression are shown.

5.3.3 Climate and local drivers of trends of eelgrass abundance in northeastern James Bay 2

23	Between 1985 to 2019, temporal trends and variation in vegetative shoot density and
4	biomass were best explained by an interaction between climate and freshwater discharge,
5	whether the anomalous high summer freshwater discharge of 1999 was included or excluded
6	from the analysis (Table 5.3, Table S.2.6). High eelgrass shoot density was associated with low
7	summer freshwater discharge and high summer temperature, whereas high above ground
8	biomass was associated with low summer freshwater discharge and high accumulated GDD
9	(Table 5.4, Figure 5.5). For both density and biomass, alternative models were not supported
10	(Table S.2.6).
11	
12 13 14 15 16 17	Table 5.3 Candidate models correlating shoot density and above ground biomass using GAMMs. The table includes Akaike information criterion values for small sample sizes (AICc), AIC weights (wAIC), and explained deviance (\mathbb{R}^2). FD, freshwater discharge; T, air temperature; and GDD for accumulated growing degree days. Only models with <i>w</i> AIC > 0.20 are presented (see Supplementary Material for Chapter 4 for a complete list of models tested).

Best model(s) from 1985 to 2019	AICc	wAIC	\mathbb{R}^2
Shoot density (no. m^{-2})			
Site + s(Mean max summer T, Summer FD T, k=6, by Site)	14662.9	0.85	0.51
Biomass (g DW m^{-2})			
Site + s(GDD, Summer FD T, k=6, by Site)	11717.9	1.00	0.52

19 20

Table 5.4 Summary of parametric estimates for generalized additive mixed models (GAMMs)23best modes fitted to vegetative shoot density and above ground biomass shoots from six eelgrass24biomass monitoring sites. EDF: Estimated degrees of freedom. ***= p < 0.001, **= p < 0.01. FD,25freshwater discharge; T, air temperature; and GDD for accumulated growing degree days.

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	Shoot density (no. m ⁻²)	Parametric terms	df	Chisq	Р
28	Model	Site	3	231.60	***
		Smooth terms	EDF	Chi.sq	р
20	Mean max T x	s(Mean max summer T, Summer FD): Site 1	3.88	222.42	***
	summer	s(Mean max summer T, Summer FD): Site 3	3.56	49.33	***
20	FD	s(Mean max summer T, Summer FD): Site 4	3.18	9.75	0.02
30		s(Mean max summer T, Summer FD): Site 6	3.01	71.57	***
21	Biomass (g DW m ⁻²)	Parametric terms	df	F	Р
51		Site	3	170.0	***
32 33		Smooth terms	EDF	F	р
	CDD y gummon ED	s(GDD, Summer FD): Site 1	4.50	18.82	***
	GDD x summer FD	s(GDD, Summer FD): Site 3	2.00	12.34	***
		s(GDD, Summer FD): Site 5	4.40	13.85	***
		s(GDD, Summer FD): Site 6	2.00	25.87	***
34					





5.3.4 Regional temporal trends of eelgrass cover

In a regional analysis, we detected a decline in eelgrass cover, estimated as the proportion of sites with eelgrass cover > 50% (Figure 5.6). The number of sites with eelgrass cover > 50% was higher in 1996 than in 1999 ($X^2 = 45.16$, p < 0.000), in 2019 than in 1999 ($X^2 = 4.74$, p = 0.03), and in 1996 than in 2019 ($X^2 = 19.48$, p < 0.000). Mean eelgrass percent cover between 2011 and 2019 ranged between 28% and 37% and did not vary systematically between years (GLMM; p = 0.27; Figure 5.7 A; see Figure S.2.3). The video footage of the same eelgrass cover monitoring sites surveyed several times between 2011 and 2019 revealed that there was no directional change for each site over time (Figure 5.7 B).



Figure 5.6 Number and location of Hydro-Québec eelgrass cover monitoring sites with eelgrass cover > 50 % and eelgrass cover < 50 % based on A-B: 1996 eelgrass distribution map (base line data prior to decline, Lalumière et al., 1999), C-D: surveys conducted in 1999 (Lalumière et al. 1999) and E-F: surveys in 2019. Figures G-H: represent eelgrass cover in five eelgrass cover classes of Hydro-Québec and CCHRP eelgrass cover monitoring sites visited in 2019. The number of sites visited each year is indicated in parentheses.



Figure 5.7 A) Boxplot of eelgrass cover (%) for each year. Black diamond indicates mean cover (%) for each year. The number of sites visited each year is in parentheses; B) Means (± 1 SE) of eelgrass cover (%) at eelgrass cover monitoring sites surveyed 2011, 2014, and 2019 along the study latitudinal gradient.

5.3.5 Regional-scale comparison of eelgrass density and shoot size in 1995 and 2019

Vegetative shoot density and biomass were lower in 2019 than 1995, prior to the decline in 1999. Mean eelgrass vegetative shoot density in 1995 was 477.67 \pm 32.30 m⁻², while mean density in 2019 across all sites was 213.49 \pm 12.51 m⁻², which represents a marginal difference in density at the *p* = 0.05 level (**Figure 5.8 A**, GLMM, *Z* = -2.00; *p* = 0.05). Mean eelgrass above ground biomass in 1995 was 214.90 \pm 16.13 g DW m⁻², while mean eelgrass above ground biomass in 2019 was 35.93 \pm 3.26 g DW m⁻², which represents a statistically significant difference in biomass (**Figure 5.8 B**, LMM, *F* = 8.44; *p* = 0.01). Mean shoot length in 2019 was 43.7 \pm 0.85 cm (min 11.3; max 104.9), while in 2020 mean shoot length was 41.6 \pm 1.00 cm (min 13.9; max 99.2). There was no significant difference between in shoot length between years (LMM, *F* = 1.79; *p* = 0.18) (**Figure 5.9**).



Figure 5.8 Boxplot of eelgrass A) shoot density m⁻² and B) above ground biomass g DW m⁻² from sites in 1995, prior to the eelgrass drastic decline, and in 2019. The X-axis indicates the site location along the eastern James Bay coast. Dashed box indicates 2019 sites that were near eelgrass biomass monitoring sites. Sites for both years were surveyed in August.



Figure 5.9 Mean \pm SE eelgrass shoot length (cm) along the study latitudinal gradient in 2019 (N = 43) and 2020 (N = 24). Vertical lines indicated maximum eelgrass shoot length reported in Lalumière et al. (1994).

5.3.6 Coastal water properties 1999-2020

Salinity and temperature were significantly different between years (LMM; surface salinity, F = 28.67, p < 0.000; water temperature, F = 42.97, p < 0.000; see **Figure S.2.4**) but we did not detect any temporal trend in salinity or temperature from 1999 to 2020. Within these 11 years, mean salinity varied from 17.1 to 21.1 across the five years it was measured, while water temperature varied from 11.5 to 14.8°C across the seven years it was measured (**Table 5.5**, **Figure 5.10**).

Table 5.5 Surface salinity and water temper	rature (°C) mean \pm	SE based or	n yearly sir	ngle-point
samples at sites visited during the summer (between July to Se	ptember) fr	om 1999 to	o 2000.

