DRIVERS OF REGIONAL-SCALE VARIABILITY IN THE ABUNDANCE OF AN INVASIVE BRYOZOAN IN THE KELP BEDS OF THE NORTHWEST ATLANTIC OCEAN

by

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Dalhousie University is located in Mi'kma'ki, the
ancestral and unceded territory of the Mi'kmaq.
We are all Treaty people.

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ABSTRACT

Species distribution models (SDMs) are important tools for predicting changes in the distribution and impact of invasive species due to climate change. In this thesis, I developed and applied SDMs predicting the abundance of *Membranipora membranacea*, a bryozoan invasive to kelp beds in the northwest Atlantic Ocean (NWA). With a large, compiled dataset, I employed a multimodel inference approach to select relevant predictor variables for SDMs for *M. membranacea*, and developed a conceptual framework from my results to guide variable selection for SDMs of other organisms (Chapter 2). I then constructed SDMs predicting the abundance of *M. membranacea* in the NWA (Chapter 3). The future abundance distribution of the bryozoan depended on the magnitude of climate change and possible invasions of *M. membranacea* from new source populations. My results are applicable to the management of *M. membranacea* and kelp beds in the NWA, and to invasive species and SDMs generally.

LIST OF ABBREVIATIONS AND SYMBOLS USED

Abbreviation/Symbol	**Definition**
%	percent
~	approximately
<	less than
≤	less than or equal to
>	greater than
Δ	delta (change in)
∑	sum of
√	square root
®	registered trademark
°C	degrees Celsius
°N	degrees north
°W	degrees west
1-I	one-month integral
1-Lin	one-month linear
1-Log	one-month logarthmic
1-M	one-month mean
1-Q	one-month quadratic
3-I	three-month integral
3-Lin	three-month linear
3-Log	three-month logarithmic
3-M	three-month mean
3-Q	three-month quadratic
6-I	six-month integral
6-Lin	six-month linear
6-Log	six-month logarithmic
6-M	six-month mean
6-Q	six-month quadratic
AC	*Agarum clathratum*

Abbreviation/Symbol	**Definition**
AIC	Akaike's information criterion
AVE	average error
b	model intercept
BEZI	zero-inflated beta distribution
b_{raw}	raw-scale regression coefficient
cm	centimetres
cond.	conditional
CR	Crooks Island
dAIC	change in AIC
df	degrees of freedom
DFO	Fisheries and Oceans Canada
E	conditional expectation
e.g.	exempli gratia (for example)
ERSST	Extended Reconstructed Sea Surface Temperature
ESI	Eastern Shore Islands
et al.	et alia
etc	et cetera
F	F test statistic
F_i	fetch
GAM	generalized additive model
GLMM	generalized linear mixed model
GoM/GOM	Gulf of Maine
GoS	Gulf of St. Lawrence
GR	growth rate
h	hour
HB	Halibut Island
i.e.	id est (that is)
IST	in situ temperature
k	number of clusters
$Kelp_R$	relative kelp density

Abbreviation/Symbol	**Definition**
Kelp_T	total kelp density
km	kilometres
LB	Labrador
LD	*Laminaria digitata*
LI	Long Island
log	logarithm
logLik	log likelihood
m	metres
m	model slope
marg.	marginal
ME	Maine
mm	millimetres
MO	The Moll
n	sample size
N	normal distribution
NB	negative binomial distribution
NB	New Brunswick
NF	Newfoundland
no.	number
NOAA	National Oceanic and Atmospheric Administration
NS	Nova Scotia
NWA	northwest Atlantic Ocean
ODMAP	Overview, Data, Model, Assessment and Prediction
p	p-value
PEI	Prince Edward Island
PSU	practical salinity units
PU	Pumpkin Island
QC	Quebec
QQ	quantile-quantile
r	Pearson correlation

Abbreviation/Symbol	**Definition**
R^2	coefficient of determination
RCP	Representative Concentration Pathway
REI	relative wave exposure index
RMSE	root mean squared error
RT	residence time
SD	standard deviation
SDM	species distribution model
SE	standard error
SL	*Saccharina latissima*
SP	Speck Island
SR	Shag Rock
SST	sea surface temperature
STR	settlement rate
T	temperature
™	trademark
TU	Tuffin Island
u_b	bottom orbital velocity
UB	Ungava Bay
var	variance
V_i	average wind speed
W_i	wind frequency
WI	White Island
x	times
y_i	predicted values
$\hat{y}_i$	observed values
Y-Lin	calendar-year linear
Y-Log	calendar-year logarithmic
Y-Q	calendar-year quadratic
α	probability of observing 0
θ	unknown parameter controlling variance

Abbreviation/Symbol	**Definition**
μ	mean
ρ	Spearman rank correlation
σ	standard deviation
τ_{00}	random intercept variance

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CHAPTER 1

INTRODUCTION

1.1 Background

Over evolutionary time scales, species are generally confined to a specific geographic range that they have evolved to inhabit, to which they are termed “native” (Webb 1985, Pyšek et al. 2004). However, through human-mediated means, organisms can sometimes become established in new areas as non-native species (Richardson et al. 2011, Jeschke et al. 2014, Gilroy et al. 2017). Invasive species are a subset of non-native species that exert negative impacts on organisms and ecosystems in their introduced range (Colautti & MacIsaac 2004, Convention on Biological Diversity 2008, Richardson et al. 2011). Invasive species affect their invaded ecosystems through numerous mechanisms (Ehrenfeld 2010; see also section 2.1 of this thesis), which are often linked to an increase in the abundance of the invader in the absence of natural competitors or predators due to a lack of shared evolutionary history between the invader and recipient biological community (David et al. 2017). To date, biological invasions have had a devastating impact globally on the biodiversity and function of ecosystems (Ricciardi & MacIsaac 2011, Simberloff et al. 2013, Gallardo et al. 2016) and the services they provide to humans (Charles & Dukes 2008, Katsanevakis et al. 2014, Vilà & Hulme 2017). Invasions are expected to increase in frequency and impact in the future due to climate change (Rahel & Olden 2008, Hellmann et al. 2008, Mainka & Howard 2010, Rehage & Blanchard 2016, Hulme 2017, Meyerson et al. 2019).

Global governance structures and the international scientific community have recognized the importance of developing strategies for managing biological invasions (Lodge et al. 2006, Convention on Biological Diversity 2010, UN 2015, Giakoumi et al. 2019). Examples of strategies employed to detect and prevent invasions, wherever possible, include ballast water treatment (Bax et al. 2003, Scriven et al. 2015, Holbech & Pedersen 2018), border searches (Hulme 2006, Simberloff 2014), and DNA-based monitoring (Porco et al. 2013, Darling et al. 2017). Established invasive species have been controlled through methods such as biological control (Hoddle 2004, Messing & Wright 2006, Heimpel & Mills 2017), physical removal and culling (Parkes & Panetta 2009, Simberloff 2014), containment (Forrest et al. 2009, Robertson et al. 2020), and protection of native ecosystems and species (Giakoumi et al. 2016, 2019, Epstein & Smale 2017). Regardless of the employed strategies, knowledge of both the current range of an invasive species and its projected future range under climate change is essential for informing prevention and management (Srivastava et al. 2019).

Species distribution models (SDMs) use data on species occurrence or abundance and a set of environmental or biotic predictor variables to generate correlative relationships (although, more rarely, mechanistic approaches are also employed; Dormann et al. 2012) which can predict the distribution of organisms in space and time (Elith & Leathwick 2009, Guisan et al. 2017). With broad accessibility of the necessary data (Guisan et al. 2017) and software (Jarnevich et al. 2015), species distribution modelling has become a widely used tool for predicting the present and future distribution of organisms (Guisan & Thuiller 2005, Elith & Leathwick 2009, Franklin 2013), and is thus commonly applied to invasive species (Jeschke & Strayer 2008, Srivastava et al. 2019). However, despite their ease of application, the utility of SDMs as an aid to invasive species management, or any other application for that matter, relies on model accuracy (Pearson 2007). The accuracy of SDMs can be affected by many factors, including data quality (Robinson et al. 2011), the appropriateness of the applied model (Jarnevich et al. 2015), and the context in which the model is applied (e.g. extent of extrapolation; Elith & Leathwick 2009, Heikkinen et al. 2012). An important factor that can be overlooked is the selection and use of appropriate predictor variables (Barbet-Massin & Jetz 2014, Fourcade et al. 2018). Multiple studies have provided recommendations on various aspects of predictor selection for SDMs (Synes & Osborne 2011, Williams et al. 2012, Barbet-Massin & Jetz 2014, Petitpierre et al. 2017, Fourcade et al. 2018), but a general framework guiding the selection of predictors for SDMs is lacking. Therefore, despite the status of SDMs as one of the most frequently used modelling techniques in the ecological literature, there are still knowledge gaps to be addressed.

1.2 Study system

Membranipora membranacea is a invasive bryozoan, a small invertebrate which forms colonies composed of multiple semi-autonomous units called zooids (Ryland 2005). Native to Europe and the west coast of North America (Schwaninger 1999, 2008), *M. membranacea* was introduced to the Gulf of Maine in 1987 (Lambert 1990) and has subsequently spread throughout the northwest Atlantic Ocean (NWA), as far north as southern Labrador (Caines & Gagnon 2012). The bryozoan grows on the blades of native kelps in the region, compromising their structural integrity (Krumhansl et al. 2011) and causing them to break off when the kelp is exposed to strong waves (Lambert et al. 1992, Scheibling & Gagnon 2009). Kelp populations in the NWA have sustained substantial losses as a result of colonization by *M. membranacea* (Lambert et al. 1992, Scheibling & Gagnon 2009, Filbee-Dexter et al. 2016), which is concerning due to the importance of kelps as a keystone species providing habitat (Gotceitas et al. 1995, Christie et al. 2009, Teagle et al. 2017) and food (Krumhansl & Scheibling 2012, Filbee-Dexter & Scheibling 2012, Wernberg et al. 2019) to a wide array of organisms. Management options for *M. membranacea* are limited; for example, the opportunity to control the establishment and spread of the bryozoan has passed, as it is long-established and widespread in the NWA. For the same reason, its eradication through physical removal or other means would require an impossibly gargantuan effort to implement. However, estimates of the present and future distribution of the bryozoan could help predict future spatial patterns of the impact of the bryozoan, as well as patterns of spread to currently unoccupied regions. These predictions could inform management actions such as the placement of marine protected areas (MPAs) for kelp (e.g. by avoiding placing MPAs in areas anticipated to be highly impacted by the bryozoan; *sensu* Giakoumi et al. 2016).

1.3 Objectives

The main objective of my thesis is to construct and employ SDMs to estimate the current and future distribution of the invasive species *M. membranacea* in the NWA. In Chapter 2, I lay the foundation for an SDM for *M. membranacea* by compiling the largest available dataset of observations of abundance and potential predictor variables and comparing multiple candidate models to select the optimal set of predictors for use in an SDM. I also use my analysis as the foundation for a conceptual framework to guide variable selection in future species distribution modelling studies. In Chapter 3, I construct an SDM for *M. membranacea* based on the results of my analysis in Chapter 2, and project the model in the NWA under present and future climate scenarios. I also investigate the evidence for a shift in the relationship of the bryozoan to its predictor variables over time within the NWA, and the potential effect of an additional invasion of *M. membranacea* from a new source population. Lastly, in Chapter 4, I synthesise my findings from Chapters 2 and 3 and discuss their implications for *M. membranacea* and for SDMs and their application to invasive species in general.

CHAPTER 2

VARIABLE SELECTION FOR SPECIES DISTRIBUTION MODELS: A CASE STUDY WITH AN INVASIVE MARINE BRYOZOAN[1]

2.1 Abstract

Invasive species in marine environments constitute a major ecological threat that necessitates management action. Management of marine invasive species can be informed by using species distribution models (SDMs) to predict their range and potential impact. However, the accuracy and utility of SDMs can be compromised when predictor variables are selected without careful consideration of their ecophysiological relevance to the focal organism. I conducted an in-depth examination of the variable selection process by evaluating predictors to be used in SDMs for *Membranipora membranacea*, an ecologically significant marine invasive species with a complex lifecycle, as a case study. Using an information-theoretic and multi-model inference approach based on generalized linear mixed models, I assessed multiple environmental variables (depth, kelp density, kelp substrate, temperature, and wave exposure) in terms of their relationships, and relative and absolute importance as predictors of the abundance of multiple life stages of *M. membranacea.* I found that the relative importance of a predictor, the metric calculated to represent a predictor, and whether a predictor was proximal or distal were

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[1] Pratt CJ, Denley D, Metaxas A. Variable selection for species distribution models: a case study with an invasive marine bryozoan. Oecologia. Submitted May 7, 2021.

I collected and analysed field data, developed the study design, conducted data analysis, and wrote the manuscript. My co-authors Anna Metaxas and Danielle Denley collected field data, supervised the study design and analysis, and edited the manuscript.

important considerations in the variable selection process. Data constraints (e.g. sample size, lack of proximal predictor data) may inhibit accurate assessment of predictor variables during variable selection. Importantly, my results suggest that species-environment relationships derived from small-scale studies can inform variable selection for SDMs at larger spatiotemporal scales. I developed a conceptual framework for variable selection for SDMs which can be applied to most contexts of species distribution modelling, but particularly those with several candidate predictors and a large dataset.

2.2 Introduction

Invasive species are a major threat to biodiversity (Bax et al. 2003, Millennium Ecosystem Assessment 2005, Halpern et al. 2008, Molnar et al. 2008, IPBES 2019), negatively affecting invaded ecosystems through different mechanisms, including competitive displacement of native species (Robinson et al. 2005, Cheng et al. 2009, Ekesi et al. 2009), habitat modification (Crooks 2002, Cuddington & Hastings 2004, Wallentinus & Nyberg 2007) and alteration of food webs (Kimbro et al. 2009, Miehls et al. 2009, David et al. 2017). The impacts of invasive species can also spread as they expand their invasive range (Sorte et al. 2010). As a result, biological invasions can reduce ecosystem services (Charles & Dukes 2008, Katsanevakis et al. 2014, Walsh et al. 2016) and have negative socioeconomic impacts (Streftaris & Zenetos 2006, Pejchar & Mooney 2009). Eradication is a viable option for many terrestrial invasive species (Parkes & Panetta 2009, Robertson et al. 2017); however, high environmental connectivity in marine environments and long-range dispersal (Geburzi & McCarthy 2018) make marine invasive species difficult to eradicate or control (Thresher & Kuris 2004, Molnar et al. 2008, Giakoumi et al. 2019). Although management options are limited, particularly for widespread marine invasive species (Forrest et al. 2006, Lehtiniemi et al. 2015), impacts from such species can still be mitigated through protection of native organisms (Giakoumi et al. 2016, Epstein & Smale 2017) and by enacting measures to delay or prevent secondary spread to new areas (Ojaveer et al. 2015).

Species distribution models (SDMs) are useful tools for informing management of marine invasive species by predicting the current distribution and future spread of the invader (Elith et al. 2010, Mainali et al. 2015, Battini et al. 2019, D'Amen & Azzurro 2020). However, although the performance of these models is contingent on the use of environmental predictors with ecophysiological relevance to the modelled organism, many species distribution modelling studies do not fully address this requirement (Elith & Leathwick 2009, Austin & Van Niel 2011, Synes & Osborne 2011). The accuracy and utility of SDMs can be compromised when commonly available predictors are used without ecological justification (Austin 2007, Elith & Leathwick 2009), linear relationships are assumed and fit for predictors which may affect species distribution non-linearly (Austin 2007, Santika & Hutchinson 2009), and predictors are not considered at appropriate spatial (Dormann 2007) or temporal (Mod et al. 2016, Gardner et al. 2019) scales or in terms of the appropriate metric (DeWeber & Wagner 2018). Inadequate knowledge of variable importance may also impair the selection of relevant and informative predictor variables (Austin & Van Niel 2011). Additionally, for organisms with complex life cycles (sensu Wilbur 1980), the predictive performance and management applicability of SDMs can be diminished if they do not consider multiple life stages, which may each respond to different predictors (Costa et al. 2015, Asch &

Erisman 2018). Therefore, variable selection involving a detailed investigation of the relationships between the focal species and its potential predictors, based on existing knowledge and ecological theory, should be undertaken prior to the construction of an SDM. Here, I provide an example of this process of variable selection for a well-studied and ecologically significant marine invasive species with a complex life cycle.