Water parameter	Year	Ν	Max	Min	Range	Mean ± SE	Median
Surface salinity	2004	56	23.5	10.0	13.5	18.8 ± 3.21	19.8
	2009	40	24.0	11.0	13.0	18.9 ± 3.02	19.5
	2011	68	24.0	11.0	13.0	21.1 ± 2.70	22.0
	2014	88	23.2	1.70	21.5	19.2 ± 3.70	20.6
	2018	90	21.5	6.8	14.7	21.5 ± 0.31	17.9
	2019	132	21.2	2.2	19.0	17.1 ± 3.54	18.0
	2020	23	21.2	7.8	13.4	21.2 ± 0.97	17.9
Water temperature (°C)	1999	61	17.0	10.5	6.5	14.1 ± 0.17	14.0
	2000	55	22.0	11.0	11.0	14.8 ± 0.32	14.0
	2004	56	17.5	5.50	12.0	11.5 ± 0.35	12.0
	2009	40	16.0	7.00	9.0	12.2 ± 0.32	12.5
	2011	68	18.5	10.0	8.5	14.6 ± 0.20	14.5
	2014	88	18.5	9.70	8.8	14.2 ± 0.19	14.1
	2018	90	20.0	5.5	14.5	13.2 ± 0.35	13.2
	2019	135	19.9	6.97	12.9	12.1 ± 0.21	11.4
	2020	23	19	10.2	8.8	13.5 ± 0.62	13.8



Figure 5.10 A) surface water surface temperature from 1999 to 2020 measured at eelgrass cover monitoring sites. The red dashed line indicates minimum temperature (10 °C) at which eelgrass flowering has been observed (Harrison & Mann, 1975) and B) surface salinity along the study latitudinal gradient from 2004 to 2020 measured at eelgrass cover monitoring sites. The red dashed line indicates the minimum salinity range limit (> 15) for optimal eelgrass growth and photosynthesis (Kamermans et al., 1999; Nejrup & Pedersen, 2008).

5.4 Discussion

The synthesis of historical observations and monitoring over the past three decades quantifies the major decline of eelgrass abundance that occurred between 1995 and 1999 at many locations along the eastern coast of James Bay and the limited post-decline recovery. Most eelgrass meadows surveyed in 2019 along the eastern coast of James Bay had eelgrass cover <50%, and had lower above ground biomass, smaller shoots and marginally lower densities compared to pre-1999 estimates. Indeed, our study showed a 40% loss of dense eelgrass meadows in eastern James Bay since 1996, which, to our knowledge, represents the largest scale eelgrass decline documented in eastern Canada. Though it has been suggested that subarctic eelgrass meadows might expand in response to climate change (Beca-Carretero et al., 2018), the eelgrass declines in James Bay occurred concurrent with environmental conditions associated with a warming climate. Within the northeastern James Bay sector, where LGR discharge is the dominant freshwater source and biomass monitoring was conducted since 1982, we find associations between low eelgrass biomass and density and an interaction between climatedriven warming and regulated freshwater discharge. Low eelgrass shoot density and low above ground biomass were associated with warmer (i.e., high summer temperature for shoot density and high accumulated GDD for biomass) and fresher conditions (i.e., high summer freshwater discharge). These results suggest that warmer and fresher conditions during the growing season are associated with declines in health of James Bay eelgrass meadows. However, the lack of control sites, limited baseline data and the absence of water quality measurements prevent drawing any cause-effect relationships from the patterns we observed. Furthermore, if freshening or another change in water properties (e.g., light penetration, nutrients) associated with river discharge plays a role in the large-scale eelgrass decline that occurred along the entire east coast of James Bay, other freshwater sources besides LGR discharge must be invoked because the LGR flows mostly northward from its river mouth in northeast James Bay. Our analyses show a significant loss of high-density eelgrass cover in southeast James Bay after 1995 but, lacking

quantitative monitoring data across the period of change, the potential environmental drivers contributing to declines in southeast James Bay remain unexplored.

5.4.1 Eelgrass status prior to the decline

Prior to 1996, maximum biomass and vegetative shoot density in northeastern James Bay were within the range of other eelgrass meadows studied in northeastern North America (Clausen et al., 2014, Olesen et al., 2015). Between 1980 to 1995, mean above ground biomass measurements in shallow and deep transects in most sites were within the biomass range based on assessments made prior to hydroelectric development (Curtis, 1974-75). Eelgrass vegetative shoot density was highest in shallow water (< 1 m at low tide), while above ground biomass was similar between shallow and deep transects. This could be attributed to the fact that, while eelgrass density was lower in deep transects, shoots in those transects were possibly taller to compensate for increased light attenuation (Krause-Jensen et al., 2000). In sites 1, 3, 4, and 6, eelgrass abundance was highest at the onset of monitoring, while at site 5 abundance fluctuated. Trends in percent of reproductive shoots from 1982 to 1995 were similar to what was previously described by Lalumière et al. (1994), with percent of reproductive shoots generally below 10%, similar to other perennial eelgrass populations (Olesen, 1999).

5.4.2 Eelgrass regional decline

Between 1995 and 1999, most eelgrass monitoring sites experienced a dramatic decline, losing between 90 and 100% of vegetative shoot density and above ground biomass in both shallow and deep transects. The abrupt decline in sites 1, 2, 3, and 6 resembles a 'threshold response'. Interactions between stressors can trigger a fast collapse of seagrass meadows without

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any major change prior to decline (Connell et al., 2017; Ceccherelli et al., 2018). The drastic decline occurred in both shallower and deeper transects, suggesting that light limitation might not have been the primary cause of the loss. Two sites (4 and 5) closest to the La Grande River showed some declining trends, albeit of lesser magnitude, but both had low density and biomass already in the late 1980s. Eelgrass cover monitoring in 1999 showed that the decline was regional, encompassing the entire eastern coast. Over 90% of the eelgrass meadows in 1999 had eelgrass cover < 50%, and low-cover sites appeared to be evenly distributed along the entire latitudinal range of the study area.

An initial hypothesis for the 1999 eelgrass was a wasting disease outbreak caused by the pathogen *Labyrinthula zosterae*, possibly triggered by the high summer temperature in 1998 (Lemieux & Lalumière, 2000). *Labyrinthula* spp. are colony-forming stramenopiles, which are omnipresent in seagrass populations and can cause black necrotic lesions on the shoots. Sometimes *L. zosterae* become virulent pathogens causing massive and sudden die-offs (Jakobsson-Thor et al., 2020). Laboratory investigations have shown that *L. zosterae* growth in eelgrass generally occurs in salinities above 12 (Sykes & Porter, 1973; McKone & Tanner, 2009) and water temperatures between 15 to 24°C (Tutin, 1938, Dawkins et al., 2018). While it is not possible to completely rule out *L. zosterae* as a potential cause of the drastic decline, the presence of the disease in the eelgrass meadows was not confirmed during the 1999 surveys (Lemieux & Lalumière, 2000). Also, the variable water temperatures and salinity levels along the entire coastline (as seen in **Figure 5.10**) would have most likely limited the rapid spread of the pathogen. Furthermore, Cree reported the drastic decline of eelgrass meadows rather than the blackening of the meadows and shoots (CGW, 2017).

5.4.3 Climate and local drivers of trends of eelgrass abundance in northeastern James Bay

Given the spatial extent and the speed at which the eelgrass decline occurred, the ultimate cause or causes are likely to be linked to large-scale regional drivers, perhaps interacting with local drivers. For northeastern James Bay, we have hypothesized that a large-scale regional driver such as climate could interact with a local driver such as the freshwater discharge of LGR. The GAMM modeling of this study revealed that high shoot density and biomass in most sites located in northeastern James Bay were associated with low summer freshwater discharges with mid to high summer temperatures and accumulated GDD, respectively. This result is consistent with interactive effects between local discharge and regional climate drivers affecting shoot density and biomass.

Although the results do clearly show that a period of climate warming and altered freshwater discharge in eastern James Bay has coincided with rapid eelgrass decline, cause-effect relationships are difficult to establish through monitoring time series, particularly given the potential for multiple stressors and cumulative impacts, which may themselves be correlated over the time series (Adams, 2005; Ban et al., 2010). Furthermore, the lack of control sites, limited baseline data, the heterogeneity of monitoring approaches, and the absence of water quality measurements at biomass monitoring sites represent additional challenges to assessing trends over time and causal relationships.

Observations from 1999 to 2020 showed the salinity and temperature ranges measured in August were well within tolerance ranges for eelgrass (**Figure 5.10**). However, water conditions in spring and early summer may have been different and could have impacted eelgrass productivity. In fact, the year 1998, a year prior to the eelgrass decline, was characterized by high June and July temperatures and accumulated GDD, as well as an exceptionally early ice

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breakup. As a result, climatic conditions of 1998 may have had a greater impact than those after 1999, albeit later conditions may have still contributed to the slow recovery.

While this study was unable to determine whether the eelgrass declines detected in the biomass monitoring sites in northeastern James Bay were primarily climate-driven or primarily due to a climate-freshwater discharge interaction, the potential ramifications of hydroelectric development and climate change on eelgrass productivity are significant enough to warrant further investigations. The methods, interpretation, and data limitations reported here can serve to direct future monitoring and research efforts.

5.4.4 The eelgrass regional status post decline

The eelgrass cover surveys suggest only modest change, following the 1999 decline, for most eelgrass meadows along the eastern coast of James Bay. Although the proportion of sites with > 50% eelgrass cover differed between 1996 and 2019, only 21% of the sites in 2019 have cover > 50%, which is 40% fewer than in 1996. Most sites surveyed in 2019 had low cover (< 25%) and very few sites had eelgrass cover > 70%.

In recent years, eelgrass is less abundant and productive than in the past. The change is detectable in multiple analyses and using different data sources for eelgrass variables. Eelgrass meadows surveyed in 2019 had lower above ground biomass and marginally lower shoot density compared to mean eelgrass biomass and density in 1995. The lower above ground biomass in 2019 is most likely due to smaller eelgrass shoots (max length of 1 m) relative to eelgrass prior to the decline (max length of 2.5 m, Lalumière et al., 1994). Eelgrass shoots appeared to be longer south of the study region, suggesting a possible latitudinal pattern of eelgrass shoot biomass south of the LGR.

While large-scale eelgrass declines typically occur in more southerly and warmer locations (Murphy et al., 2021), widespread declines in northern regions have occurred in recent decades, with important losses reported in the White Sea and along Norway, Sweden, and Denmark coastal waters due to wasting disease outbreaks and eutrophication (Boström et al., 2015; Krause-Jensen et al., 2020). Similar to what was observed in eastern James Bay, many estuaries in these regions have not fully recovered decades after the decline, despite substantial water quality mitigations (Boström et al., 2015). While the ability to recover from perturbation can vary between eelgrass populations due to environmental factors influencing growth and productivity (O'Brien et al., 2018), subarctic eelgrass populations that have slow vegetative spreading, low sexual shoot recruitment, slow biomass turnover, and concomitantly lower genetic diversity may take longer to recover after large-scale declines (Olesen & Sand-Jensen, 1994, Hughes & Stachowicz, 2004, Ehlers et al., 2008, Olesen et al., 2015).

5.5 Conclusion

In the context of eastern James Bay, eelgrass meadows are part of social-ecological systems and provide critical support to animals and humans alike. This study's synthesis of 38 years of eelgrass monitoring in the region corroborates Cree Land Users knowledge. They have observed a gradual decline of eelgrass at some sites in the LGR sector of the coast (the only sector for which there are 1980s monitoring data) during the late 1990s, followed by a drastic decline that appears to have affected eelgrass all along the coast. Cree knowledge of coastal ecosystems extends beyond what monitoring has described in both space and time. The eelgrass changes reported in this study represent only a fraction of what the coastal Eeyou Istchee Cree

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have experienced and observed over the last decades. Changes in eelgrass biomass in northeastern James Bay could be the result of regional climate drivers acting synergistically with local drivers, including the seasonality of LGR freshwater discharge but additional monitoring and assessment, guided by both Cree knowledge and scientific research are required to better resolve how climate change and hydroelectric development affect eelgrass meadows and the services they provide.

Environmental fluctuations in coastal ecosystems where eelgrass is present are common but with ongoing climate changes, fluctuations of salinity, temperature, and nutrient concentrations (to name just a few) may become more frequent and acute in coming decades. These changes can have serious implications for coastal social-ecological systems throughout North America and Europe (IPCC, 2013). In eastern James Bay, however, flow modification related to hydroelectric development and regulation represent an additional local driver for environmental change, which is also likely to change over time, as a further result of climate change. Confidently attributing eelgrass change to regional and local drivers, and identifying possible mitigations against these drivers, represents a necessary and critical step in future management of coastal ecosystems in eastern James Bay and for the continuity of the culture and livelihoods of the Eeyou Istchee Cree who have historically depended on them.

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Chapter 6: General Discussion

Seagrasses, including eelgrass Zostera marina, are critical to animals and humans alike. As anthropogenic pressure in coastal ecosystems is expected to increase in the following decades (Hewitt et al., 2016), monitoring seagrass ecosystems to better understand and predict how these ecosystems respond to change will become an integral aspect of seagrass research. The objectives of this thesis were to contribute to better understanding eelgrass ecosystems by testing a novel approach to retrospective satellite imagery analysis, assessing the spatiotemporal dynamics of eelgrass meadows in subarctic Canada using long-term monitoring data, and evaluating the importance of eelgrass to Canada Geese during their fall migration. In doing so, I have demonstrated that eelgrass meadows can be highly dynamic, with meadows showing different directions of change within one estuary (Chapter 2). I have also demonstrated that the subarctic eelgrass meadows along the eastern coast of James Bay, once considered to be amongst the most extensive in North America (Lalumière et al., 1994), have not fully recovered after a recorded collapse in the late 1990s (Chapter 4). These changes can significantly influence the abundance and distribution of species that rely on eelgrass for habitat or food, such as Canada Geese, that depend upon eelgrass meadows during their fall migration in eastern Canada (Chapter 3).