Membranipora membranacea is a widely distributed, invasive bryozoan inhabiting kelp bed ecosystems in the northwest Atlantic Ocean. Native to Europe and the western coast of North America (Schwaninger 2008), the bryozoan was first observed in the northwest Atlantic in the Gulf of Maine in 1987 (Berman et al. 1992) and has since spread to occupy a large range including Nova Scotia (Watanabe et al. 2010), coastal Newfoundland and southern Labrador (DFO 2011, Caines & Gagnon 2012), and the Gulf of St. Lawrence (Denley et al. 2019b). The bryozoan has an annual, complex lifecycle in which planktonic larvae settle out of the water column (Saunders & Metaxas 2007) and grow to form large, encrusting colonies on kelps (Berman et al. 1992, Scheibling et al. 1999). Encrustation by *M. membranacea* weakens the tissue of kelp blades (Krumhansl et al. 2011) increasing their susceptibility to breakage during periods of high wave action (Lambert et al. 1992, Scheibling & Gagnon 2009). Consequently, *M. membranacea* has been linked to large-scale declines in kelp populations in its invasive range (Filbee-Dexter et al. 2016). Since the abundance of the bryozoan increases with temperature, its negative impact on kelp bed ecosystems is predicted to increase with ocean warming due to climate change (Saunders et al. 2010, Denley et al. 2019a). Because of the ecological and economic importance of kelp bed ecosystems (Wernberg et al. 2019), robust SDMs are needed for the abundance of *M. membranacea* in the northwest Atlantic to inform critical management strategies.

Variable selection for *M. membranacea* is facilitated by past studies that have identified both environmental factors and biological characteristics of kelp beds affecting the abundance of multiple life stages (newly settled and adult colonies) of the bryozoan in its invasive range. Sea water temperature can affect the abundance of both newly settled and adult colonies (Saunders & Metaxas 2007, Scheibling & Gagnon 2009, Caines & Gagnon 2012). Wave exposure has been shown to have a negative quadratic relationship with the abundance of newly settled colonies (Caines & Gagnon 2012). Wave exposure may also affect the abundance of adults, as flow velocity affects adult colony abundance (Pratt 2008, Arkema 2009). Depth has been positively correlated with the abundance of newly settled colonies in multiple studies (Saunders & Metaxas 2007, Denley & Metaxas 2017b). Lastly, the species of kelp on which *M. membranacea* grows can influence the abundance of both settler and adult life stages (Saunders & Metaxas 2009b), and the relative abundance of kelp species within mixed species kelp beds may affect the abundance of adult colonies of *M. membranacea* by altering its population dynamics (Denley et al. 2019a).

Although past research has identified multiple factors affecting the abundance of *M. membranacea*, existing knowledge is insufficient to select the most relevant predictors for use in SDMs for this species. Firstly, there is a mismatch between the large spatial (>2000 km) and temporal (decadal) scales of the invasion of *M. membranacea* and those of these past studies, which were conducted over limited temporal (n = 2-3 years) and geographic (<50 km) ranges. Additionally, the relative importance of the predictors of abundance of *M. membranacea*, as well as the absolute importance (sensu Galipaud et al. 2017) of some candidate predictors (e.g. wave exposure and kelp density), have not been established. Lastly, multiple details regarding the effects of temperature and wave exposure on the abundance of newly settled and adult colonies of the bryozoan are not well-established, including: 1) the temporal windows over which these metrics should be considered; 2) the shapes of the potential relationships between wave exposure and the abundance of *M. membranacea*; and 3) whether the mean or thermal integral (cumulative sum) of temperature over a given temporal window is the superior metric for prediction.

Although SDMs should ideally employ the most ecologically relevant, proximal predictors, data for these are often unavailable at the requisite spatiotemporal scales. For example, in the case of benthic marine organisms, *in situ* temperature at depth (IST) is often an ecologically relevant proximal predictor. However, because of limited availability of IST data, the distal predictor sea surface temperature (SST) is often the only option for large-scale modelling efforts (Stobart et al. 2016). When SST is used in SDMs where observations have been collected from multiple depths, depth should also be incorporated into the models to account for depth-based temperature variability (Duffy & Chown 2017). However, SST and depth may not be an adequate approximation of IST in all cases and relationships are not consistent in space and time (Castillo & Lima 2010, Stobart et al. 2016).

In this study, I demonstrate a detailed process of predictor variable selection that is often absent from the current SDM literature, using the invasive bryozoan *M. membranacea* as a case study. Specifically, I model the relationships between two life history stages (newly settled and adult colonies) of the bryozoan and their potential predictors using the largest available dataset to date of observations throughout the northwest Atlantic Ocean. After using past findings and ecological reasoning to identify relevant predictor variables and their appropriate metrics, I take an information-theoretic, multi-model inference approach to fulfill the following objectives: 1) determine the optimal metrics and most relevant temporal scales for environmental predictors of abundance; 2) quantify the relationships and determine the importance of environmental predictors in driving the abundance of different life history stages; 3) compare my quantified relationships and variable importance to the results of past studies conducted at smaller spatiotemporal scales; and 4) compare the performance of models based on a distal (SST) and proximal (IST) predictor of temperature. This study provides a conceptual framework for selecting variables for inclusion in SDMs that is especially applicable to organisms with numerous potential drivers of abundance for which ample species and predictor data are available.

2.3 Materials and methods

2.3.1 Dataset

I compiled a dataset of all available observations of the abundance of adult colonies (measured as the percent cover of adult colonies per unit area of kelp blade) and newly settled colonies (settler density, measured as the number of newly settled colonies per unit area of kelp blade) of *M. membranacea* on the three numerically dominant kelp species (*Agarum clathratum, Laminaria digitata,* and *Saccharina latissima*) in the northwest Atlantic Ocean, along with data on their potential environmental drivers [depth, kelp density, kelp substrate (species), sea surface temperature (SST), *in situ* temperature (IST), and wave exposure]. The dataset included historical data from the literature spanning over 2800 km and 30 years (n = 20 and 13 sites, for percent cover and settler density, respectively) and new data I collected from 9 additional sites on the Atlantic coast of Nova Scotia, Canada in 2018 and 2019 (Figure 2.1, Table A.1; for details, see Appendix A.1).

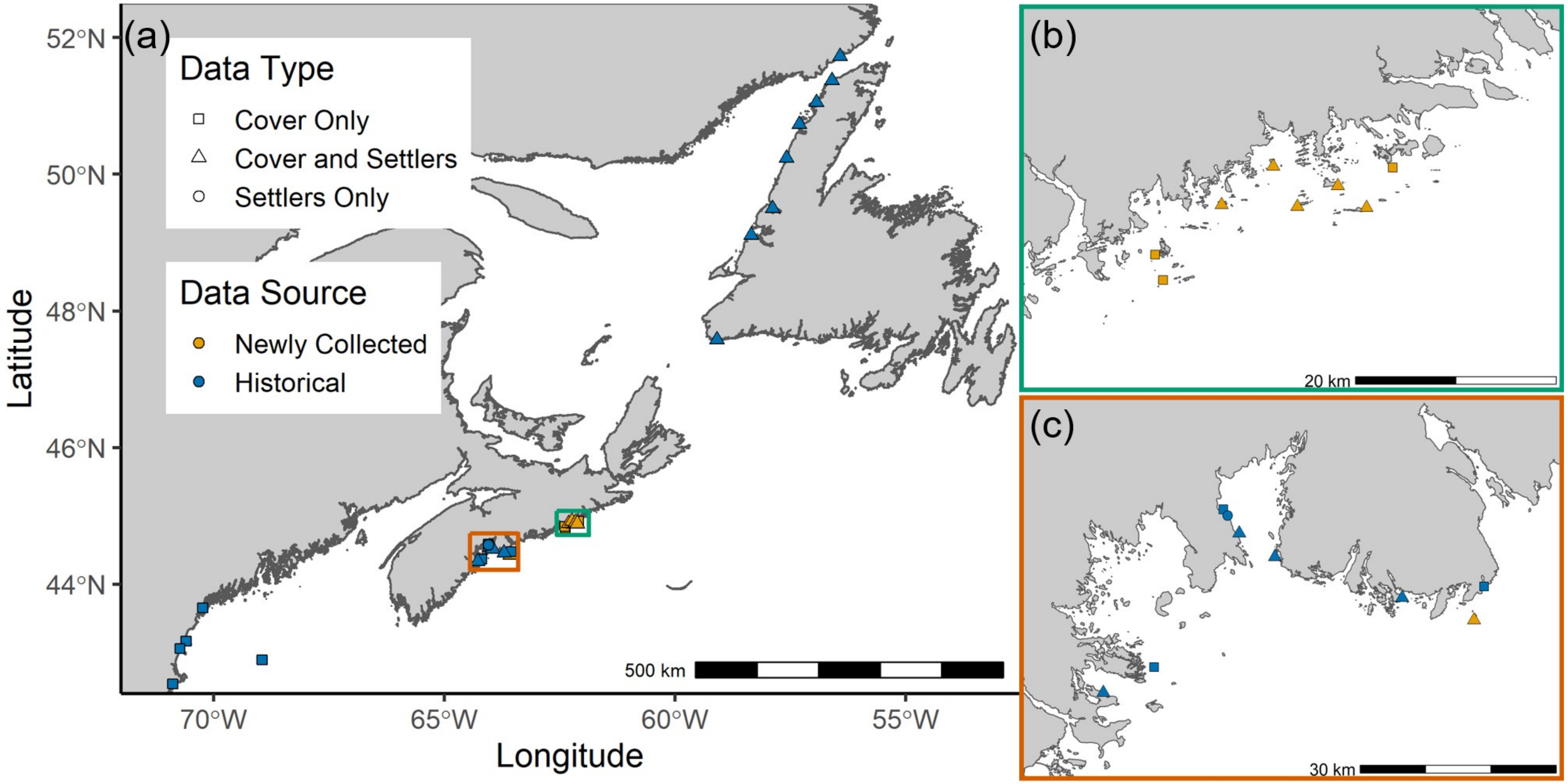

Figure 2.1 (a) Locations of historical (1987-2017) and newly collected (2018-2019) observations of percent cover and settler density of *Membranipora membranacea* in the northwest Atlantic Ocean. Insets show sites in (b) the Eastern Shore Islands and (c) the southwestern shore of Nova Scotia, corresponding to green and orange boxes in (a), respectively.

2.3.2 Calculation of response variables

Percent cover of *M. membranacea* in all previous studies and new collections was either measured directly on individual kelp blades or estimated from imagery (as for my newly collected data as detailed in Appendix A.1.1). I found no difference in estimates of percent cover between methods (Appendix A.2) and therefore combined percent cover data from all studies irrespective of collection method.

Although all previous studies and my new collections used the same method to enumerate settler density on individual collected kelp blades (for details see Appendix A.1.1), the definition of a settler varied among studies: settlers were defined either as colonies <1 cm in diameter or as colonies with ≤2 zooid rows (typically 0.5 - 0.9 mm in diameter; Saunders & Metaxas 2007). I used concurrent observations of abundance for multiple colony size classes from Caines and Gagnon (2012) to generate a relationship between colonies ≤2 zooids and <1 cm in diameter. I then used this relationship to estimate the abundance of colonies with ≤2 zooid rows in studies which defined settlers as colonies <1 cm (Appendix A.3). This allowed us to combine data across studies by standardizing settlers as colonies with ≤2 zooid rows.

I averaged percent cover and settler density across all individuals of a given kelp species within each depth, site, and sampling date, and bounded the data between May and November to encompass the approximate annual growth period of *M. membranacea* (Table A.1; Appendix A.4).

2.3.3 Identification and calculation of relevant predictor variables

2.3.3.1 Temperature

I obtained time series of daily sea surface temperature (SST) data from NOAA's "CoralTemp" dataset (NOAA Coral Reef Watch 2020) at a 5-km spatial resolution for the six months leading up to the sampling date for each observation of percent cover and settler density in my dataset. In cases where SST data were unavailable at a given site, I used the mean value from all grid cells within a 6-km radius of the site. I also compiled *in situ* temperature (IST) data corresponding to observations of percent cover and settler density from past studies (only available from sites in Nova Scotia; Table A.1).

I calculated multiple temperature metrics, consisting of the mean and thermal integral over different time periods prior to a given observation of percent cover or settler density, for both IST and SST data (Table 2.1). For each period prior to the date of observation of percent cover or settler density, I calculated thermal integrals by summing standardized daily temperatures (calculated by adding 1.8°C to daily average temperatures to avoid negative values; Saunders & Metaxas 2007). To calculate thermal integral, gaps in IST data (n = 1-15 days) were filled using the mean temperature for the given month, site, and depth. Mean temperature metrics were calculated as the mean of daily average temperatures over the given period prior to the date of observation of percent cover or settler density. Thermal integral can effectively predict percent cover (Scheibling & Gagnon 2009, Caines & Gagnon 2012) and settler density of *M. membranacea* (Saunders & Metaxas 2007, Caines & Gagnon 2012). However, I also investigated mean temperature metrics since they do not rely on time series of continuous daily temperature and, therefore, offer greater flexibility in the temperature data that can be used in predictive models. I investigated three-month temperature metrics as predictors of percent cover based on the findings of Scheibling & Gagnon (2009) that the three-month integral of temperature had a strong relationship with annual peak percent cover. I also assessed six-month temperature metrics to account for the potential effects of temperature on *M. membranacea* over longer timescales that encompass multiple stages in its lifecycle (larvae, reproduction, etc.; Saunders & Metaxas 2008, Caines & Gagnon 2012). For settler density, I investigated one-month temperature metrics since larvae of *M. membranacea* have an average planktonic larval duration of 4 weeks (Yoshioka 1982), and three- and six-month metrics because the abundance of settlers may be explained by thermal indices which affect both the planktonic larval period and the adult colonies producing the larvae (Caines & Gagnon 2012).

Table 2.1 Summary of candidate temperature (SST or IST) and REI metrics considered as predictors of percent cover and settler density. Time periods in the metrics refer to the period prior to a given observation of percent cover or settler density over which temperature or wind data (for REI) were averaged or summed. One-month metrics were only considered as candidate predictors in models for settler density.

Model Type	Temperature		REI	
	Metric	Abbreviation	Metric	Abbreviation
Settler density models only	one-month integral	1-I	one-month linear	1-Lin
	one-month mean	1-M	one-month logarithmic	1-Log
			one-month quadratic	1-Q
Percent cover and settler density models	three-month integral	3-I	three-month linear	3-Lin
			three-month logarithmic	3-Log
	three-month mean	3-M	three-month quadratic	3-Q
			six-month linear	6-Lin
	six-month integral	6-I	six-month logarithmic	6-Log
			six-month quadratic	6-Q
	six-month mean	6-M	calendar-year linear	Y-Lin
			calendar-year logarithmic	Y-Log
			calendar-year quadratic	Y-Q

I examined the relative effects of seasonal temperature variation (day of year) and site- or year-specific thermal anomalies using residual regression (Graham 2003). I generated generalized additive models (GAMs) of the non-linear relationship between day of the year (1-365; independent variable) and all observations of each temperature metric (log-transformed if necessary to satisfy model assumptions) and used the residuals to represent temperature anomalies in subsequent GLMMs (SST anomaly in section 2.3.4.3). I used the day of the year to represent seasonal average temperature variation in the northwest Atlantic (seasonal SST in section 2.3.4.3).

2.3.3.2 Wave exposure

I calculated wave exposure using the relative wave exposure index (REI) after Krumhansl & Scheibling (2011):

$$REI = \sum_{i=1}^{16} (V_i \times W_i \times F_i) \tag{2.1}$$

where V_i and W_i are average wind speed (km h^{-1}) and wind frequency over a given temporal window, and F_i is fetch (km; bounded at 2000 km for a given direction) from the *i*th cardinal direction (north, north-northeast, northeast, east-northeast, etc.), in 16 bins of 22.5° centred on each direction. I obtained wind data from weather stations within a maximum distance of ~100 km from each site, based on data availability, proximity, and geographical representativeness, from Environment and Natural Resources Canada's Historical Climate Database (http://climate.weather.gc.ca) for Canadian sites and NOAA's National Data Buoy Center (https://www.ndbc.noaa.gov) for sites in the Gulf of Maine (Figure A.3). REI was linearly related to *in situ* wave exposure measured as bottom orbital velocity at 5 sites (Appendix A.5).