Access to information regarding the distribution of seagrass habitats is critical for seagrass management and conservation. Due to the increase accessibility to low-cost satellite imagery, the use of satellite imagery to monitor marine and coastal ecosystems is on the rise (Murray et al., 2018). However, compared to tropical and subtropical regions, mapping seagrass in temperate and subarctic areas can be challenging as the water in those regions tends to be more turbid and the substrate on which seagrasses grow is much darker (O'Neil & Costa, 2013;

Reshitnyk et al., 2014; Clyne et al., 2021). These characteristics may restrict the use of satellite imagery in temperate and subarctic regions. Still, several studies have demonstrated that mapping seagrass meadows in temperate regions with mid to high accuracy is achievable under the appropriate conditions (i.e., clear water and continuous seagrass meadows) (Hogrefe et al., 2014; Blakey et al., 2015; Wilson et al., 2019; Forsey et al., 2020). The study presented in Chapter 3, which aimed to map eelgrass in an estuary located in eastern Canada and published in the Canadian Journal of Remote Sensing, has demonstrated the potential of freely available Landsat imagery to map eelgrass habitat in eastern Canada. Results from Chapter 3 also promote the use of Landsat images to better assess seagrass meadows spatiotemporal dynamics. This information will help understand how seagrass meadows respond to climate change which currently represent an important threat to seagrass ecosystems globally (Short & Neckles, 1999). In Chapter 3, I also demonstrate how the information generated by a time-series analysis of satellite images can be used to identify environmental drivers of seagrass change, formulate different hypotheses of change, and complement data collected at different spatial and temporal scales.

While mapping efforts have grown in recent years, the current map depicting the distribution of eelgrass meadows in Canada is incomplete (Environment and Climate Change Canada, 2020). The data used for the eelgrass distribution maps comes from many sources using various methods, including historical data, single observations, and monitoring data. Most of the information compiled is comprised of single observations indicating the presence/absence of eelgrass (Environment and Climate Change Canada, 2020). The mapping approach tested in Chapter 3 could be used to enhance mapping efforts at a national scale and assess eelgrass

change in different bioregions where eelgrass is found (see Murphy et al., 2021), particularly in remote locations that are not readily accessible (Clyne et al., 2021).

Maintaining consistency in sampling design when monitoring ecosystems is critical for detecting changes. Long-term monitoring data can be used to distinguish trends that deviate from recurrent fluctuations (Krause-Jensen et al., 2004; Duarte et al., 2006; Lindenmayer & Likens, 2010), and, when combined with appropriate environmental data, identify drivers underpinning these changes. In Chapter 5, using long-term historical data, I verified a decline in eelgrass density and biomass in northeastern James Bay between 1995 and 1999, and I demonstrated a lack of recovery during the following decades. However, I could not assess the effect of important factors known to influence eelgrass health, such as light availability, salinity, and temperature, because these factors were not measured after 1985 in the eelgrass monitoring stations. As a result, despite monitoring eelgrass meadows in eastern James Bay for almost four decades, several questions about what influences eelgrass abundance and distribution in this region remain unanswered. Collecting information at various spatial scales ranging from chemical constituents in eelgrass tissue that can indicate light or nutrient availability to eelgrass abundance (above ground biomass, shoot density, and percent cover) and meadow size (via remote sensing) could contribute to a better understanding of the factors influencing eelgrass growth and productivity in this region. Measuring water parameters such as salinity, temperature, nutrients, and light availability at high temporal resolution is critical for linking eelgrass growth and productivity to environmental conditions. Most importantly, future monitoring strategies in eastern James Bay must be co-developed with Cree Land Users, local stakeholders, and local and regional Cree governments, allowing for efficient management of eelgrass habitats at the local and regional levels.

Understanding the reciprocal relationships between seagrass and the species that rely on it another important component of efficient eelgrass habitat management and conservation. Compared to Canada Geese populations migrating through the continental interior, populations migrating along coastal routes rely more on coastal resources as staging areas (Reed et al., 1996; Murphy et al., 2021). While eelgrass has a lower energy content than managed terrestrial vegetation (Fox & Abraham, 2017), dense and continuous eelgrass meadows represent an important food source to migratory waterfowl, particularly when no alternative feeding habitats are available (Seymour et al., 2002). In Chapter 4, I demonstrated the influence of eelgrass on Canada Geese distribution, supporting the findings by Seymour et al. (2002) that eelgrass is an important food source during the fall migration in eastern Canada. I also demonstrated how human activities in coastal zones such as hunting influence Canada Geese spatiotemporal distribution, supporting findings of other studies that human disturbances influence stopover behaviour of migratory waterfowl (Béchet et al., 2003; LeTourneux et al., 2021). Simultaneously analyzing the impact of eelgrass and human disturbance on Canada geese habitat use can inform migratory waterfowl management and protect eelgrass-rich coastal estuaries.

Waterfowl (ducks, geese, and swans) are the primary seagrass herbivores in temperate regions and their impact on seagrass above ground biomass varies between species and locations (Valiela, 1995; Kollars et al., 2017). Species such as Brant (*Branta bernicla*) have been observed to regraze the same places every four days, removing approximately 30% of the above ground biomass (Prins et al., 1980). However, the impact on seagrass was shown to be negligible, as a clipping experiment demonstrated that a harvesting regime of about 30% of the above ground biomass gave the highest regrowth of new shoots. While overgrazing of eelgrass by Canada Geese is rare, overgrazing has been observed when birds consume the entire shoots or damage

the meristems. Overgrazing on eelgrass by Canada Geese was observed in 2003 near the Portsmouth River (Great Bay estuary, USA) when their regular food resources were inaccessible due to snow (Rivers & Short, 2007). While the findings in Chapter 3 indicate an eelgrass loss in the Tabusintac Estuary, overgrazing by Canada Geese is unlikely to be a cause of this decline, as the findings in Chapter 3 indicate that geese generally avoided locations where declines were detected. To assess Canada Geese top-down and bottom-up impacts on eelgrass in the Tabusintac Estuary, future studies should consider field observations in combination with exclosure experiments.

Chapter 7: Final Conclusion

Using open-source software, a novel approach to the time-series analysis of Landsat imagery, field surveys, and long-term monitoring data, this thesis contributes to our understanding of eelgrass spatiotemporal dynamics and their importance to migratory waterfowl. Overall, this thesis contributes to advanced knowledge about eelgrass (*Zostera marina*) ecology in Canada. As coastal ecosystems continue to change because of climate change and anthropogenic impacts, it will be critical to assess seagrass changes quickly and effectively. Resource managers, researchers, and local and regional stakeholders will want to use easy-toimplement tools and robust yet straightforward monitoring strategies to evaluate the magnitude and direction of change over large areas to identify stressors before eelgrass collapse occurs. As seagrass ecosystems deteriorate, so do coastal assemblages that depend on eelgrass as habitat and food. Therefore, future seagrass monitoring programs or networks should strive to establish an ecosystem approach to consider broader seagrass ecosystem functions and services when planning and developing monitoring and management strategies.

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Appendix: Supplementary Materials for All Chapters



S.1 Supplementary Material for Chapter 3

Figure S.1.1 Frequencies of the number of gunshots per hour in 2016 and 2017, Tabusintac, New Brunswick, Canada.

Table S.1.1 *P*-values of post hoc comparisons with Holm-Bonferroni adjustment testing for difference in Canada Geese flock size. Values are statistically significant if **p**-values are \leq 0.005; bolded values are significant. Three hunting periods are prior to hunting, high hunting (High H) and low hunting (Low H).