To calculate metrics of REI for each observation, I first averaged hourly wind data over the same time periods as for the temperature metrics (one, three and six months), as well as over the calendar year of a given observation to describe the average exposure conditions at that site. I then transformed the time-averaged REI values into linear, logarithmic, and quadratic forms to test different hypotheses regarding relationships between REI and percent cover and settler abundance of *M. membranacea* (Table 2.1). A negative linear relationship between REI and the abundance of *M. membranacea* may be possible because high wave exposure could physically inhibit larval settlement (Koehl 2007) and slow the growth of adult colonies due to the energetic costs of producing protective structures in response to high wave action (Bayer et al. 1997). Similarly, a negative log-linear relationship could occur if a threshold exists beyond which settlement or colony growth is impeded by the above mechanisms. Lastly, a quadratic relationship reflects possible inhibitory effects of both high and low wave exposure on settlement (Pawlik & Butman 1993) and the feeding success of adult colonies (Pratt 2008, Arkema 2009), respectively.

2.3.3.3 Kelp Density

For sites where all three kelp species were present, I calculated the site-and depth-specific mean density of each species of kelp from July-September (summer), October-December (autumn), January-March (winter), and April-June (spring). I then calculated the relative densities of *L. digitata* and *S. latissima* (species-specific kelp density divided by total kelp density; Kelp_R) and total kelp density (kelp density summed across all 3 species; Kelp_T) for each depth, site, and period. I considered quadratic Kelp_R (of *L. digitata* and *S. latissima*) as predictors of percent cover of *M. membranacea* based on the prediction of Denley et al. (2019a) that percent cover is highest for mixed-species kelp beds (i.e. percent cover should be greatest at intermediate values of Kelp_R). I hypothesised that, if larval supply limits settlement of *M. membranacea* as for other marine invertebrates (e.g. Gaines et al. 1985), a linear relationship could exist between Kelp_T and settler density: positive if physical factors such as the roughness (Eckman 1990) and internal flow attenuation (Eckman et al. 1989) of kelp beds enhance settlement, or negative if the presence of kelp does not induce settlement (Denley & Metaxas 2017b) but higher densities of kelp spread settlers over a larger surface area of kelp and thus decrease their density.

Preliminary analyses revealed moderate collinearity between the optimal REI metric (log of six-month REI; see sections 2.3.4.1 and 2.4.1) and the relative density of *L. digitata* ($r = 0.43$) and *S. latissima* ($r = -0.34$). To examine the effect of kelp density on percent cover independently from that of REI, I conducted residual regression (Graham 2003) using linear models with Kelp_R as the dependent variable and the log of six-month REI as the independent variable. I used the residuals of these models as the Kelp_R variables in subsequent GLMMs for percent cover.

2.3.4 Assessment of Predictor Variables

I used an information-theoretic multi-model inference approach, based on generalized linear mixed models (GLMMs), to assess the relative and absolute importance of candidate predictors (and metrics) and the relationships of these predictors with percent cover and settler density of *M. membranacea* (Figure 2.2; for complete detailed schematic, see Figure A.5). I conducted all analyses in R, version 3.6.2 (R Core

Team 2020) in the R Studio environment (RStudio Team 2020). I fit GLMMs using glmmTMB (Brooks et al. 2017), validated them with DHARMa (Hartig 2020), and conducted model averaging with MuMIn (Barton 2019). See Appendix A.7 for a full list of packages used.

2.3.4.1 Selection of optimal SST and REI metrics for predicting percent cover and settler density

To determine the optimal REI and SST metrics for predicting percent cover and settler density, I compared the performance of GLMMs containing each candidate metric (Table 2.1) using ratios of their Akaike weights (Wagenmakers & Farrell 2004). First, I standardized all continuous predictor variables by subtracting the sample mean from each observation (Schielzeth 2010) and dividing by 2 standard deviations (Gelman 2008), and applied a sum-to-zero contrast to the kelp substrate variable (Schielzeth 2010). Standardization allowed comparison of parameter estimates among models to assess relative effect size, while the sum-to-zero contrast simplified the interpretation of model-averaged interaction terms (Schielzeth 2010). After standardization, I examined collinearity between predictors by calculating pairwise correlations and variance inflation factors (Dormann et al. 2013). I then fit GLMMs composed of: 1) all candidate predictor variables except kelp density (depth, kelp substrate, REI, and SST) as fixed effects; 2) an interaction between temperature and kelp substrate, which was identified as significant in preliminary analyses; and 3) crossed random intercepts for study site and study year, to account for the blocked nature of the data within these factors (Table 2.2). GLMMs were fit using maximum likelihood. For models of percent cover, I used a beta model with an intercept-only zero-inflation term and a logit link function (Ospina & Ferrari 2012). For models of settler density, I used a negative binomial model with a log link function. I validated the GLMMs by visually assessing QQ plots and plots of simulated residuals vs. fitted values.

To determine optimal metrics, I first compared models fit with each REI metric, using the same temperature metric (six-month mean of SST [SST 6-M]) as the SST metric in each model (Figure 2.2, arrow 1). I selected the optimal REI metric by identifying the metric generating the model with the highest Akaike weight, and compared its performance relative to other REI metrics using ratios of their Akaike weights (evidence ratios; Wagenmakers & Farrell 2004). Using this optimal REI metric in each model, I then compared models fit using each SST metric, and selected the optimal SST metric using Akaike weights (Figure 2.2, arrow 2).

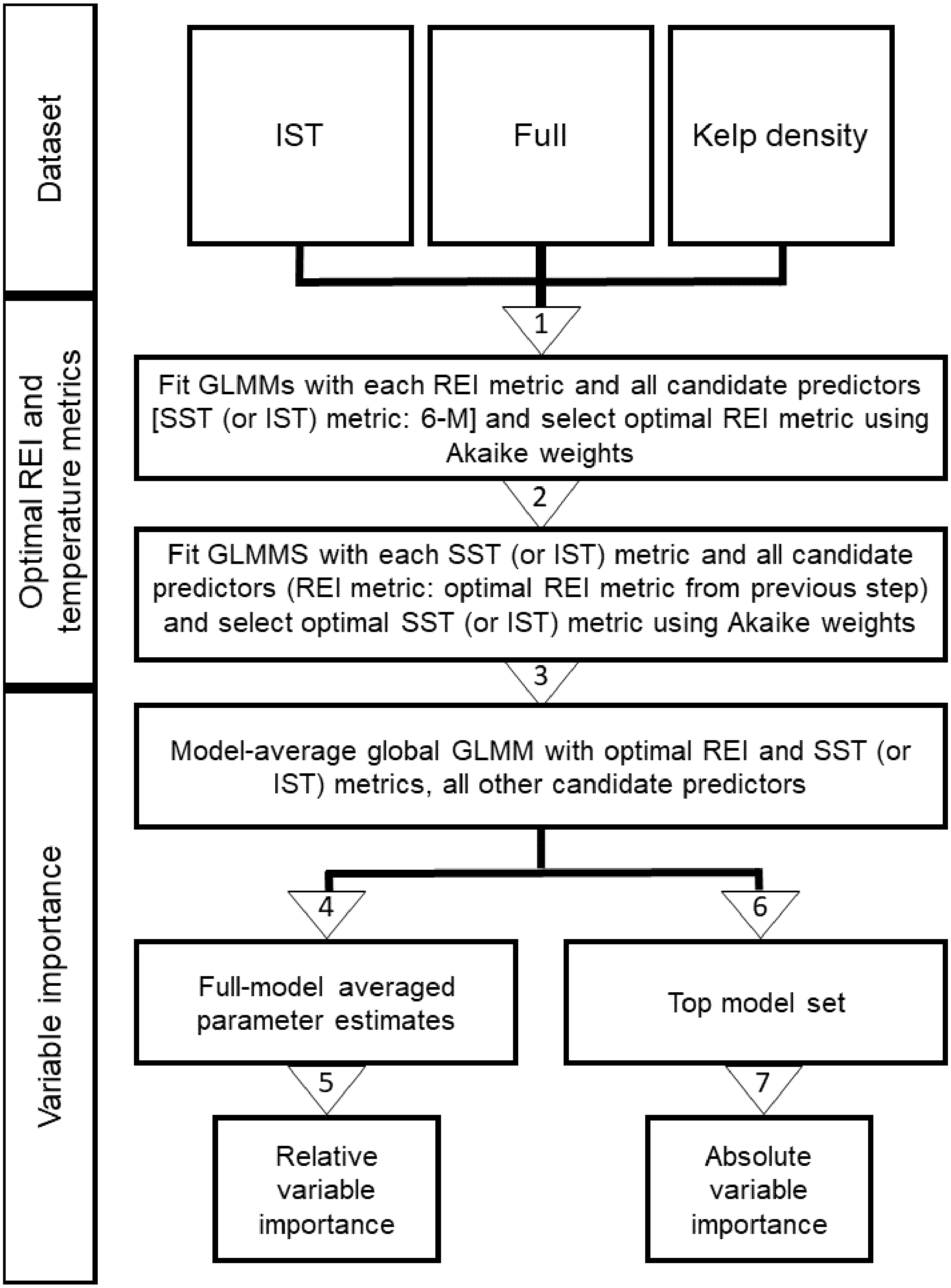

Figure 2.2 Flow of data processing and modelling procedures used to assess the importance of predictors in contributing to observed patterns in percent cover and settler density of *M. membranacea* in the northwest Atlantic Ocean over broad spatial and temporal scales. Numbered arrows correspond to modelling procedures described in sections 2.3.4.1 and 2.3.4.2.

Table 2.2 General forms of global generalized linear mixed models for percent cover and settler abundance, where Percent Cover$_{ijk}$ and Settler Density$_{ijk}$ are the *k*th observation at site *i* in year *j*, μ is the mean, α is the probability of observing 0, θ is unknown parameter controlling the variance, and k is the dispersion parameter. BEZI represents a zero-inflated beta distribution and NB represents a negative binomial distribution. LD and SL are abbreviations for *L. digitata* and *S. latissima*, respectively.

Equation	Percent cover	Settler density
Error distribution	$\text{Percent Cover}_{ijk} \sim \text{BEZI}(\alpha, \mu_{ijk}, \theta)$	$\text{Settler Density}_{ijk} \sim \text{NB}(\mu_{ijk}, \text{k})$
Conditional mean function	$\text{E}(\text{Percent Cover}_{ijk}) = (1-\alpha)\mu_{ijk}$	$\text{E}\left(\text{Settler Density}_{ijk}\right) = \mu_{ijk}$
Variance function	$\text{var(Percent Cover)}_{ijk} =$ $\alpha(1-\alpha)\left(-\mu_{ijk}\right)^2 \times (1-\alpha)\dfrac{\mu_{ijk}(1-\mu_{ijk})}{1+\theta}$	$\text{var(Settler Density)}_{ijk} = \mu_{ijk} + \dfrac{\mu_{ijk}^2}{\text{k}}$
Model equation	$\text{logit}(\mu_{ijk}) = \text{Depth}_{ijk}$ $+ \text{Kelp Substrate}_{ijk} + \text{REI}_{ijk}$ $+ \text{Temperature}_{ijk}$ $(+ \text{Kelp}_{\text{R}}\ \text{LD}_{ijk} + \text{Kelp}_{\text{R}}\ \text{SL}_{ijk})$ $+ \text{Temperature}_{ijk} \times \text{Kelp Substrate}_{ijk}$ $+ \text{Site}_i + \text{Year}_j$	$\log(\mu_{ijk}) = \text{Depth}_{ijk}$ $+ \text{Kelp Substrate}_{ijk} + \text{REI}_{ijk}$ $+ \text{Temperature}_{ijk}\ \left(+ \text{Kelp}_{\text{T}\,ijk}\right)$ $+ \text{Temperature}_{ijk} \times \text{Kelp Substrate}_{ijk}$ $+ \text{Site}_i + \text{Year}_j$
Random intercept distributions	$\text{Site}_i \sim N(0, \sigma^2_{Site})$ $\text{Year}_j \sim N(0, \sigma^2_{\text{Year}})$	$\text{Site}_i \sim N(0, \sigma^2_{Site})$ $\text{Year}_j \sim N(0, \sigma^2_{\text{Year}})$

2.3.4.2 Importance of candidate predictors of percent cover and settler density

For percent cover and settler density, I fit a global GLMM (using the same procedure described above in section 2.3.4.1) with depth, kelp substrate, the optimal REI metric, the optimal SST metric, an interaction between SST and kelp substrate, and random intercepts for site and year. To evaluate variable importance, I conducted model averaging on the global GLMM and derived a complete model set, consisting of all possible sub-models (combinations of fixed effects) of the global GLMM (Figure 2.2, arrow 3; Burnham & Anderson 2002). I calculated full-model averaged parameter estimates (Symonds & Moussalli 2011) and their unconditional 95% confidence intervals (Burnham & Anderson 2004) for each predictor variable from the complete model set (Figure 2.2, arrow 4). I assessed the relationship between the predictor variable and percent cover or settler density based on the sign of its estimate (i.e. positive or negative; or the relative magnitude of the parameter estimates for each species, in the case of kelp substrate) and compared the magnitude of parameter estimates between predictors to assess relative variable importance (Figure 2.2, arrow 5).

To determine absolute variable importance, I ranked the models in the complete model set in order of increasing AIC and derived a top model set containing models for which ΔAIC (the increase in AIC of a given model compared to the top-ranked model) was less than 7, creating a top model set 95% likely to contain the actual best model (Figure 2.2, arrow 6; Burnham & Anderson 2002, Richards 2005). I excluded models for which a less complex nested model with an equal or lower AIC value was also included in the top model set (Richards 2008, Richards et al. 2011). I considered predictor variables retained in all models within the top model set to be informative predictors (sensu Leroux 2019) of percent cover or settler density (Figure 2.2, arrow 7). If a predictor variable was not included in all models in the top model set, I used ΔAIC to compare models with and without the parameter and also examined if the 95% confidence interval for its parameter estimate included zero to further assess its importance (Grueber et al. 2011). To test for significant differences among kelp substrate species and kelp-SST interactions, I conducted Tukey tests using the top-ranked model in each model set. Lastly, I determined the goodness-of-fit of the models in the top model set using Nakagawa's R^2 (Nakagawa et al. 2017).

I investigated the relative and absolute importance of kelp density separately from the other predictors (Appendix A.6), since substantially fewer data on kelp density were available and therefore assessing the importance of kelp density with the other predictors would have greatly reduced my sample size. However, kelp density was not an informative predictor for explaining patterns of percent cover and settler density (Appendix A.6). Therefore, I excluded kelp density and constructed models based on the full available dataset for all other analyses.

2.3.4.3 Importance of seasonal SST and SST anomaly in predicting percent cover and settler density

My dataset contained observations of percent cover and settler density over the entire growing season of *M. membranacea* (May-November) from different sites over different years and thus may have been influenced by both seasonal patterns in temperature and temperature variability between sites and years. To investigate the relative influence of these components of temperature variability as predictors of the abundance of *M. membranacea*, I constructed global models for cover and settler density with depth, kelp substrate, the optimal REI metric, seasonal SST and SST anomaly (using the optimal SST metric) as fixed effects, an interaction between kelp substrate and seasonal SST, and site and year as random intercepts. I then derived complete model sets from these global models, and assessed variable importance using model averaging.

2.3.4.4 IST- versus SST-based models

To investigate the suitability of SST as a proxy for IST when predicting the abundance of *M. membranacea,* I examined differences in relative and absolute variable importance between models based on temperature data from IST and SST. For this comparison, I ran models using the subset of the full datasets for which IST data were available (IST datasets; n = 165 for percent cover, n= 192 for settler density, Table A.1). First, I identified the optimal REI and temperature metrics using IST- and SST-based models for percent cover and settler density, using the procedure in section 2.3.4.1. Then, I assessed relative variable importance and absolute variable importance as described in section 2.3.4.2. Lastly, I compared variable importance results and top model fit from the IST- and SST-based models for percent cover and settler density.

2.4 Results

2.4.1 Optimal SST and REI metrics for predicting percent cover and settler density

The optimal SST metric for explaining observed patterns in percent cover was the six-month mean of SST (SST 6-M); however, the Akaike weight of the model containing SST 6-M was only 1.11 times greater than that containing the six-month integral of SST

(SST 6-I; Table 2.3a). Akaike weights of the models with both six-month metrics were approximately three orders of magnitude greater than those with both three-month metrics. For predicting settler density, the optimal SST metric was SST 6-I (Table 2.3b), with Akaike weight of the model containing SST 6-I being 1.80 times greater than that with SST 6-M. Akaike weights for models with both six-month metrics were over 3 orders of magnitude greater than those for three-month and one-month metrics.