	Comparison	Estimate	S.E.	Z-ratio	P-value
Between AM	Prior to hunting – High H	0.31	0.05	6.39	<0.001
	Prior to hunting – Low H	-0.51	0.03	-18.37	<0.001
	High HA- Low H	-0.82	0.05	-16.28	<0.001
Between PM	Prior to hunting – High H	-0.35	0.02	-14.92	<0.001
	Prior to hunting – Low H	-0.35	0.02	-14.92	<0.001
	High HA- Low H	0.02	0.02	0.74	1.000
Between AM-PM	Prior to hunting	-0.06	0.02	-2.42	0.23
	High H	-0.73	0.05	-15.18	<0.001
	Low H	0.10	0.03	3.67	0.004



Figure S.1.2 Canada Geese flock presence in 375 x 375 m grid for each hunting period for 2016 and 2017, Tabusintac, New Brunswick, Canada.
S.2 Supplementary Material for Chapter 4

S.2.1 Eelgrass shoots collection methods

From 1982 to 1986, sampling of above- and below-ground eelgrass biomass was conducted using a boat-based coring device with a surface area of 0.04 m². Starting in 1988, above ground eelgrass biomass was collected by SCUBA divers within 0.15 m² quadrats (Lalumière 1988b).

From 1982 to 1990, sampling grids from which above ground eelgrass biomass was collected consisted of one or two transects perpendicular to the shore at 0.5 m depth intervals, where five to ten eelgrass samples were collected along the transects. From 1991 to 2009, the sampling sites included five 20 m equidistant line-transects perpendicular to the shore. Six samples were collected along each transect, which was set at different water depths at 0.5 m increments (minimum depth 0.5; maximum depth 2 m).

Eelgrass shoots collected in cores and quadrats were scraped free of epiphytes, counted, and dried before weighing at 105 °C for 24 hrs in 1982 and 1985, and at 70 °C for 72 hrs from 1986 to 2009. Comparative analysis showed no significant difference in eelgrass dry biomass weight between the two different drying methods (Lalumière 1986). In 1982, the above-and belowground biomasses were not separated and only eelgrass vegetative and reproductive shoot densities were retained for that year. Lalumière (1986) estimated that eelgrass dry weight in samples collected in cores in 1985, 1986, and 1987 only represented 60 % of the eelgrass biomass in the samples due to the inability of the boat-based cores to retrieve eelgrass shoots completely intact.

X 7	
Year	Reference
1982	Roche ltée. (1982). Etudes océanographiques de la côte est de la baie James. Tome III. La végétation
1702	littorale. Rapport réalisé pour le compte de la SEBJ. 105 pages + annexes.
1085	Roche ltée. (1985). Études de la végétation aquatique de l'estuaire de la Grande Rivière et de la côte est de la
1965	Baie James. Rapport réalisé pour le compte de la SEBJ. 105 pages + annexes.
	Lalumière, R. (1986). Étude de la zostère marine (Zostera marina) sur la côte est de la baie James – été 1986.
1986	Rapport de Gilles Shooner et Associés pour la Direction Ingénierie et Environnement de la SEBJ. 80 pages. +
	annexes.
	Lalumière, R. (1987a). Caractérisation bio-écologique de quelques zostéraies de la côte est de la baie James.
1987	Rapport de Gilles Shooner et Associés pour la Direction Ingénierie et Environnement de la SEBJ. 82 pages. +
	annexes.
	Lalumière, R. (1988a). Suivi des stations permanentes d'étude de la zostère marine sur la côte est de la baie
1988	James – été 1988. Rapport de Gilles Shooner et Associés pour la Direction Ingénierie et Environnement de la
	SEBJ. 30 pages. + annexes.
	Lalumière, R. & Belzile, L. (1989). Suivi des stations permanentes d'étude de la zostère marine sur la côte est
1989	de la baie James – été 1989. Rapport de Gilles Shooner et Associés pour la Direction Ingénierie et
	Environnement de la SEBJ. 30 pages. + annexes.
	Lalumière, R. & Belzile, L. (1990). Production de zostère marine à la sation Kakassituq, côte est de la Baie
1990	James – 1990. Rapport de Gilles Shooner et Associés pour la Direction Ingénierie et Environnement de la
	SEBJ. 24 pages. + annexes.
	Lalumière, R., Belzille, L. & Lemieux, C. (1992) Étude de la zostère marine le long de la côte nord-est de la
1991	baie James (été 1991). Rapport di Groupe-conseil Génivar inc. Pour le compte du Service écologique de la
	SEBJ. Québec. 20 pages+ annexes.
	Lalumière, R. & Lemieux, C. (1993). Étude de la zostère marine le long de la côte nord-est de la baie James
1993	(1993). Rapport di Groupe-conseil Génivar inc. Pour le compte du Service écologique de la SEBJ. Québec.
	20 pages + annexes.
	Lalumière, R. & Lemieux, C. (1994). Étude de la zostère marine le long de la côte nord-est de la baie James
1994	(1994). Rapport di Groupe-conseil Génivar inc. Pour le compte du Service écologique de la SEBJ. Québec.
	34 pages + annexes.
	Lalumière, R. & Lemieux, C. (1995). Étude de la zostère marine le long de la côte nord-est de la baie James
1995	(1995). Rapport di Groupe-conseil Génivar inc. Pour le compte du Service écologique de la SEBJ. Québec.
	36 pages + annexes.
	Lemieux, C., Lalumière, R., & Laperle, M. (1999). Complexe La Grande. Suivi environnemental 1999. Les
1000	habitats côtiers de la baie James et la végétation aquatique de La Grande Rivière. Rapport présenté à la
1999	Direction Expertise et Support technique de production, Unité Hydraulique et Environnement Hydro-Québec,
	par le Groupe conseil Génivar inc. 73 page + annexes.
	Lemieux, C. & Lalumière, R. (2000). Complexe La Grande. Suivi environnemental 2000 Les habitats côtiers
2000	de la baie James et la végétation aquatique de La Grande Rivière. Rapport présenté à la Direction Expertise et
2000	Support technique de production, Unité Hydraulique et Environnement Hydro-Québec, par le Groupe conseil
	Génivar inc. 68 page + annexes.
	Genivar. (2010). Centrales de l'Eastmain-1-A et de la Sarcelle et dérivation Rupert. Suivi de la zostère
2009	marine de la côte nord-est de la baie James – État de référence 2009. Rapport de GENIVAR Société en
	commandite pour Hydro-Québec et la Société d'énergie de la Baie James. 54 p et annexes.

Table S.2.1 List of reports from which data from eelgrass monitoring sites was compiled.Reports are available at the Hydro-Québec online library (www.cherloc.ca).

Table S.2.2 Eelgrass biomass sampling methods for each site located in northeastern James Bay, Québec, Canada, 1985-2009. Methods defined as follows: C, coring, 0.04 m²; D, dive, 0.15m²; in parentheses is the sampling depth in m; Q/T, number of quadrats per transect, and Q, total number of quadrats. Stations in reports referred to as Site 1 (Attikuan I), Site 2 (Attikuan II), Site 3 (Kakassituq), Site 4 (BMI 2a), Site 5 (Tees Bay), and Site 6a, b (Dead Duck Bay).