The log of six-month REI (REI 6-Log) was the optimal REI metric for predicting percent cover (Table 2.3a), followed closely by the log of three-month REI (REI 3-Log) and the log of calendar-year REI (REI Y-Log). REI Y-Log was the optimal REI metric for predicting settler density, with the Akaike weight of the model containing REI Y-Log being 1.06 times greater than that with REI 6-log (Table 2.3b).

Table 2.3 Results of GLMMs comparing REI and SST metrics as predictors of a) percent cover and b) settler density. Models of the form shown in Table 2 (excluding kelp density as a predictor) were fit using each REI and SST metric. For comparison of REI metrics, SST Six-Month Mean was the temperature metric in the model. For comparison of SST metrics, the optimal REI metric was employed as the REI metric in the model. AIC, dAIC (change in AIC relative to top-ranked model) and Akaike weight were calculated for each model. REI and SST metrics are ranked in order of descending model performance and are abbreviated as per Table 2.1.

(a)

Variable	Metric	AIC	dAIC	weight
REI	6-Log	-1282.436	0.000	0.258
	3-Log	-1282.130	0.306	0.222
	Y-Log	-1281.523	0.913	0.164
	6-Lin	-1280.866	1.570	0.118
	Y-Lin	-1279.936	2.500	0.074
	3-Lin	-1279.766	2.670	0.068
	6-Q	-1278.873	3.563	0.044
	Y-Q	-1277.938	4.498	0.027
	3-Q	-1277.780	4.656	0.025
SST	6-M	-1282.436	0.000	0.527
	6-I	-1282.222	0.214	0.473
	3-I	-1265.605	16.831	<0.001
	3-M	-1265.438	16.998	<0.001

(b)

Variable	Metric	AIC	dAIC	weight
REI	Y-Log	3699.284	0.000	0.339
	6-Log	3699.392	0.108	0.321
	6-Q	3700.559	1.275	0.179
	Y-Q	3702.862	3.578	0.057
	3-Log	3704.073	4.789	0.031
	1-Log	3705.668	6.384	0.014
	1-Lin	3705.900	6.616	0.012
	3-Lin	3706.007	6.723	0.012
	Y-Lin	3706.042	6.758	0.012
	6-Lin	3706.210	6.926	0.011
	3-Q	3707.164	7.880	0.007
	1-Q	3707.329	8.045	0.006
SST	6-I	3698.044	0.000	0.650
	6-M	3699.284	1.240	0.350
	3-I	3722.245	24.201	<0.001
	3-M	3722.513	24.469	<0.001
	1-M	3834.331	136.287	<0.001
	1-I	3834.575	136.530	<0.001

2.4.2 Importance of candidate predictors of percent cover and settler density

My top-ranked GLMMs for percent cover and settler density both attained marginal R^2 values of over 0.5 (Table 2.4a,b). SST was the most important predictor of both percent cover and settler density, with a parameter estimate more than twice as large as the next largest (kelp substrate; Figure 2.3a,b). Both seasonal SST and SST anomaly were informative individual predictors of percent cover and settler density of *M. membranacea*, both appearing in all models in the top model sets; however, seasonal SST was approximately 2 times more important than SST anomaly in both cases (Figure A.6, Table A.2).

SST had a positive relationship with cover and settler density but the strength of this relationship was strongly dependent on kelp substrate (Figure 2.4d,h). The positive relationship between SST and percent cover was stronger for *L. digitata* than for *S. latissima* or *A. clathratum* while the positive relationship between SST and settler density was significantly lower for *A. clathratum* than *L. digitata* or *S. latissima* (Tukey test, $p<0.01$; Figure 2.3a,b). The second most important predictor of percent cover and settler density was kelp substrate (Figure 2.3a,b). Mean percent cover was significantly higher on *L. digitata* than on *S. latissima* or *A. clathratum* while mean settler density was significantly lower on *A. clathratum* than on *L. digitata* or *S. latissima* (Tukey test, $p<0.01$; Figure 2.3a,b; Figure 2.4b,f). Depth was the third most important predictor of percent cover and the least important for settler density (Figure 2.3a,b) with a negative and positive relationship, respectively (Figure 2.4a,e). The negative, logarithmic relationship with REI was the least important predictor of percent cover (Figure 2.3a;

Figure 2.4c) although it was the third most important predictor of settler density (Figure 2.3b; Figure 2.4g). For percent cover, all candidate variables except REI were included in both models in the top model set; there was a ΔAIC of <1 when REI was removed from the top model in the model set (Table 2.4a) and its 95% confidence interval included zero (Figure 2.3a), providing little evidence that it is an informative predictor. For settler density, all predictors appeared in both models in the top model set except REI, which only appeared in the top-ranked model; there was a ΔAIC of over 4 when REI was removed in the second-ranked model (Table 2.4b) and its 95% confidence interval did not include zero (Figure 2.4b), indicating that it is an informative predictor.

Table 2.4 Sets of top models (models with ΔAIC<7) explaining observed patterns in a) percent cover and b) settler density of *M. membranacea* in the northwest Atlantic. REI and SST model terms are abbreviated as per Table 2.1. Marg. and Cond. R^2 are the marginal and conditional R^2 values for the GLMM. Random Effect SD is the standard deviation of each random intercept.

(a)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Depth + REI 6-Log + Kelp Substrate + SST 6-M + Kelp Substrate:SST 6-M	12	653.218	-1282.436	0.000	0.581	0.588	0.766	Site = 0.566 Year = 0.142
Depth + Kelp Substrate + SST 6-M + Kelp Substrate:SST 6-M	11	651.858	-1281.717	0.719	0.405	0.558	0.758	Site = 0.592 Year = 0.142

(b)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Depth + REI Y-Log + Kelp Substrate + SST 6-I + Kelp Substrate:SST 6-I	11	-1838.022	3698.044	0.000	0.891	0.542	0.778	Year = 0.845 Site = 0.654
Depth + Kelp Substrate + SST 6-I + Kelp Substrate:SST 6-I	10	-1841.444	3702.888	4.844	0.079	0.494	0.775	Year = 0.849 Site = 0.788

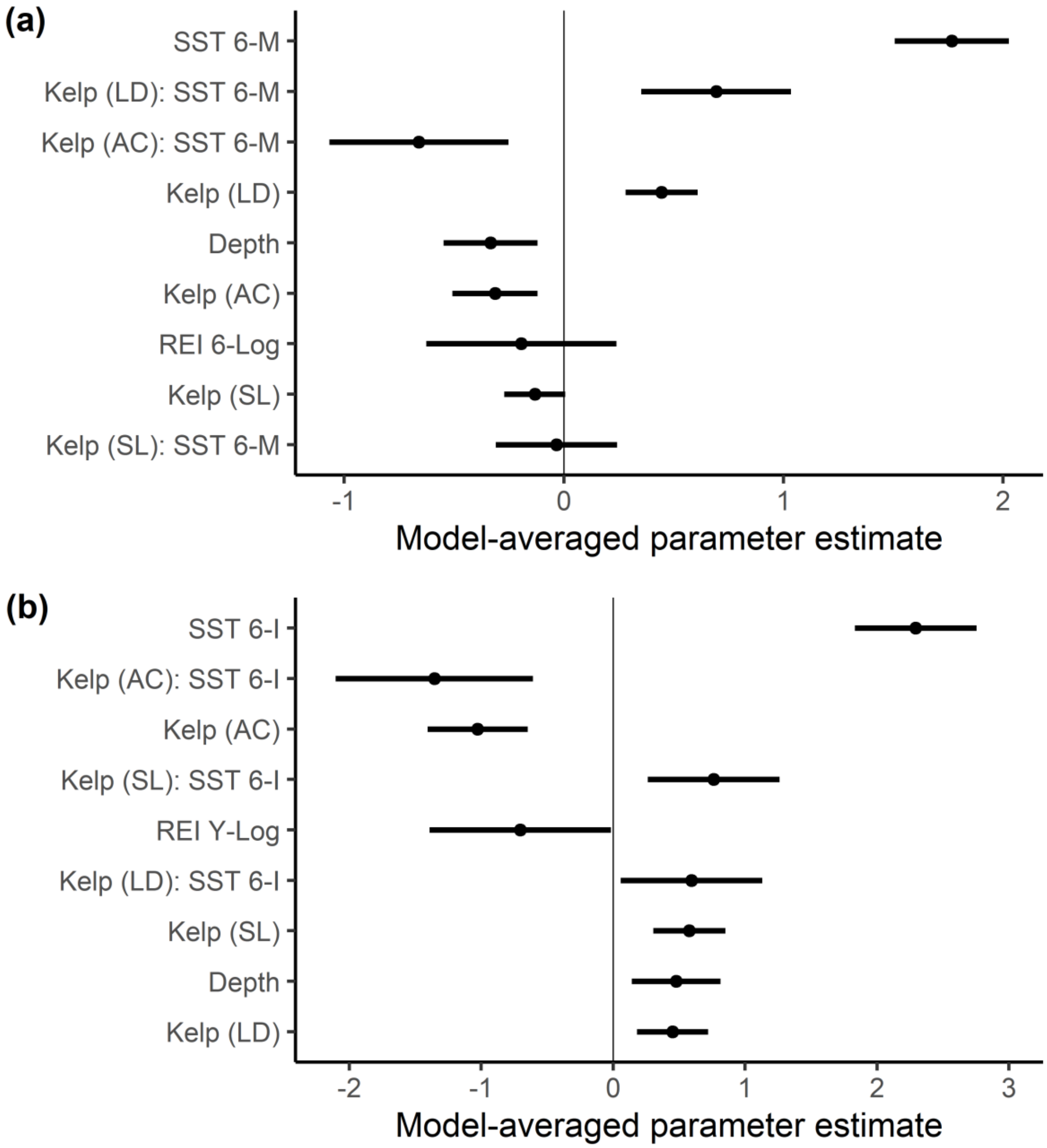

Figure 2.3 Full-model averaged standardized parameter estimates for depth, kelp substrate, REI and SST as predictors of a) percent cover and b) settler density, arranged in descending order of magnitude. REI and SST metrics are abbreviated as per Table 2.1. Error bars represent 95% confidence intervals based on unconditional standard error. AC = *A. clathratum*, LD = *L. digitata*, SL = *S. latissima.*

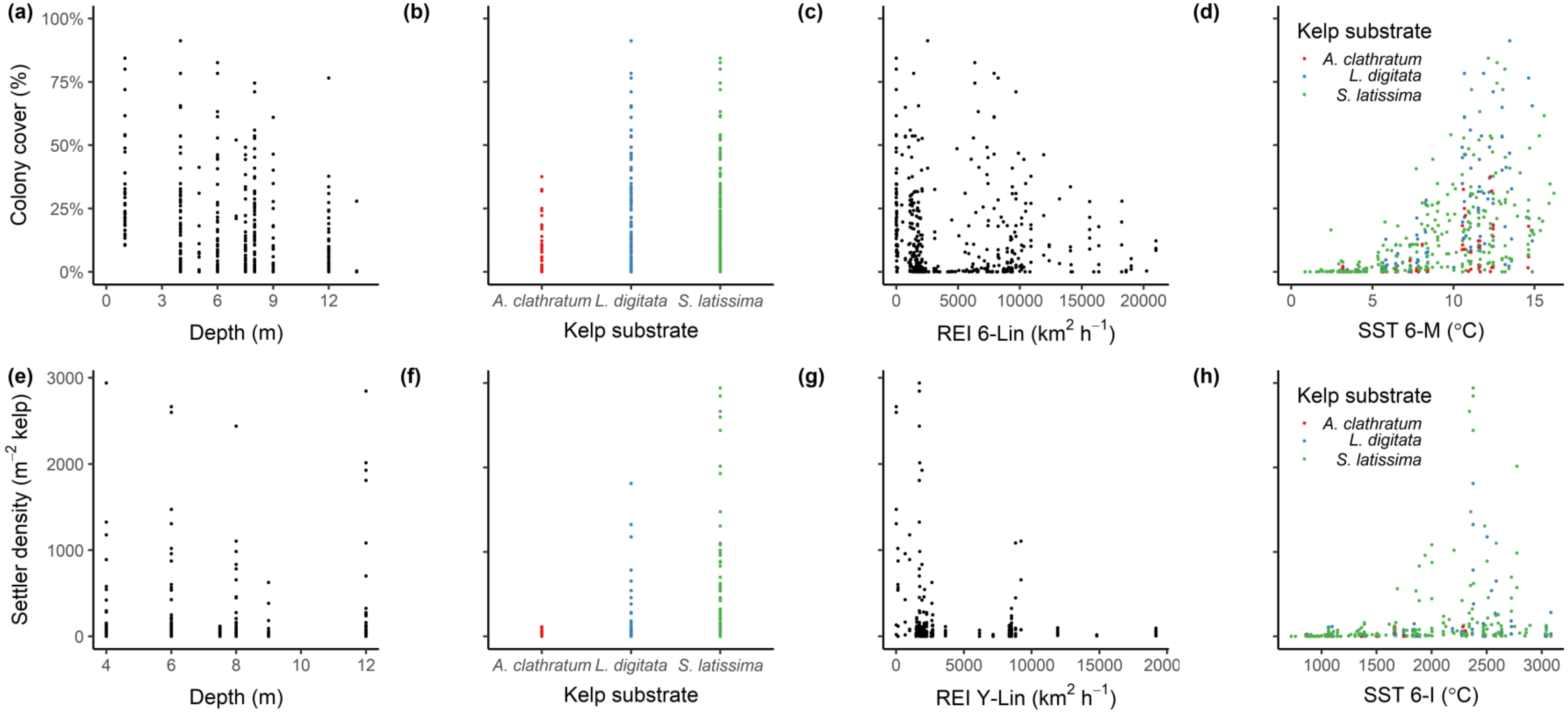

Figure 2.4 Candidate predictors of the percent cover (a-d) and settler density (e-h) of *M. membranacea* in the northwest Atlantic. Percent cover of colonies of *M. membranacea* on kelp blades (kelp species-specific means for each depth, site, and sampling date) as a function of a) depth, b) kelp substrate species, c) six-month mean REI, and d) six-month mean SST separated by kelp substrate. Settler density (no. individuals per m^2 kelp; kelp species-specific means for each depth, site, and sampling date) as a function of e) depth, f) kelp substrate species, g) mean REI over the calendar year, and h) six-month integral SST separated by kelp substrate.

2.4.3 IST- vs SST-based models

I compared the results of SST-based models to those of IST-based models to assess the suitability of SST as a proxy for IST for predicting the abundance of *M. membranacea* (for detailed results, see Table A.4 and Table A.5). The optimal temperature metric was the three-month integral in SST-based models and the three-month mean in IST-based models of percent cover (Table 2.5a; Table A.4a,b). For settler density, the optimal temperature metric was the three-month integral in SST-based models and the one-month integral in IST-based models (Table 2.5b). For both percent cover and settler density, there were no notable differences in the rankings of REI metrics between IST- and SST-based models (Table A.4). For IST- and SST-based models of settler density, quadratic six-month mean REI (REI 6-Q) produced the model with the highest Akaike weight. However, the quadratic relationship between REI 6-Q and settler density seems to be an artifact of the dataset (few datapoints at intermediate values; Figure A.7) rather than a real effect. Consequently, I elected to use the log of one-month mean REI (REI 1-Log), which had a parameter estimate of almost identical magnitude to REI 6-Q, as the optimal REI metric for subsequent analyses.

For percent cover, relative variable importance rankings were similar for IST- and SST-based models except depth, which had a higher relative importance in SST-based models than in IST-based models (Table 2.5a, Figures A.9a,c). Absolute variable importance was also the same in IST- and SST-based models except depth, which was an informative predictor in SST- but not IST-based models (Table 2.5a, Tables A.5a,b, Figures A.9a,c). The top-ranked IST-based model performed better in terms of model fit (higher marginal R^2 and lower AIC) than the top-ranked SST-based model (Table 2.5a;

Tables A.5 a,b). For settler density, the relative importance of depth and REI was higher in IST-based models than in SST-based models, while the rankings of temperature, kelp substrate and REI were the same (Table 2.5b, Figures A.9b,d). Absolute variable importance did not differ between IST- and SST-based models, with depth, temperature and kelp substrate being informative. The top-ranked IST-based model had lower AIC but also slightly lower marginal R^2 than the top-ranked SST-based model (Table 2.5b; Tables A.5c,d).

Table 2.5 Comparison of SST- and IST-based models fit using the subset IST dataset for a) percent cover and b) settler abundance. Optimal temperature and REI metrics indicate the metrics producing models with the largest Akaike weight when compared to models fit using other metrics and are abbreviated as per Table 2.1. Relative variable importance indicates the ranking of candidate predictor variables by their full-model averaged parameter estimates. Absolute variable importance indicates the variables which were included as predictors in models in the top model set (i.e. informative predictors). Top model R^2 is the marginal R^2 for the top-ranked GLMM in the model set.

(a)

Temperature Data Source	Optimal Temperature Metric	Optimal REI Metric	Relative Variable Importance	Absolute Variable Importance	Top Model AIC	Top Model R^2
SST	SST 3-I	REI 6-Log	SST>Depth>Kelp Substrate>REI	Depth, Kelp Substrate, SST	-470.658	0.586
IST	IST 3-M	REI 3-Lin	IST>Kelp Substrate>Depth>REI	Kelp Substrate, IST	-483.565	0.616

(b)

Temperature Data Source	Optimal Temperature Metric	Optimal REI Metric	Relative Variable Importance	Absolute Variable Importance	Top Model AIC	Top Model R^2
SST	SST 3-I	REI 1-Log	SST>Kelp> Depth>REI	Depth, Kelp Substrate, SST	1875.898	0.327
IST	IST 1-I	REI 1-Log	IST>Depth>Kelp Substrate>REI	Depth, Kelp Substrate, IST	1857.641	0.275

2.5 Discussion

As a result of a detailed process of variable selection, the top-ranked models in this study explained a substantial amount of the variability (>50%; Cohen 1988, Møller & Jennions 2002) in the abundance of multiple life stages of the invasive bryozoan *M. membranacea*. With few exceptions, variable importance and the relationships between environmental predictors and abundance revealed in my large-scale study aligned with those of past studies conducted at smaller spatiotemporal scales. This case study using *M. membranacea,* a well-studied invasive species for which abundance data were available, may represent a best-case scenario for variable selection for SDMs. However, the framework I used can be applied widely in species distribution modelling to select relevant predictor variables, including for organisms for which data are available as presence-absence or presence-only (Figure 2.5).

My comparisons of models based on different temperature data sources indicated that the suitability of distal predictors (e.g. depth and sea surface temperature [SST]) as proxies for their *in situ* counterparts (e.g. *in situ* temperature [IST]) should be investigated whenever possible in the context of SDM (Figure 2.5, step 3). Rankings of metrics and variable importance were similar and model fit was only slightly improved in IST- compared to SST-based models of percent cover, indicating that depth and SST can be used to approximate IST in SDMs for percent cover of *M. membranacea*. However, rankings of temperature metrics and the relative importance of depth differed between SST- and IST-based models of settler density, potentially due to confounding effects of another depth-dependent variable on settler density. The differences between SST- and IST-based models for settler density, as well as the spatial limitation of the IST dataset to a subset of my study region (Nova Scotia), underscore the necessity to evaluate the suitability of SST and depth as a proxy for IST on a case-by-case basis.

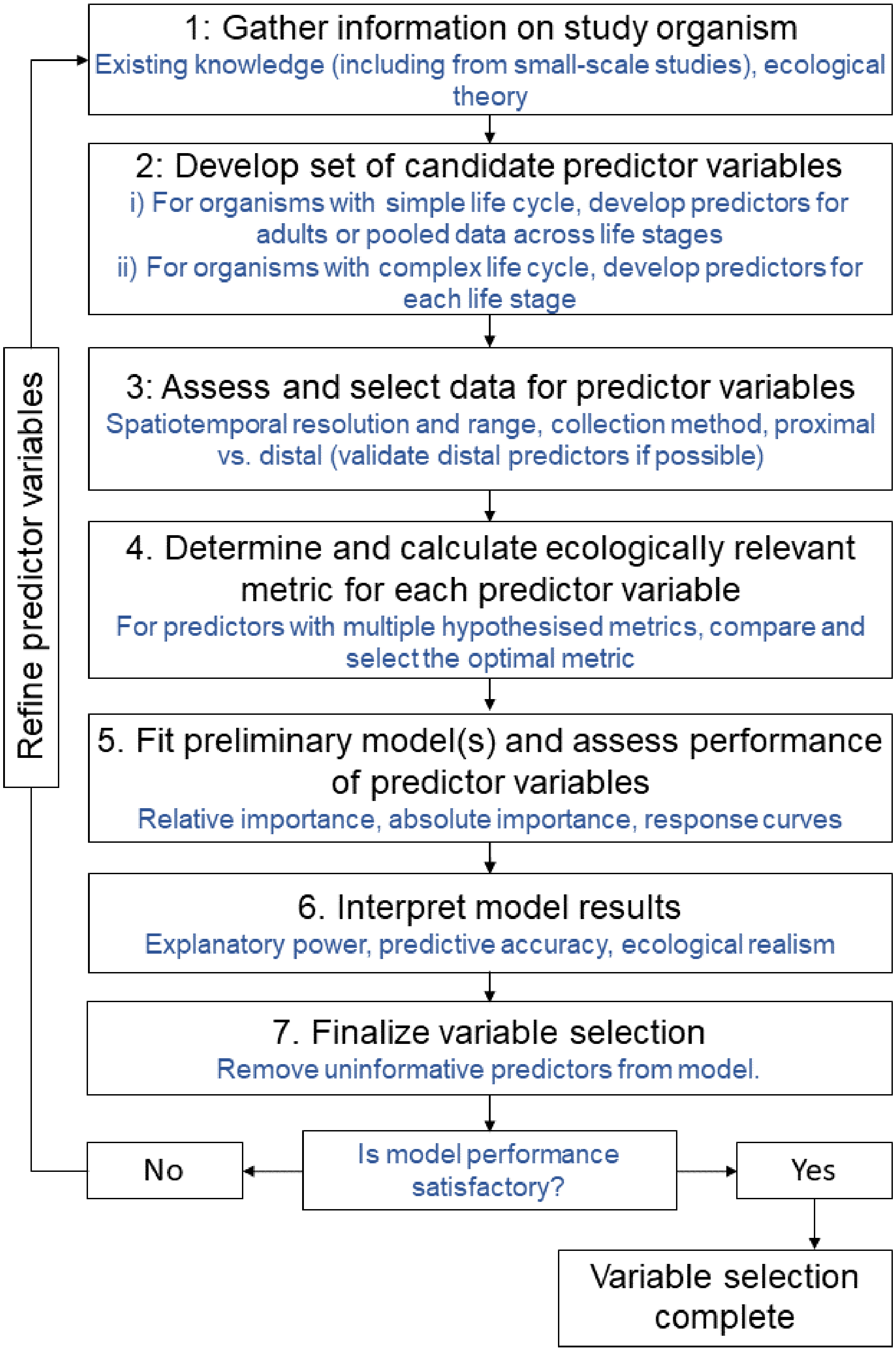

Figure 2.5 Conceptual framework for variable selection in species distribution modelling. Numbered black text shows each step in the variable selection process, blue text details considerations at a given step.

My results highlight the importance of carefully selecting metrics used to summarise environmental data employed in SDMs to match the scale of the ecological processes affecting the organism or life stage being modelled (Figure 2.5, step 4). Firstly, the six-month thermal windows of the optimal SST metrics in this study were consistent with previous studies, showing that the abundance of both settlers and adult colonies depends on the thermal history affecting the current and previous life stage (Saunders et al. 2010, Caines & Gagnon 2012). Secondly, I found that thermal integrals of SST explained patterns in settler density better than mean temperature, but that thermal integrals and means explained patterns in percent cover equally well. These results were likely caused by differences in thermal sensitivity between settlers and adult colonies of the bryozoan. Early life stages of marine ectotherms are often more sensitive to temperature than adults (Pörtner et al. 2007, Putnam et al. 2010, Pineda et al. 2012, Reglero et al. 2014, Pandori & Sorte 2019) and, as a result, thermal integrals may be superior to mean temperature in predicting the recruitment of *M. membranacea* (Neuheimer & Taggart 2007, Metaxas & Saunders 2009). Consequently, the suitable temporal resolution of environmental data may differ between organisms or life stages (Figure 2.5, step 3), as the calculation of thermal integrals requires daily temperature data whereas means can be calculated from data at a lower temporal resolution.

Additionally, my findings demonstrate that the knowledge gained by assessing relative variable importance in an SDM can affect subsequent modelling decisions (Figure 2.5, step 5). Consistent with previous smaller-scale studies of the bryozoan (Saunders & Metaxas 2007, Scheibling & Gagnon 2009, Caines & Gagnon 2012), temperature was the most important predictor of percent cover and settler density in my models, with a positive effect on abundance in both life stages. Notably, I found that although seasonal changes in temperature were most strongly associated with abundance, temperature anomalies among sites and years were also informative predictors of percent cover and settler density, providing evidence that spatial and interannual difference in temperature drive variability in the abundance of *M. membranacea*. The strong, positive, and direct effect of temperature on abundance reinforces the conclusions of previous studies (Saunders et al. 2010, Denley et al. 2019a) that the abundance of *M. membranacea* will increase with climate change-induced warming in the northwest Atlantic, and emphasises the need for SDMs predicting these future increases. Further, kelp substrate was the second most important predictor of both percent cover and settler abundance, suggesting that SDMs predicting future temperature-induced changes in the abundance of the bryozoan must account for the substrate on which it is being measured. These inferences highlight that identifying the relative importance of candidate predictors is needed to inform the construction and implementation of SDMs.

Even when a variable is an informative predictor in an SDM, the data used to calculate the predictor may not be sufficient to fully capture the ecological mechanism by which the predictor affects the focal organism (Figure 2.5, step 6). This is illustrated in this study by the emergence of mean REI over the calendar year as the optimal REI metric for predicting settler density. The negative logarithmic relationship between REI and settler density is ecologically justifiable, implying that settlement sharply decreases beyond a threshold value of REI. Since post-settlement mortality is low for *M. membranacea* (Yoshioka 1982, Denley & Metaxas 2016), this decrease is likely related to an inhibitory effect of wave action on larval settlement (Koehl 2007) rather than an effect on post-settlement mortality. However, it is not clear that calendar year as the optimal temporal window for calculating REI has an ecological basis because it incorporates at least some wind data that could not have affected the bryozoan. Rather, this indicates that my models could not elucidate the real temporal window over which REI has the greatest effect on the settlement of *M. membranacea*. The type of data used to represent an environmental predictor can affect the ability of SDMs to account for and model the details of species-environment relationships, affecting their ecological realism (Figure 2.5, step 6). This outcome underscores the importance of carefully assessing and selecting predictor data prior to modelling (Figure 2.5, step 3).

My investigations of kelp density as a candidate predictor of bryozoan abundance illustrate that, in some instances, it can be difficult to determine whether the low importance of a predictor indicates that it is truly uninformative or that the result is an artifact of data analysis. Here, I hypothesised that total density of kelp would influence settler density and that the relative density of the 3 dominant kelp species in the northwest Atlantic would affect percent cover of the bryozoan. Contrary to my expectations, I found that neither the density nor species composition of kelps affected the abundance of *M. membranacea*. However, unlike previous studies, my analyses relating relative kelp density to percent cover only focussed on mixed kelp beds where all three kelp species were present; previous predictive models compared population growth of *M. membranacea* for mixed kelp beds and mono-specific beds of the same density (Denley et al. 2019a). Additionally, my datasets for kelp density were considerably smaller than those for the other candidate predictors, possibly affecting my ability to detect an effect of kelp density. In my models, I was able to explain a substantial amount of variance in the abundance of *M. membranacea* despite kelp density being an uninformative predictor. However, in cases where a predictor hypothesised as important is found to be uninformative, it may be necessary to deem the resultant model unsatisfactory and return to the beginning of the variable selection process (Figure 2.5, step 7).

2.6 Conclusions

Using a detailed variable selection procedure grounded in ecological reasoning and decades of past research, I determined relevant predictors and their optimal metrics for use in SDMs for multiple life stages of *M. membranacea* in the northwest Atlantic. My analyses revealed general conclusions relevant to variable selection for SDMs : 1) Relative variable importance can and should be used to inform species distribution modelling decisions; 2) Species-environment relationships derived from small-scale studies can be applied (if ecologically justified) to regional scales for the purposes of variable selection for species distribution modelling; 3) The use of distal predictors in SDMs can be justified; however, the interpretation of such predictors may be limited by confounding variables and their suitability will likely be study specific; 4) Temporal windows and descriptive statistics (e.g. mean, cumulative sum, maximum) for continuous environmental predictors should be selected to match the ecology and life stage of the focal organism; 5) Data constraints (e.g. sample size, lack of proximal data) may affect the performance of candidate predictor variables in SDMs. I recommend that future studies on species distribution modelling consider these conclusions and follow my proposed framework (Figure 2.5) to improve the selection of variables for inclusion in SDMs. This framework is particularly relevant when multiple predictors (or predictor metrics) are hypothesised to affect the focal organism and sufficient data on species occurrence and predictors are available to conduct a detailed exploration.

CHAPTER 3

CLIMATE CHANGE INCREASES THE THREAT OF AN INVASIVE BRYOZOAN TO KELP BEDS IN THE NORTHWEST ATLANTIC OCEAN

3.1 Abstract

Climate change is expected to create more favourable climate conditions for many invasive species, increasing their abundance and spread. One such invasive species is *Membranipora membranacea*, an epiphytic bryozoan causing defoliation of kelp beds in the northwest Atlantic Ocean (NWA). The impact of *M. membranacea* is directly linked to its abundance, which is anticipated to increase due to climate change. Additionally, further range expansion may threaten Arctic kelp beds in the future. I constructed a species distribution model (SDM) to predict the abundance of *M. membranacea* in the NWA under present and future climate scenarios. I also assessed the potential effect of an invasion of *M. membranacea* from populations in Norway by comparing NWA- and Norway-based SDMs. The projected future abundance distribution of *M. membranacea* in the NWA differed substantially depending on the future climate scenario employed, but the bryozoan was predicted to occur in the Arctic at low abundances regardless of scenario. However, I also found that *M. membranacea* in Norway achieve much higher abundances at low temperatures compared to NWA populations, and could pose a dire threat to kelp beds in the NWA and southern Arctic if introduced in these regions. Although my SDMs performed well under internal validation, estimating the impact of *M. membranacea* is complicated by the context-dependent response of kelp communities

to coverage by the bryozoan. Nonetheless, this study assesses the potential response of an ecologically significant invasive species to climate change and is of broader relevance to the study of other invasive organisms.

3.2 Introduction

Climate change and invasive species are two of the greatest drivers of global ecological change, and are expected to act synergistically in causing further perturbation to ecosystems in the future (Hellmann et al. 2008, Mainka & Howard 2010). By favoring invasive species due to their broad environmental tolerances and capacity for rapid range shifts (Hellmann et al. 2008), climate change is expected to increase the frequency of species invasions (Rahel & Olden 2008, Rehage & Blanchard 2016) and exacerbate the negative impacts of already-established invasive species through increases in their range and abundance (Stachowicz et al. 2002, McDowell et al. 2014, Hulme 2017). Predictions of such responses of invasive species to environmental change are therefore needed, and species distribution models (SDMs) can be effective tools for this purpose (Elith 2017, Srivastava et al. 2019). However, the most commonly employed SDMs only predict the probability of presence or presence/absence of invasive species, not accounting for abundance (Bradley 2013, Ashcroft et al. 2017, Bradley et al. 2018) which is critical in determining impact (Parker et al. 1999, Ricciardi 2003, Kulhanek et al. 2011). This is likely due to the difficulty of predicting species abundances resulting from: 1) the paucity of reliable data on abundance for many species (Guisan et al. 2017, Bradley et al. 2018); and 2) the dependence of abundance on population and demographic processes that necessitate mechanistic modelling (i.e. SDMs composed of multiple mathematical functions predicting functional traits and life history; Dormann et al. 2012), and thus substantial amounts of data (Ehrlén & Morris 2015, Briscoe et al. 2019). However, for invasive species with available abundance data and for which abundance distribution is not heavily dependent on population processes or demography, correlative SDMs can be used to predict abundance. These models can provide valuable information on the potential impacts of the species throughout their invasive range (e.g. Strubbe et al. 2010, Risch et al. 2020).