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6a	Site 6b
1982			C (0.5-1.5 m);			C (0.5-0.7 m);	
			5 Q/T; 10 Q			5Q/T; 10Q	
1985			C (0.5-1.5 m);			C (0.5-0.7 m);	
			5 Q/T; 10 Q			5Q/T; 10Q	
1986	C (0.5-1.5 m);		C (0.5-1.5 m);		C (0.5-1.5 m);	C (0.5-0.7 m);	
	5 Q/T; 10 Q		5 Q/T; 10 Q//		5Q/T; 10Q	5Q/T; 10Q	
			D (0.5m); 26Q				
1987			D (1.5 m); 6Q	D (1.2 m); 5Q			
1988	D (0.5, 1.0, 1.5, 2.0m);		D (0.5, 1.0, 1.5 m);		D (0.5, 1.0, 1.5 m);		
	10 Q/T; 40 Q		5Q/T; 15Q		5Q/T; 15Q		
1989	D (0.5, 1.0, 1.5, 2.0m);	D (0.5, 1.0, 1.5 m);	D (0.5, 1.0, 1.5 m);		D (T0.5, 1.0, 1.5 m);		D (0.5, 1.0, 1.5 m);
	10 Q/T; 40 Q	10 Q/T; 30 Q	10Q/T; 30Q		10Q/T;30Q		10Q/T; 30Q
1990			D (0.5, 1.0, 1.5 m);				
			10Q/T; 30Q				
1991	D (0.5, 1.0, 1.5, 2.0m);	D (0.5, 1.0, 1.5 m);		D (0.5, 1.0, 1.5 m);			
	10 Q/T; 40 Q	10 Q/T; 30 Q	10Q/T; 30Q	10Q/T; 30Q	10Q/T; 30Q		10Q/T; 30Q
1993	D (0.5, 1.0, 1.5, 2.0m);		D (0.5, 1.0, 1.5 m);				
	10 Q/T; 40 Q		10Q/T; 30Q				
1994	D (0.5, 1.0, 1.5, 2.0m);	D (0.5, 1.0, 1.5 m);		D (0.5, 1.0, 1.5 m);			
	10 Q/T; 40 Q	10 Q/T; 30 Q	10Q/T; 30Q	10Q/T; 30Q	10Q/T; 30Q		10Q/T; 30Q
1995	D (0.5, 1.0, 1.5, 2.0m);	D (0.5, 1.0, 1.5 m);		D (0.5, 1.0, 1.5 m);			
	10 Q/T; 40 Q	10 Q/T; 30 Q	10Q/T; 30Q	10Q/T; 30Q	10Q/T; 30Q		10Q/T; 30Q
1999	D (0.5, 1.0, 1.5, 2.0m);	D (0.5, 1.0, 1.5 m);		D (0.5, 1.0, 1.5 m);			
	10 Q/T; 40 Q	10 Q/T; 30 Q	10Q/T; 30Q	10Q/T; 30Q	10Q/T; 30Q		10Q/T; 30Q
2000	D (0.5, 1.0, 1.5, 2.0m);	D (0.5, 1.0, 1.5 m);		D (0.5, 1.0, 1.5 m);			
	10 Q/T; 40 Q	10 Q/T; 30 Q	10Q/T; 30Q	10Q/T; 30Q	10Q/T; 30Q		10Q/T; 30Q
2009	D (0.5, 1.0, 1.5, 2.0m);	D (0.5, 1.0, 1.5 m);		D (0.5, 1.0, 1.5 m);			
	10 Q/T; 40 Q	10 Q/T; 30 Q	10Q/T; 30Q	10Q/T; 30Q	10Q/T; 30Q		10Q/T; 30Q



Table S.2.3 List of reports from which water parameters and eelgrass cover-abundance class data were compiled. The reports are available at Hydro-Québec online library

(www.cherloc.ca).

Year	Reference	Water parameters	Data extracted from the reports	Raw observations (underwater videos or photos)
1999	Lemieux, C., Lalumière, R., & Laperle, M. (1999). Complexe La Grande. Suivi environnemental 1999. Les habitats côtiers de la baie James et la végétation aquatique de La Grande Rivière. Rapport présenté à la Direction Expertise et Support technique de production, Unité Hydraulique et Environnement Hydro-Québec, par le Groupe conseil Génivar inc. 73 page + annexes.	Temperature	Eelgrass abundance class for 1996 and 1999	NA
2000	Lemieux, C. & Lalumière, R. (2000). Complexe La Grande. Suivi environnemental 2000 Les habitats côtiers de la baie James et la végétation aquatique de La Grande Rivière. Rapport présenté à la Direction Expertise et Support technique de production, Unité Hydraulique et Environnement Hydro-Québec, par le Groupe conseil Génivar inc. 68 page + annexes.	Temperature		NA
2002	Lalumière, R. & Lemieux, C. (2002). Suivi environnemental des projets La Grande-2-A et La Grande-1. La zostère marine de la côte nord-est de la baie James. Rapport synthèse pour la période 1988-2000. Rapport de GENIVAR Groupe Conseil inc. pour la Direction Barrages et Environnement, Hvdro-Ouébec Production. 92 p. et annexes	Temperature		NA
2004	Lemieux, C. & Lalumière, R. (2004). État des zostéraies de la côte est de la baie James, été 2004. Rapport de GENIVAR Groupe Conseil inc. à la Direction Barrages et Environnement, Hydro- Québec Production. 33 p. et annexes.	Temperature Salinity		NA
2009	Genivar. (2010). Centrales de l'Eastmain-1-A et de la Sarcelle et dérivation Rupert. Suivi de la zostère marine de la côte nord-est de la baie James – État de référence 2009. Rapport de GENIVAR Société en commandite pour Hydro-Québec et la Société d'énergie de la Baie James. 54 p. et annexes.	Temperature Salinity		NA
2011	Consortium Waska-Genivar. (2011). Centrales de l'Eastmain-1-A et de la Sarcelle et dérivation Rupert. Suivi de la zostère marine de la côte nord- est de la baie James. Rapport d'étude 2011. Rapport du Consortium Waska-GENIVAR inc. pour Hydro- Québec Production. 57 p et annexes.	Temperature Salinity		Video footage for 12 sites
2014	CGW – Consortium Genivar-Waska. (2017). Eastmain-1-A and Sarcelle Powerhouses and Rupert Diversion. Followup of Eelgrass Meadows on the Northeast Coast of Baie James (James Bay) – Study Report 2014. Report prepared by Consortium GENIVAR-Waska for Hydro-Québec Production. 83 pages and appendices.	Temperature Salinity		Video footage for 11 sites
2019*	Englobe corporation. (2019). Rapport de mission Suivi de la zostère marine de la côte nord-est de la baie James. Rapport préparé pour Hydro-Québec, Montréal, Québec. 7 pages.	Temperature Salinity		Video footage for 71 sites

* Internal report provided by Englobe, which is not available at Hydro-Québec online library

(www.cherloc.ca),

- 29 Table S.2.4 Correlation matrix for predictor factors used in GAMMs (GDD, Accumulated
- 30 Growing Degree Days; IBU, ice breakup dates; FD, freshwater discharge; T, air temperature;
- 31 SST, sea surface temperature). The lower diagonal contains Pearson's correlation
- 32 coefficients, upper diagonal contains p-values. The higher Pearson's correlation coefficients33 are in bold.
- 33 are

	GDD	IBU	Summer	Mean	Max	Min	Summer
			FD	summer	summer	summer	SST
				Т	Т	Т	
GDD	-	0.00	0.13	0.00	0.00	0.00	0.11
IBU	-0.67	-	0.08	0.18	0.27	0.14	0.01
Summer FD	0.38	-0.43	-	0.83	0.80	0.56	0.98
Mean summer T	0.73	-0.34	0.06	-	0.00	0.00	0.37
Max summer T	0.66	-0.28	-0.07	0.96	-	0.00	0.31
Min summer T	0.73	-0.37	0.15	0.94	0.84	-	0.58
Summer SST	0.40	-0.57	0.01	0.23	0.26	0.14	-