Membranipora membranacea is an invasive epiphytic bryozoan in the northwest Atlantic Ocean (NWA) responsible for severe defoliation of kelp beds (Saunders & Metaxas 2008, Scheibling & Gagnon 2009, Filbee-Dexter et al. 2016), which support diverse communities and provide valuable ecosystem services (Teagle et al. 2017, Wernberg et al. 2019). The extent of kelp defoliation in a given area is related to the percentage of kelp blade surface area covered by colonies of *M. membranacea* and, specifically, the peak percent cover of the bryozoan during its annual life cycle (Scheibling & Gagnon 2009). Temperature is the primary driver of peak percent cover of *M. membranacea* (Scheibling & Gagnon 2009), suggesting that the abundance and negative impact of the bryozoan on kelp beds in the region will increase with climate change (Saunders et al. 2010, Denley et al. 2019a). Additionally, ocean warming may facilitate the range expansion of *M. membranacea* into Arctic kelp ecosystems (Goldsmit et al. 2018, Denley et al. 2019b). Habitat suitability models predicting the presence of *M. membranacea* have been developed previously (Goldsmit et al. 2018, Lyons et al. 2020); however, SDMs predicting the abundance (i.e. peak percent cover) of the bryozoan are needed to more accurately forecast the impact of this invasive species on kelp beds in the NWA and beyond.

As mentioned above, mechanistic SDMs have been recommended for the accurate prediction of abundance (Ehrlén & Morris 2015, Evans et al. 2015). However, while mechanistic SDMs may be necessary to predict the abundance of other organisms, multiple characteristics of *M. membranacea* make it an excellent candidate for the use of correlative species distribution modelling to predict its abundance. For example, while dispersal constraints and biotic interactions can limit the ability of organisms to colonize suitable habitat and thus affect the accuracy of correlative SDM projections (Wiens et al. 2009, Boulangeat et al. 2012, Ehrlén & Morris 2015), *M. membranacea* disperses rapidly and has saturated its available range in the northern NWA (Denley et al. 2019b), indicating that dispersal limitations do not prevent *M. membranacea* from colonizing suitable habitat in the region. Also, *M. membranacea* is the competitively dominant kelp epiphyte in the NWA (Berman et al. 1992, Yorke & Metaxas 2011) and is not affected by predation in the region (Pratt & Grason 2007); thus, biotic interactions are unlikely to confound SDM predictions of range and abundance. Percent cover of *M. membranacea* on kelp blades is largely dependent on colony growth (Saunders & Metaxas 2009a, Saunders et al. 2010) which, in turn, is mainly determined by temperature (Saunders & Metaxas 2009a). Additionally, the bryozoan has an annual life cycle (Saunders & Metaxas 2007) and, consequently, abundance in a given year is unrelated to that of previous years. These characteristics allow the accurate prediction of annual peak abundance based solely on correlative relationships with temperature (Scheibling & Gagnon 2009, Saunders et al. 2010), depth, and kelp substrate (Chapter 2).

Correlative SDMs characterise the realised niche of a species, and assume that this niche is conserved (i.e. that the relationship of the species to its predictor variables does not change over space and time; Wiens et al. 2009)); however, realised niche of an invasive species, as characterised by an SDM, can change in its invaded range through multiple mechanisms (Gallien et al. 2010), which can cause the SDM to perform poorly (Václavík & Meentemeyer 2012). For one, invasive species can encounter novel environmental and biotic conditions in their invaded range, changing their realised niche and rendering SDMs calibrated on data from the species' native range ineffective (Broennimann et al. 2007, Fitzpatrick et al. 2007, Zimmermann et al. 2010). SDMs fit to data from the invaded range of a species can also perform poorly when they are calibrated early in the invasion, as the realised niche of the invader will change over time as it fills its suitable habitat in the invaded range (Zimmermann et al. 2010, Václavík & Meentemeyer 2012). However, the realised niche of an invasive species can also change as a result of a shift in its fundamental niche in its invaded range. For example, invasive species may phenotypically or genetically adapt to new conditions upon introduction (Gallien et al. 2010, Chapman et al. 2017, Elith 2017), or multiple invasions by genetically-distinct source populations can enhance adaptive capability and lead to range expansion (Jeffery et al. 2017, Zhu et al. 2017). As *M. membranacea* has long been established in its invaded range in the NWA, ample data are available from the invaded range for SDM training (see Chapter 2) and the bryozoan appears to have saturated its suitable habitat in the region (Denley et al. 2019b), minimizing the risk of mischaracterising its realised niche. However, it is unknown whether *M. membranacea* has adapted to its invaded environment in the NWA and, although there is no evidence of multiple invasions in the region, the potential impact of a future additional invasion of *M. membranacea* has not been predicted. It is therefore important to investigate the possibility of the above scenarios to provide additional context and assess the applicability of SDMs for *M. membranacea* in the region.

Based on the predictor variables found to be important in Chapter 2 (temperature, kelp substrate, and depth) we constructed a correlative SDM for the peak percent cover of *M. membranacea* in the NWA to project the abundance distribution of the bryozoan under present and future climate scenarios in the region and assess the potential for *M. membranacea* to spread and impact Arctic kelp ecosystems. I also trained SDMs on data from the early and late stages of the invasion of the bryozoan and compared the models to assess the evidence for changes in the response of *M. membranacea* to its environment over the course of its invasion of the NWA. Finally, to predict the effect of a future additional invasion of the bryozoan, I constructed an SDM using abundance data for *M. membranacea* from Norway and compared it to the NWA-based model. This study provides valuable projections of future changes to the range and impact of this ecologically significant invasive species, and the implications of these changes for kelp bed ecosystems.

3.3 Methods

3.3.1 Study Region

I defined the northwest Atlantic Ocean (NWA) in my study as the area bounded by the southern Gulf of Maine in the south (42°N), the St Lawrence Estuary in the west (72°W), the east coast of Newfoundland in the east (52°W), and the northern tip of Labrador in the north (61°N; Figure 3.1). This area encompasses the latitudinal and longitudinal extent of observations of percent cover of *M. membranacea* in my dataset.

To assess the potential northward spread of the bryozoan with climate change, the domain is also extended northward beyond the extent of the known range of the bryozoan to include the southern Arctic areas of the eastern coast of Labrador and Ungava Bay, Quebec.

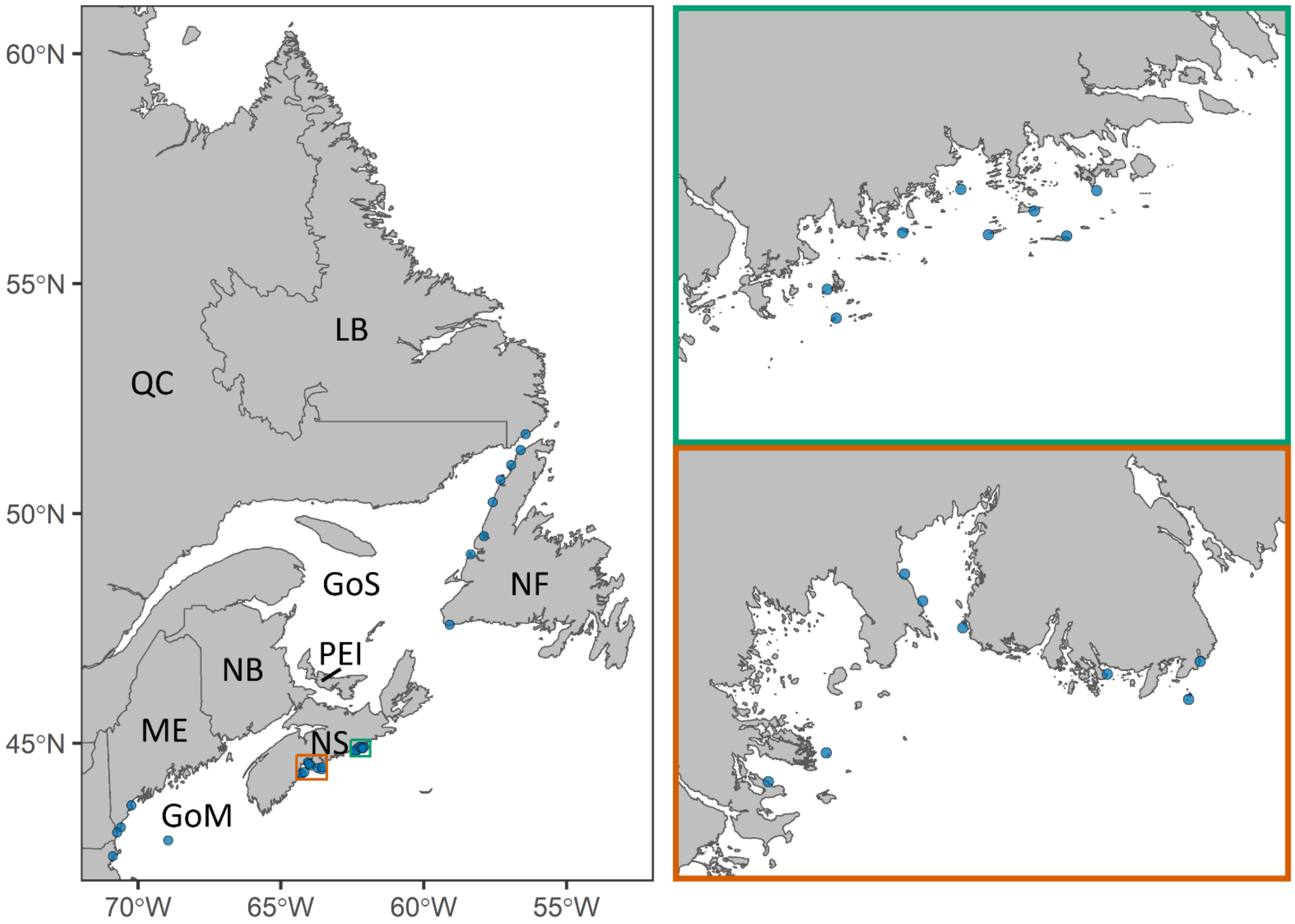

Figure 3.1 Map of the study region in the northwest Atlantic Ocean. Blue points represent sites from which data on percent cover of *Membranipora membranacea* were obtained. The green and orange insets show the Eastern Shore Islands and Southwestern Shore of Nova Scotia, respectively. GoM = Gulf of Maine, GoS = Gulf of St Lawrence, LD = Labrador, ME = Maine, NB = New Brunswick, NF = Newfoundland, NS = Nova Scotia, PEI = Prince Edward Island, and QC = Quebec.

3.3.2 Biological Data

I obtained observations of percent cover of *M. membranacea* from 20 subtidal sites (1-13.5 m depth) in the northwest Atlantic Ocean, collected during the annual growth period of *M. membranacea* (1 May – 30 November; Chapter 2) between 1987 and 2020 (n = 607). These data consisted of historical observations obtained from the literature and new data I collected from 9 sites along the Atlantic coast of Nova Scotia between 2018 and 2020. Each datapoint represents the mean percent cover of *M. membranacea* across all individuals of one of the three numerically dominant kelp species in the NWA (*Agarum clathratum, Laminaria digitata, Saccharina latissima*) at a given depth, site, and sampling date (see Chapter 2, except 2020, when new data were collected in July and October from 6 sites in the Eastern Shore Islands [Halibut Island, Long Island, The Moll, Speck Island, Tuffin Island, and White Island] using video-based percent cover estimation methods). No observations of percent cover were available on *Alaria esculenta*, a dominant kelp species in the northern Gulf of St Lawrence and northern Newfoundland (Adey & Hayek 2011); however, *A. esculenta* has thin blades (Kraan & Guiry 2000, Adey & Hayek 2011) which can erode rapidly, and was more prone to biofouling than *S. latissima* in a comparative study (Kerrison et al. 2020), and is therefore likely to be affected by *M. membranacea* to a similar or greater extent than the kelp species included in my dataset.

3.3.3 Environmental Data

In a comprehensive variable selection analysis, I found that sea surface temperature (SST; averaged over the previous six months), kelp substrate (the species of kelp on which the bryozoan is growing), and depth were informative predictors of percent cover of *M. membranacea* in the NWA, in order of decreasing importance (Chapter 2). Kelp substrate and depth were recorded when observations of percent cover were collected (allowing SDMs to be trained using these data) and parameterized as constants when projecting the SDMs (see section 3.3.4.3). Thus, I only obtained data layers for SST to train and project SDMs for *M. membranacea*.

I obtained rasters of daily SST for the NWA at a 0.05° (~5-km) spatial resolution from NOAA's "CoralTemp" dataset (NOAA Coral Reef Watch 2020) from 1987 to 2020. I then extracted time series of SST at each site where percent cover of *M. membranacea* was sampled. For sites that were not covered by the SST raster, I extracted the time series of the nearest neighbouring cell. From the timeseries at each site, I calculated mean temperature over the six months (180 days) prior to each observation of percent cover. These temperature values were used to train the SDMs (section 3.3.4).

To prepare SST data for projecting annual peak percent cover of *M. membranacea* throughout the NWA, I began by identifying the most suitable period to represent present-day SST conditions for the NWA (i.e. the most recent group of years with similar SST; see Appendix B.1 for details), and found this period to be 2010-2020. I elected to choose my own range of years to represent present-day SST conditions because I judged the range of years for "present-day" conditions used by common databases like Bio-ORACLE (2000-2014; Assis et al. 2018b) and MARSPEC (2002-2010; Sbrocco & Barber 2013) to no longer be representative of current SST conditions, due to rapid climate warming during the 2010s (NOAA National Centers for Environmental Information 2020). For each year from 2010 to 2020, I: (1) calculated the daily six-month mean SST for each cell in the study area using the CoralTemp data; (2) identified the maximum value (SST 6-max) for each year; and (3) averaged these SST 6-max values across years to create a present-day temperature climatology for projecting percent cover throughout the NWA.

To project percent cover in the NWA under future climate change scenarios, I was unable to use SST data from CoralTemp since this dataset does not provide future climate projections. Instead, I obtained “present-day” (2000-2014) and future (2040-2050 and 2090-2100) mean SST climatologies from Bio-ORACLE (Assis et al. 2018b) in order to generate rasters of the difference in SST between current and future climate scenarios, which could then be added to existing CoralTemp data to estimate future changes in SST 6-max. For each future time period, I selected Representative Concentration Pathways (RCPs) 4.5 (to represent a “likely” future climate pathway) and 8.5 (to represent a “worst-case scenario” future climate pathway; Hausfather & Peters 2020a), for a total of 4 future temperature scenarios. To obtain an estimate of mean SST 6-max for future scenarios, I first calculated the difference between mean “present-day” and future SST in the NWA for each cell in the Bio-ORACLE data. I then calculated SST 6-max for each year (as above) between 2000 and 2014 using the CoralTemp data and averaged across years, to provide a baseline value for each cell for the timeframe for “present-day” temperature from Bio-ORACLE. I generated future rasters of SST 6-max by adding the mean temperature difference between present and future scenarios (from Bio-ORACLE) to the mean SST 6-max for 2000-2014 (from CoralTemp). Since the resolution of the Bio-ORACLE data is coarser (0.08° or 9.2 km; Assis et al. 2018b) than that of CoralTemp (0.05° or 5 km; Skirving et al. 2020), I used bilinear interpolation to resample the temperature-difference rasters derived from Bio-ORACLE to match the resolution of the CoralTemp data prior to summing the two rasters.

3.3.4 SDM

3.3.4.1 Construction

Following Chapter 2, I trained an abundance SDM on my full dataset of percent cover using a generalized linear mixed model (GLMM) fit with maximum likelihood, with fixed effects for six-month mean SST, depth, and kelp substrate, an interaction between SST and kelp substrate, and crossed random intercepts for study site and year (to account for the blocked nature of my data within these factors). I standardized SST and depth by 2 standard deviations and applied a sum-to-zero contrast to kelp substrate prior to modelling, which decreased collinearity between main effects and interactions terms and improve the interpretability of the model coefficients (Gelman 2008, Schielzeth 2010). I used a beta error distribution for the model, to limit percent cover between 0 and 100% (expressed as a proportion between 0 and 1), and employed a zero-inflation model (Ospina & Ferrari 2012) parameterised with the same terms as the conditional model. Although I employed an intercept-only zero inflation model in Chapter 2 for the purposes of variable selection, preliminary analyses for Chapter 3 determined that a fully parameterized zero-inflation model improved the predictive performance of the SDM. Depth was non-significant in the zero-inflation model, but I retained it to comply with the ecological reasoning that depth affects the probability of measuring 0% cover.

3.3.4.2 Validation

To perform model validation, I employed the 0.632+ bootstrap method with 200 repetitions, following Potts and Elith (2006), because it provides a more accurate estimate of model performance than cross-validation techniques. Specifically, I calculated 5 metrics of performance for abundance models : 1) Pearson correlation between observed and predicted values (*r*); 2) Spearman rank correlation between observed and predicted values (ρ); 3) model calibration, where a linear regression model is fit between predicted and observed values (observed ~ *m*[predicted] + *b*) and the intercept (*b*) and slope (*m*) of the regression provide measures of bias and consistency of bias for the SDM, respectively; 4) root mean squared error (RMSE; Eq. 3.1) and average error (AVE; Eq. 3.2), where *n* is the sample size, $\hat{y}_i$ are the predicted values, and y_i are the observed values (Potts & Elith 2006).

$$\text{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(\hat{y}_i - y_i)^2} \tag{3.1}$$

$$\text{AVE} = \frac{1}{n}\sum_{i=1}^{n}(\hat{y}_i - y_i) \tag{3.2}$$

Lastly, I produced maps of model standard error (SE) to assess the magnitude and spatial distribution of uncertainty in the projections of percent cover (Guisan et al. 2017; see section 3.3.4.3).

3.3.4.3 Projection

I projected the SDM (percent cover and SE) onto present-day and future rasters of SST 6-max while keeping depth and kelp substrate constant. I chose to project at a constant depth because I were unable to obtain bathymetric rasters for the NWA at a high enough resolution to accurately reflect depths in the shallow subtidal zone over which my data ranged (1-13.5 m). Instead, I projected the model assuming a constant depth of 7.5 m, the median depth of the observations of percent cover in my dataset and also a depth commonly inhabited by all three kelp species in my dataset, as well as *Alaria esculenta* (Adey & Hayek 2011). Accordingly, I restricted the model domain to raster cells in contact with land, assuming these cells to contain a 7.5-m depth contour.

For kelp substrate, I made separate predictions of percent cover for each kelp species assuming it was present across the model domain. Although species distribution models for *L. digitata* and *S. latissima* exist for the NWA (Khan et al. 2018, Assis et al. 2018a, Wilson et al. 2019), these models did not consider the effects of *M. membranacea*. Furthermore, to my knowledge, no SDMs exist for *A. clathratum* in the NWA. Given these uncertainties and my study's focus on habitat suitability for *M. membranacea* (rather than its realized distribution on different kelp species), I chose to not incorporate kelp distribution models into this study.

Prior studies have suggested that low salinity may negatively affect *M. membranacea* (Forbord et al. 2020). Preliminary analyses indicated there was no relationship between percent cover and salinity for my data, but sites in my dataset represented a narrow range of relatively high salinity habitats relative to other areas within the NWA. I therefore determined the lowest salinity at which *M. membranacea* has been recorded in the NWA (21.2 PSU) and limited the SDM domain above this salinity level for my projections (see Appendix B.2 for details).

3.3.4.4 Effect of invasion stage on SDM performance

To determine whether species-environment relationships of *M. membranacea* have changed over time in the NWA, I first divided the data into "early-stage" and "late-stage" observations on which to train separate SDMs. To facilitate comparison between SDMs trained on the early- and late-stage datasets, I restricted the data to Nova Scotia for this analysis. *M. membranacea* was first documented in Nova Scotia in 1992 (Scheibling et al. 1999) and was the focus of a long-term study for the rest of the decade, from which I obtained records of percent cover ending in 1999 (Scheibling & Gagnon 2009). After 1999, the next records of percent cover in my dataset are from 2005 (Saunders & Metaxas 2009b), shortly before the bryozoan was observed at sites throughout Nova Scotia (Watanabe et al. 2010). I therefore selected 1999 as the cut-off year between early (1999 and before) and late (2005-2020) invasion stages. However, early-stage data only contained observations on *S. latissima* and contained considerably fewer observations (n=43) than the late-stage data (n=492). To make SDMs based on the late-stage data more comparable to the early-stage models, I limited the late-stage data to observations of percent cover on *S. latissima* and subsetted it via random sampling to match the sample size of the early-stage data prior to modelling.

For the dataset from each invasion stage, I fit an SDM as in section 3.3.4.1, but without kelp substrate (data in this analysis were restricted to a single kelp species [*S. latissima*]), as well as the random intercepts for site and year from the zero-inflation model due to low variance (Bolker et al. 2009). To assess model performance, I validated each model by predicting to the dataset from the opposite time period (i.e. early-stage SDM was validated on late-stage data, and vice versa) and calculating the 5 model validation metrics described in section 3.3.4.2. Lastly, I compared the distribution of percent cover in the NWA under present-day SST conditions projected using both the early- and late-stage models.

3.3.4.5 Comparison of NWA- and Norway-based SDMs

I obtained percent cover data (n=118) from multiple studies in Norway (Førde et al. 2016, Matsson et al. 2019, Forbord et al. 2020), which were collected from *S. latissima* growing at aquaculture sites distributed along a large latitudinal gradient (58-70°N). I retrieved SST data from CoralTemp and calculated six-month mean SST to match these percent cover records as per section 3.3.3. I then predicted percent cover for these data using the SDM trained on data from the NWA and assessed model performance using the 5 metrics detailed in section 3.3.4.2.

For comparison with the NWA-based model, and to assess the effect of any differences in species-environment relationships for *M. membranacea* between Norway and the NWA, I also trained an SDM for percent cover on the Norway dataset. I fit the model with the same specifications as the NWA-based SDM (section 3.3.4.1), except for kelp substrate, because all data from Norway were collected on the same kelp species (*S. latissima*), and random intercepts for site and year, which were removed from the zero-inflation model due to low variance (Bolker et al. 2009). I calculated raw-scale regression coefficients (b_{raw}; Schielzeth 2010) to compare the effect sizes of SST and depth between the NWA and Norway-based SDMs. I then predicted peak percent cover of *M. membranacea* in the NWA using the Norway-based model, under the present and future climate scenarios detailed in section 3.3.3, to simulate the potential effect of an invasion of Norwegian *M. membranacea* in the NWA.

I conducted all analyses in R, version 4.0.3 (R Core Team 2020) in the R Studio environment (RStudio Team 2020). I worked with raster data using the *raster* package (Hijmans 2020), used the *glmmtmb* package to fit GLMMs (Brooks et al. 2017) and checked GLMM assumptions (fit of data to specified error distribution, homogeneity of variance, collinearity between variables, spatial and temporal autocorrelation) using the *DHARMa* (Hartig 2020) and *performance* packages (Lüdecke et al. 2020). I created figures using *ggplot2* (Wickham 2016), *sf* (Pebesma 2018), and *rnaturalearth* (South 2017), and arranged them using *patchwork* (Pedersen 2020). Other packages used are listed in Appendix B.3. In addition to the description above, my methods are also detailed according to ODMAP protocol (Zurell et al. 2020) in Appendix B.4.

3.4 Results

3.4.1 Model performance

The SDM for *M. membranacea* in the NWA (Table 3.1) performed well, as indicated by the model validation statistics resulting from 0.632+ bootstrap analysis (Table 3.2). There was a high Pearson correlation (r) between observed and predicted values, and the high Spearman rank correlation (ρ) (Cohen 1988, Møller & Jennions 2002) indicated that the rank order of observations was preserved even when exact values were not predicted correctly. The model was almost perfectly calibrated, with no consistent bias ($b = 0.00$) and a slight overprediction of percent cover for high values ($m=0.97$). The model predictions of percent cover deviated from observed values by 12%

on average (RMSE = 0.12) and average model predictions were slightly lower than observed values (AVE = -0.01). Model standard error was less than 10% cover for all kelp substrate species and temperature scenarios and was highest for percent cover on *A. clathratum*, followed by *L. digitata* and *S. latissima* (Figures A.2-A.4).

Table 3.1 Model summary table for the SDM for peak percent cover of *M. membranacea*, trained on the full NWA dataset (section 3.3.4.1). Predictors were standardized by 2 standard deviations prior to modelling, and a sum-to-zero contrast was set for kelp substrate. Due to sum-to-zero contrast for kelp substrate, statistics for kelp substrate and kelp:SST use the intercept and the main effect for SST as reference categories, respectively. AC = *A. clathratum*, LD = *L. digitata*, SL = *S. latissima.* Significant p-values in **bold** ($\alpha = 0.05$). σ^2 is the residual variance and τ is the between-group variance for random intercepts.

Predictors	Estimates	Std. error	*z* value	*p*-value
Conditional Model				
(Intercept)	-2.36	0.15	-16.21	**<0.001**
Depth	-0.36	0.10	-3.70	**<0.001**
Kelp (AC)	-0.25	0.10	-2.53	**0.011**
Kelp (LD)	0.38	0.08	4.53	**<0.001**
Kelp (SL)	-0.13	0.07	-1.85	**0.064**
Six-Month Mean SST	1.79	0.14	13.18	**<0.001**
Kelp (AC): Six-Month Mean SST	-0.59	0.20	-2.88	**0.004**
Kelp (LD): Six-Month Mean SST	0.61	0.17	3.56	**<0.001**
Kelp (SL): Six-Month Mean SST	-0.02	0.14	-0.153	0.879
Zero-Inflation Model				
(Intercept)	-3.66	0.78	-4.67	**<0.001**

Predictors	Estimates	Std. error	*z* value	*p*-value
Depth	-0.22	0.44	-0.51	0.611
Kelp (AC)	2.72	0.60	4.51	**<0.001**
Kelp (LD)	-3.11	1.05	-2.95	**0.003**
Kelp (SL)	0.39	0.58	0.68	**0.499**
Six-Month Mean SST	-7.40	1.14	-6.48	**<0.001**
Kelp (AC): Six-Month Mean SST	3.29	1.13	2.90	**0.004**
Kelp (LD): Six-Month Mean SST	-5.52	1.95	-2.83	**0.005**
Kelp (SL): Six-Month Mean SST	2.23	1.08	2.08	**0.038**
Random Effects				
σ^2	0.45			
$\tau_{00\ \text{site}}$	0.23			
$\tau_{00\ \text{year}}$	0.06			

Table 3.2 Model validation statistics for all models assessed in this study. *r* is Pearson's correlation coefficient, *ρ* is Spearman's rank correlation coefficient, *b* is the intercept and *m* is the slope of model calibration linear model (observed ~ *m*[predicted] + *b*), RMSE is the root mean squared error, and AVE is the average error (following Potts & Elith 2006).

Training Data	Validation Method	*r*	*ρ*	Model Calibration		RMSE	AVE
				b	*m*		
NWA	0.632+ bootstrap	0.70	0.84	0.00	0.97	0.12	-0.01
NWA Early-Stage	Test data (late-stage dataset)	0.46	0.68	0.02	0.67	0.15	-0.02
NWA Late-Stage	Test data (early-stage dataset)	0.74	0.80	-0.03	1.15	0.11	-0.01
NWA	Test data (Norway dataset)	0.42	0.58	-0.05	3.78	0.26	0.10
Norway	0.632+ bootstrap	0.69	0.84	0.01	0.99	0.14	-0.01

3.4.2 Distribution of peak percent cover under present-day and future climate scenarios

Under present-day temperature conditions (2010-2020), peak percent cover of *M. membranacea* in the NWA varied substantially between different areas and generally decreased with increasing latitude. The area of highest predicted cover was the southern Gulf of Maine, with up to 65% cover on *L. digitata* (Figure 3.2), 35% cover on *S. latissima* (Figure 3.3), and 20% cover on *A. clathratum* (Figure 3.4). In contrast, the lowest cover was predicted for the east coast of Labrador (LB) and Ungava Bay (UB) (≤5%) for all three species (Figures 3.2-3.4). Intermediate levels of cover were predicted in the other regions.

Under RCP 4.5, the SDM projected modest increases in peak percent cover of *M. membranacea*, compared to present-day cover, on all three kelp species and in most areas of the NWA by 2040-2050 (up to 10% on *L. digitata*, Figure 3.2; 5% on *S. latissima*, Figure 3.3; and 2% increase on *A. clathratum*, Figure 3.4), with further increases expected by 2090-2100 (up to 15% on *L. digitata*, Figure 3.2; 8% on *S. latissima*, Figure 3.3; and 4% increase on *A. clathratum*, Figure 3.4). The largest projected increases in cover did not occur in areas with the highest present-day cover; for example, on the east coast of Cape Breton Island in Nova Scotia, where present-day cover was intermediate and ranged from 13% on *A. clathratum* (Figure 3.4) to 40% on *L. digitata* (Figure 3.2), cover increased to 17% (Figure 3.4), and 55% (Figure 3.2), respectively, by 2090-2100. Unlike the rest of the NWA, increases in cover were negligible in northern Newfoundland, LB, and UB on all three kelp species. In some embayments (e.g. Bay of Fundy, Nova Scotia; Chaleur Bay, New Brunswick; Notre Dame Bay, Newfoundland), cover was projected to decrease (Figures 3.2-3.4); in these areas temperature projections for 2090-2100 under RCP 4.5 have already been surpassed by 2010-2020 temperatures.

Peak percent cover projections under RCP 8.5 for 2040-2050 were almost identical to 2090-2100 projections under RCP 4.5 (Figures 3.2-3.4). However, by 2090-2100, substantial increases in percent cover were projected on all kelp species. Cover is projected to be the highest in the southern Gulf of Maine and the Maritime provinces (Nova Scotia, New Brunswick and Prince Edward Island), with up to 80% cover on *L. digitata* (Figure 3.2), 50% cover on *S. latissima* (Figure 3.3), and 30% cover on *A. clathratum* (Figure 3.4). These cover levels are increases of up to 30%, 25%, and 15% compared to present-day cover, respectively. While cover on *A. clathratum* and *S. latissima* is expected to remain low in LB and UB (Figures 3.3, 3.4), cover on *L. digitata* will reach up to 20% in southeastern LB and 10% in UB (Figure 3.2).

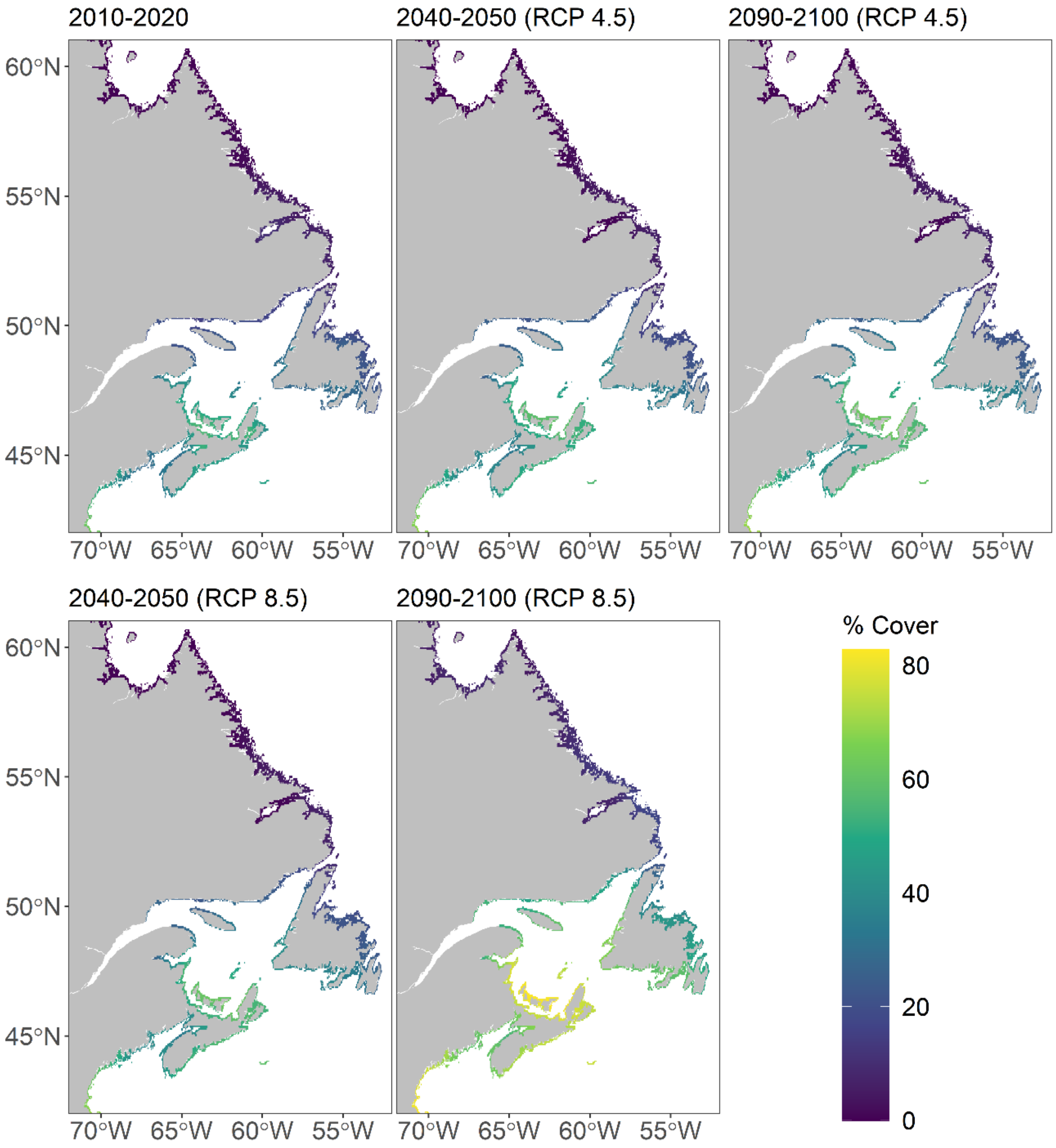

Figure 3.2 SDM projections of peak percent cover of *M. membranacea* on *L. digitata* for present-day (2010-2020) and future SST scenarios. RCP is the Representative Concentration Pathway under which SST has been predicted for each future time period