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37 **Table S.2.5** Summary of parametric estimated for generalized additive mixed models

(GAMMs) time series fitted to A- vegetative shoot density, B- above ground biomass, and
 percent of reproductive shoots from six eelgrass biomass monitoring sites. EDF: Estimated

40	degrees of freedom.	***= P < 0.001, **=P<0.01.	
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41 42

A- Vegetative shoot density Site 1 (n = 340) Chi.sq Parametric terms df Р *** $R^{2}_{adj} = 0.63$ 682.9 Depth 1 EDF Smooth terms Chi.sq Ρ *** Year, deep eelgrass 4.00 19532 *** Year, shallow eelgrass 4.00 15158 Site 2 (n = 240) Parametric terms df Chi.sq Р $R^{2}_{adj} = 0.84$ *** 1426 Depth 1 Smooth terms EDF Chi.sq Р *** Year, deep eelgrass 4.00 13473 *** Year, shallow eelgrass 4.00 21020 **Site 3** (n = 347) df Parametric terms Chi.sq Р $R^{2}_{adj} = 0.54$ Depth 1 4113 *** Smooth terms EDF Р Chi.sq *** Year, deep eelgrass 6.00 23239 *** Year, shallow eelgrass 6.00 24220 **Site 4** (n = 184) Parametric terms df Chi.sq Р $R^{2}_{adj} = 0.45$ *** Depth 1 177.1 Smooth terms EDF Chi.sq Р *** Year, deep eelgrass 4.00 8702 Year, shallow eelgrass 3.98 7618 *** **Site 5** (n = 245) Р Parametric terms df Chi.sq *** $R^{2}_{adj} = 0.26$ 927.3 1 Depth EDF Smooth terms Chi.sq Р *** Year, deep eelgrass df 3618 *** Year, shallow eelgrass 3.98 1909 Site 6 (n = 247) Parametric terms df Chi.sq Р $R^{2}_{adj} = 0.58$ *** Depth 1 409.1 Smooth terms EDF Chi.sq Р *** 15256 Year, deep eelgrass 3.00 *** Year, shallow eelgrass 3.00 15063

45 46

Site 1 $(n = 340)$	Parametric terms	df	F	
$R^{2}_{adj} = 0.45$	Depth	1	21.1	
5	Smooth terms	EDF	F	
	Year, deep eelgrass	2.99	72.81	
	Year, shallow eelgrass	2.11	18.89	
Site 2 (n = 239)	Parametric terms	df	F	
$R^{2}_{adj} = 0.72$	Depth	1	3.06	
	Smooth terms	EDF	F	
	Year, deep eelgrass	2.97	159.23	
	Year, shallow eelgrass	2.90	52.64	
Site 3 (n = 337)	Parametric terms	df	F	
$R^2_{adj} = 0.61$	Depth	1	2.49	
	Smooth terms	EDF	F	
	Year, deep eelgrass	4.90	50.00	
	Year, shallow eelgrass	4.89	56.82	
Site 4 (n=185)	Parametric terms	df	F	
$R^{2}_{adj} = 0.39$	Depth	1	0.86	
	Smooth terms	EDF	F	
	Year, deep eelgrass	2.94	25.29	
	Year, shallow eelgrass	2.83	16.11	
Site 5 (n =245)	Parametric terms	df	F	
$R^2_{adj} = 0.35$	Depth	1	6.83	
	Smooth terms	EDF	F	
	Year, deep eelgrass	3.81	28.89	
	Year, shallow eelgrass	1.04	24.66	
Site 6 (n=240)	Parametric terms	df	F	
$\mathrm{R}^2_{\mathrm{adj}} = 0.71$	Depth	1	51.92	
	Smooth terms	EDF	F	
	Year, deep eelgrass	3.85	90.18	
	Year, shallow eelgrass	3.76	41.97	

Site 1 (n = 340)	Parametric terms	df	Chi.sq	
$R_{adj}^2 = 0.00$	_ Depth	1.00	0.00	1
-	Smooth terms	EDF	Chi.sq	
	Year, deep eelgrass	1.00	0.00	1
	Year, shallow eelgrass	1.00	0.00	
Site 2 (n = 239)	Parametric terms	df	Chi.sq	
$R^{2}_{adj} = 0.14$	Depth	1	0.00	(
-	Smooth terms	EDF	Chi.sq	
	Year, deep eelgrass	1.00	4.96	(
	Year, shallow eelgrass	1.00	0.00	1
Site 3 (n = 337)	Parametric terms	df	Chi.sq	
$R_{adj}^2 = 0.26$	Depth	1.00	0.00	1
-	Smooth terms	EDF	Chi.sq	
	- Year, deep eelgrass	1.00	0.00	
	Year, shallow eelgrass	1.00	0.00	
Site 4 (n=185)	Parametric terms	df	Chi.sq	
$R^{2}_{adj} = 0.00$	_ Depth	1.00	0.00]
	Smooth terms	EDF	Chi.sq	
	- Year, deep eelgrass	1.00	0.00	1
	Year, shallow eelgrass	1.00	0.00	
Site 5 (n = 245)	Parametric terms	df	Chi.sq	
$R_{adj}^2 = 0.00$	Depth	1.00	0.00]
	Smooth terms	EDF	Chi.sq	
	Year, deep eelgrass	1.00	0.00	1
	Year, shallow eelgrass	1.00	0.00	
Site 6 (n=240)	Parametric terms	df	Chi.sq	
$R^2_{adj} = 0.00$	Depth	1.00	0.00	1
	Smooth terms	EDF	Chi.sq	

Year, deep eelgrass

Year, shallow eelgrass

1.00

1.00

0.00

0.00

0.5

1.00

57 58 59



Figure S.2.2 Mean \pm SE percentage of reproductive shoot for each site from 1982 to 2009 for sites (S) 1 to 4 and from 1982 to 2019 for sites 5 and 6.

Table S.2.6 Candidate models correlating A- shoot density and B- above ground biomass using GAMMs (C- shoot density and D- above ground biomass excluding 1999). The table includes Akaike information criterion values for small sample sizes (AICc), AIC weights (wAIC), and explained deviance (\mathbb{R}^2) (GDD, Accumulated Growing Degree Days; IBU, ice breakup dates; FD, freshwater discharge; T, air temperature; SST, sea surface temperature).

A- Shoot density (no. m ⁻²) from 1985 to 2019				
Model	logLik	AICc	delta	weight
Site + s(Summer FD, Mean max T, k=6, by=Site)	-7312.12	14662.9	0.00	0.85
Site + s(Summer FD, Mean T, k=6, by=Site)	-7314.29	14667.2	4.34	0.10
Site + s(GDD, Summer FD, k=6, by=Site)	-7314.98	14668.6	5.71	0.05
Site + s(Summer FD, Mean min T, k=6, by=Site)	-7317.48	14673.6	10.72	0.00
Site + s(Summer FD, SST, k=6, by=Site)	-7330.93	14700.5	37.61	0.00
Site + s(Summer FD, k=5,by=Site)	-7341.74	14713.9	50.99	0.00
Site + s(GDD, SST, k=6, by=Site)	-7342.83	14724.3	61.41	0.00
Site + s(GDD, k=5, by=Site)	-7361.34	14753.1	90.19	0.00
Site + $s(SST, k=5, by=Site)$	-7389.51	14809.4	146.54	0.00
Site + s(IBU, Mean max T, k=6, by=Site)	-7388.71	14816.1	153.18	0.00
Site + $s(Mean min T, k=5, by=Site)$	-7398.48	14827.4	164.47	0.00
Site + s(IBU, k=5,by=Site)	-7405.68	14841.8	178.87	0.00
Site + s(IBU, Mean min T, k=5, by=Site)	-7405.57	14849.8	186.90	0.00
Site + s(IBU, JJ, k=5, by=Site)	-7412.47	14863.6	200.70	0.00
Site + $s(Mean T, k=6,by=Site)$	-7427.76	14885.9	223.03	0.00
Site + s(Mean max T, $k=6$, by=Site)	-7493.15	15016.7	353.81	0.00
Site	-7608.05	15230.2	567.28	0.00
Null model	-7685.20	15378.4	715.52	0.00

B- Above ground biomass (g DW m ⁻²) from 1985 to 2019						
Model	logLik	AICc	delta	weight		
Site + s(GDD, Summer FD, k=6, by=Site)	-5839.63	11717.9	0.00	1.00		
Site + s(Summer FD, Mean max T, k=6, by=Site)	-5845.42	11729.5	11.59	0.00		
Site + s(Summer FD, Mean T, k=6, by=Site)	-5846.89	11732.4	14.52	0.00		
Site + s(Summer FD, SST, k=6, by=Site)	-5848.69	11736.0	18.12	0.00		
Site + s(Summer FD, Mean min T, k=6, by=Site)	-5848.69	11736.0	18.12	0.00		
Site + s(Summer FD, k=6,by=Site)	-5859.32	11749.1	31.15	0.00		
Site + $s(SST, k=6, by=Site)$	-5885.76	11801.9	84.01	0.00		
Site + s(GDD, SST, k=6, by=Site)	-5887.33	11813.3	95.41	0.00		
Site + s(GDD, k=6, by=Site)	-5895.22	11820.9	102.94	0.00		
Site + $s(Mean min T, k=6, by=Site)$	-5906.58	11843.6	125.66	0.00		
Site + s(Mean T, k=6,by=Site)	-5949.66	11929.7	211.81	0.00		
Site + s(IBU, Mean max T, k=6, by=Site)	-5967.61	11973.9	255.97	0.00		
Site + s(Mean max T, $k=6$, by=Site)	-5981.12	11992.7	274.73	0.00		
Site + s(IBU, Mean min T, k=6, by=Site)	-5977.40	11993.5	275.55	0.00		
Site + s(IBU, k=6,by=Site)	-5984.52	11999.5	281.55	0.00		
Site $+$ s(IBU, T, k=6, by=Site)	-5981.10	12000.9	282.94	0.00		
Site	-6105.52	12225.1	507.21	0.00		
Null model	-6248.35	12504.7	786.81	0.00		

Table S.2.6 Continued

C- Shoot density (no. m ⁻²) from 1985 to 2019 excluding 1999						
Model	logLik	AICc	delta	weight		
Site + s(Summer FD, Mean max T, k=6, by=Site)	-6767.83	13574.4	0.00	0.84		
Site + s(Summer FD, T, k=6, by=Site)	-6769.49	13577.7	3.32	0.16		
Site + s(Summer FD, Mean min T, k=6, by=Site)	-6773.53	13585.8	11.40	0.00		
Site + s(GDD, Summer FD, k=6, by=Site)	-6774.16	13587.1	12.65	0.00		
Site + s(Summer FD, k=5,by=Site)	-6793.70	13617.9	43.47	0.00		
Site + s(Summer FD, SST, k=6, by=Site)	-6793.18	13625.1	50.70	0.00		
Site + $s(Mean T, k=6,by=Site)$	-6799.80	13630.1	55.65	0.00		
Site + s(GDD, SST, k=6, by=Site)	-6801.60	13642.0	67.54	0.00		
Site + $s(SST, k=5, by=Site)$	-6812.41	13655.3	80.88	0.00		
Site + s(GDD, k=5, by=Site)	-6813.30	13657.1	82.65	0.00		
Site + s(Mean max T, $k=6$, by=Site)	-6813.80	13658.1	83.66	0.00		
Site + $s(Mean min T, k=5,by=Site)$	-6815.24	13661.0	86.54	0.00		
Site + s(IBU, Mean max T, k=6, by=Site)	-6832.71	13704.2	129.76	0.00		
Site $+$ s(IBU, mean T, k=5, by=Site)	-6856.95	13752.6	178.23	0.00		
Site + s(IBU, k=5,by=Site)	-6865.12	13760.7	186.3	0.00		
Site + s(IBU, Mean min T, k=5, by=Site)	-6863.10	13764.9	190.53	0.00		
Site	-6922.77	13859.6	285.23	0.00		
Null model	-7002.11	14012.2	437.83	0.00		

Table S.2.6 Continued

D- Above ground biomass (g DW m ⁻²) from 1985 to 2019 excluding 1999						
Model	logLik	AICc	delta	weight		
Site + s(GDD, Summer FD, k=6, by=Site)	-5424.59	10887.9	0.00	0.97		
Site + s(Summer FD, Mean max T, k=6, by=Site)	-5428.53	10895.8	7.87	0.02		
Site + s(Summer FD, Mean T, k=6, by=Site)	-5429.57	10897.9	9.96	0.01		
Site + s(Summer FD, Mean min T, k=6, by=Site)	-5432.50	10903.8	15.83	0.00		
Site + s(Summer FD, k=6,by=Site)	-5441.38	10913.2	25.31	0.00		
Site + s(Summer FD, SST, k=6, by=Site)	-5437.46	10913.7	25.75	0.00		
Site $+ s(SST, k=6, by=Site)$	-5454.69	10939.9	51.93	0.00		
Site + s(GDD, SST, k=6, by=Site)	-5452.25	10943.2	55.32	0.00		
Site + s(Mean T, k=6,by=Site)	-5457.55	10945.6	57.65	0.00		
Site $+$ s(Mean min T, k=6,by=Site)	-5462.43	10955.3	67.39	0.00		
Site + s(GDD, k=6, by=Site)	-5463.89	10958.2	70.31	0.00		
Site + s(Max mean T, k=6, by=Site)	-5471.32	10973.1	85.18	0.00		
Site + s(IBU, k=6,by=Site)	-5496.00	11022.5	134.55	0.00		
Site + s(IBU, Mean min T, k=6, by=Site)	-5502.14	11043.0	155.10	0.00		
Site + s(IBU, Mean T, k=6, by=Site)	-5523.13	11085.0	197.07	0.00		
Site + s(IBU, Mean max T, k=6, by=Site)	-5528.41	11095.6	207.64	0.00		
Site	-5624.00	11262.1	374.19	0.00		
Null model	-5766.37	11540.8	652.85	0.00		



Figure S.2.3 Mean \pm SE eelgrass cover (%) along the study latitudinal gradient in A- 2011, B- 2014, C- 2018, and D- 2019. Vertical dashed line showing sites across years with eelgrass cover (%) between 0 to 50 %. The number of sites visited each year is indicated in parentheses.



Figure S.2.4 Boxplot of A- salinity and B- surface water temperature. Black diamond indicating mean for each year. Different letters above the boxplot indicate significant differences between years. The number of sites visited each year is indicated in parentheses.