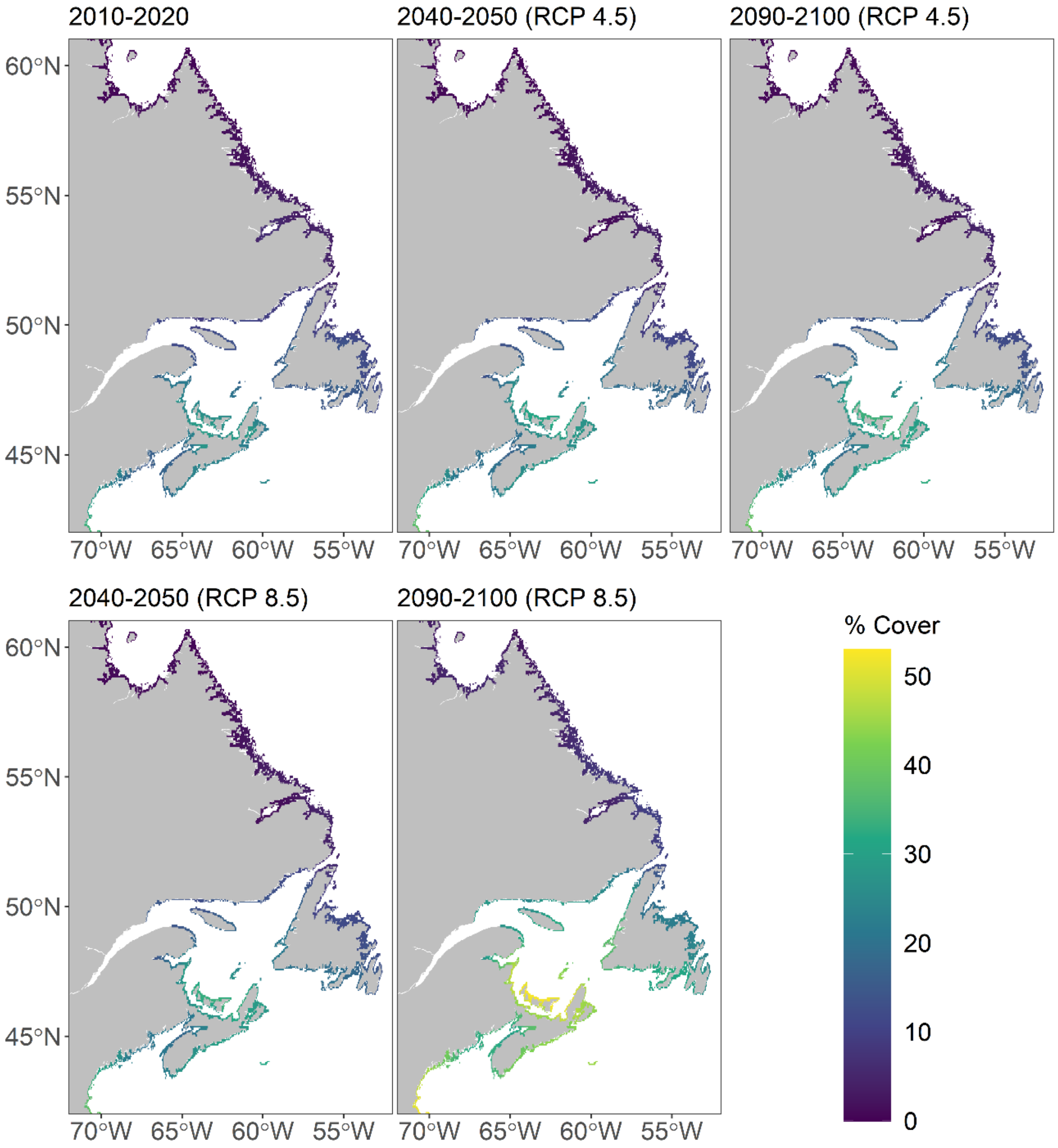

Figure 3.3 SDM projections of peak percent cover of *M. membranacea* on *S. latissima* for present-day (2010-2020) and future SST scenarios. RCP is the Representative Concentration Pathway under which SST has been predicted for each future time period

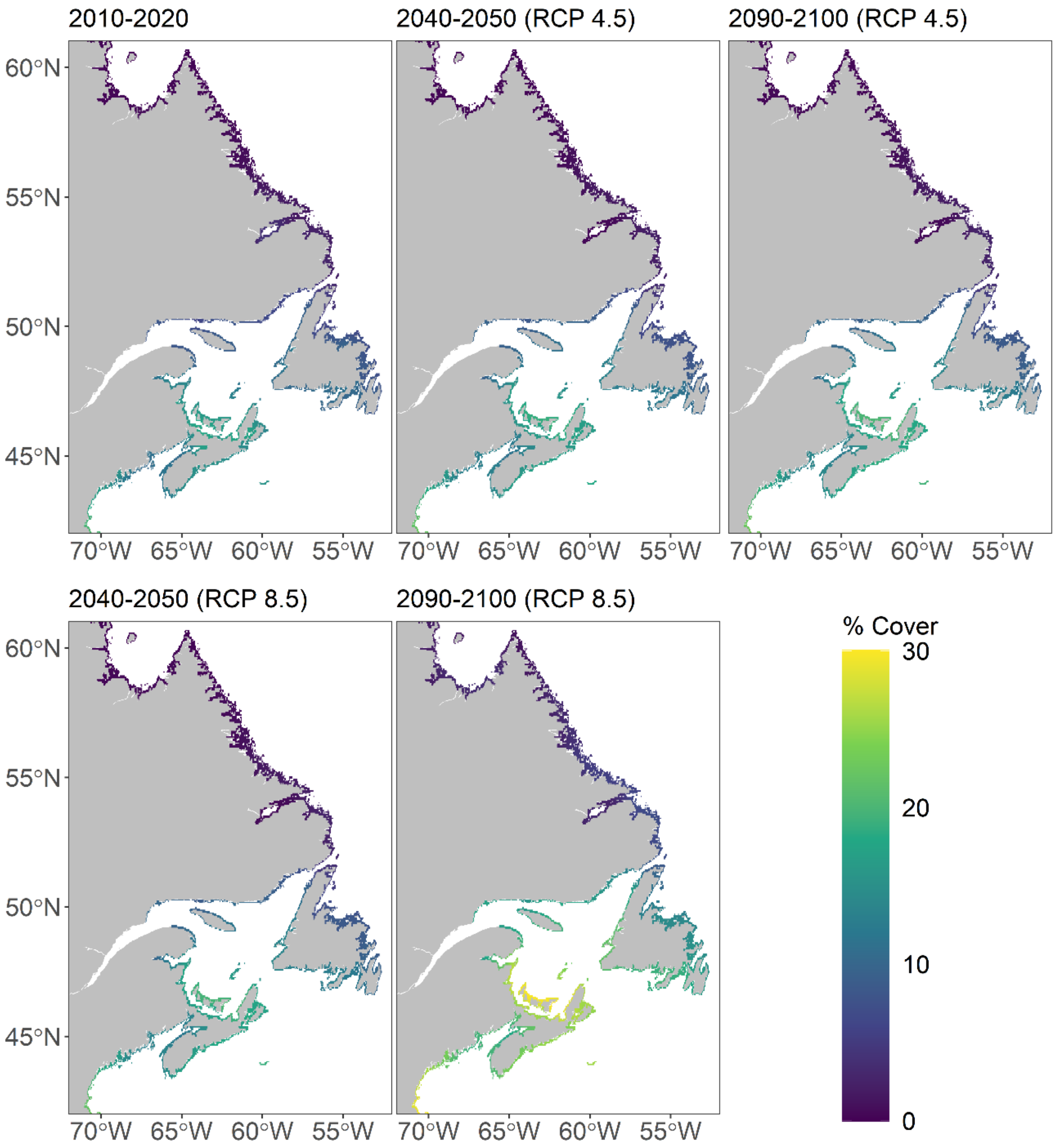

Figure 3.4 SDM projections of peak percent cover of *M. membranacea* on *A. clathratum* for present-day (2010-2020) and future SST scenarios. RCP is the Representative Concentration Pathway under which SST has been predicted for each future time period

3.4.3 Effect of invasion stage on SDM performance

The SDM trained on late-stage invasion data (2005-present) performed substantially better when extrapolating to early-stage observations (1999 and earlier) than the early-stage model when extrapolating to late-stage data (Table 3.2). The early-stage model over-estimated higher observations of percent cover for the late-stage data (m = 0.67; Table 3.2). When projected to the NWA under present-day conditions, the early-stage model also over-estimated cover compared to the SDM trained on all observations from Nova Scotia (Figure 3.5). In contrast, the late-stage model slightly underestimated cover for the early-stage observations within the larger cover ranges (m = 1.15; Table 3.2) and produced present-day projections of percent cover similar to those of the SDM trained on all observations from Nova Scotia (Figure 3.5)

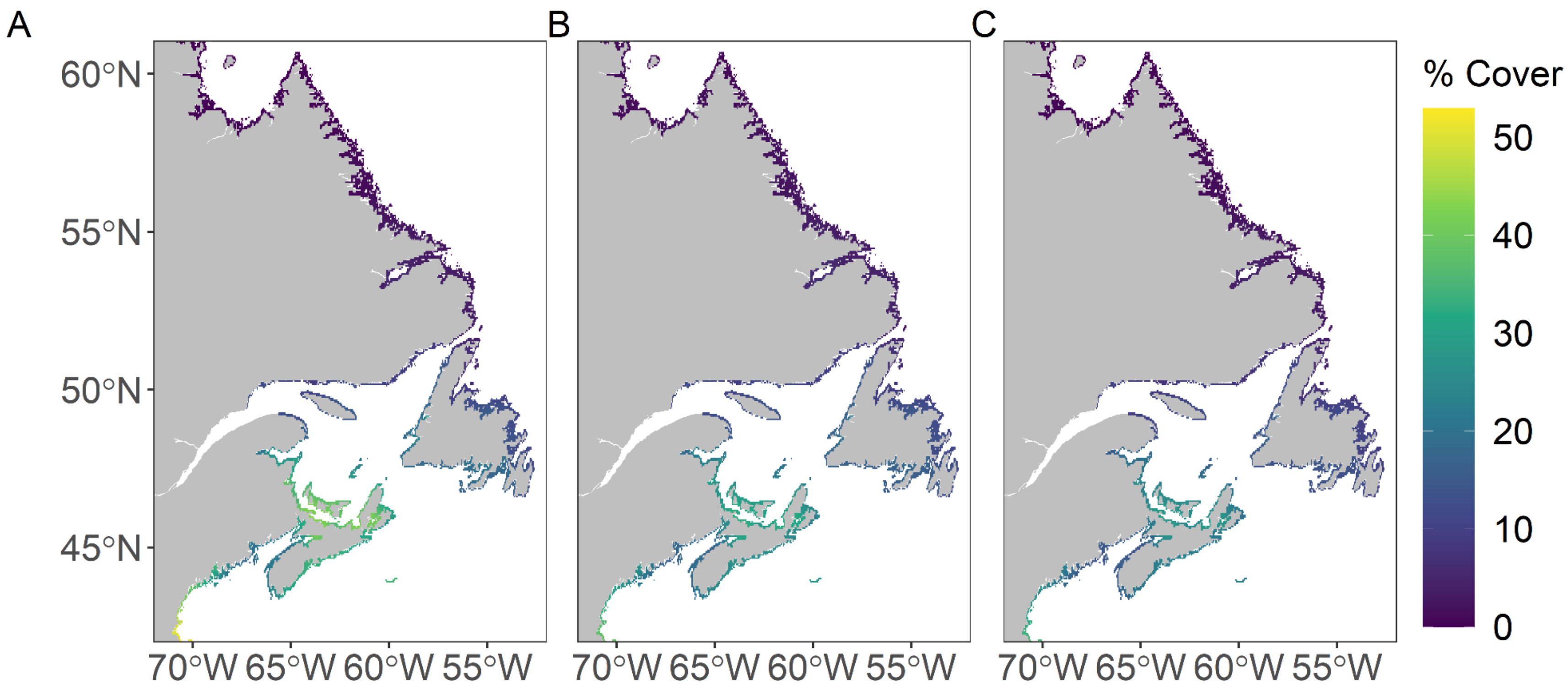

Figure 3.5 Projections of peak percent cover of *M. membranacea* on *S. latissima*, under present-day (2010-2020) SST conditions, by SDMs trained on A) data from Nova Scotia collected in 1999 or before, B) data from Nova Scotia collected in 2005 or after (subset to match sample size of data from 1999 or before), and C) all data from Nova Scotia.

3.4.4 Comparison of NWA- and Norway-based SDMs

The SDM trained on data from the NWA exhibited poor performance when validated against percent cover data from Norway, with low correlations (r and ρ) between observed and fitted values, high error (RMSE and AVE), and drastically underestimated percent cover (m = 3.78; Table 3.2). When compared to the NWA-based model, the SDM trained on the Norway data (Table 3.3) had a much larger raw-scale parameter estimate for SST (b_{raw} Norway: 0.28; b_{raw} NWA: 0.07), indicating that percent cover of *M. membranacea* in Norway reaches high levels at lower temperatures than in the NWA. Additionally, there was a positive relationship between depth and percent cover in Norway (Table 3.3) in contrast to the negative relationship between depth and percent cover in the NWA (Table 3.2). When the Norway-based SDM was projected for cover on *S. latissima* in the NWA, cover was predicted to be 40-50% higher throughout the NWA (excluding LB and UB) than that predicted by NWA-based model under all scenarios (Figure 3.6). For example, projected present-day cover by the Norway-based SDM ranged between 40-90% and cover in 2090-2100 under RCP 8.5 was between 90-100%. For LB and UB, the Norway-based SDM projected low cover in all scenarios except for RCP 8.5 2090-2100, where up to 45% cover was projected for southern LB and up to 15% cover was projected for UB (Figure 3.6).

Table 3.3 Model summary table for the SDM for peak percent cover of *M. membranacea*, trained on the Norway dataset (section 3.3.4.5). Predictors were standardized by 2 standard deviations prior to modelling. Significant p-values in **bold** ($\alpha = 0.05$). σ^2 is the residual variance and τ is the between-group variance for random intercepts.

Predictors	Estimates	Std. error	*z* value	*p*-value
Count Model				
(Intercept)	-1.47	0.16	-9.32	**<0.001**
Depth	0.73	0.23	3.12	**0.002**
Six-Month Mean SST	1.62	0.31	5.21	**<0.001**
Zero-Inflated Model				
(Intercept)	-1.25	0.30	-4.24	**<0.001**
Depth	0.68	0.49	1.38	0.166
Six-Month Mean SST	-4.61	0.91	-5.07	**<0.001**
Random Effects				
σ^2	0.49			
$\tau_{00\ \mathrm{site}}$	0.00			
$\tau_{00\ \mathrm{Year}}$	0.00			

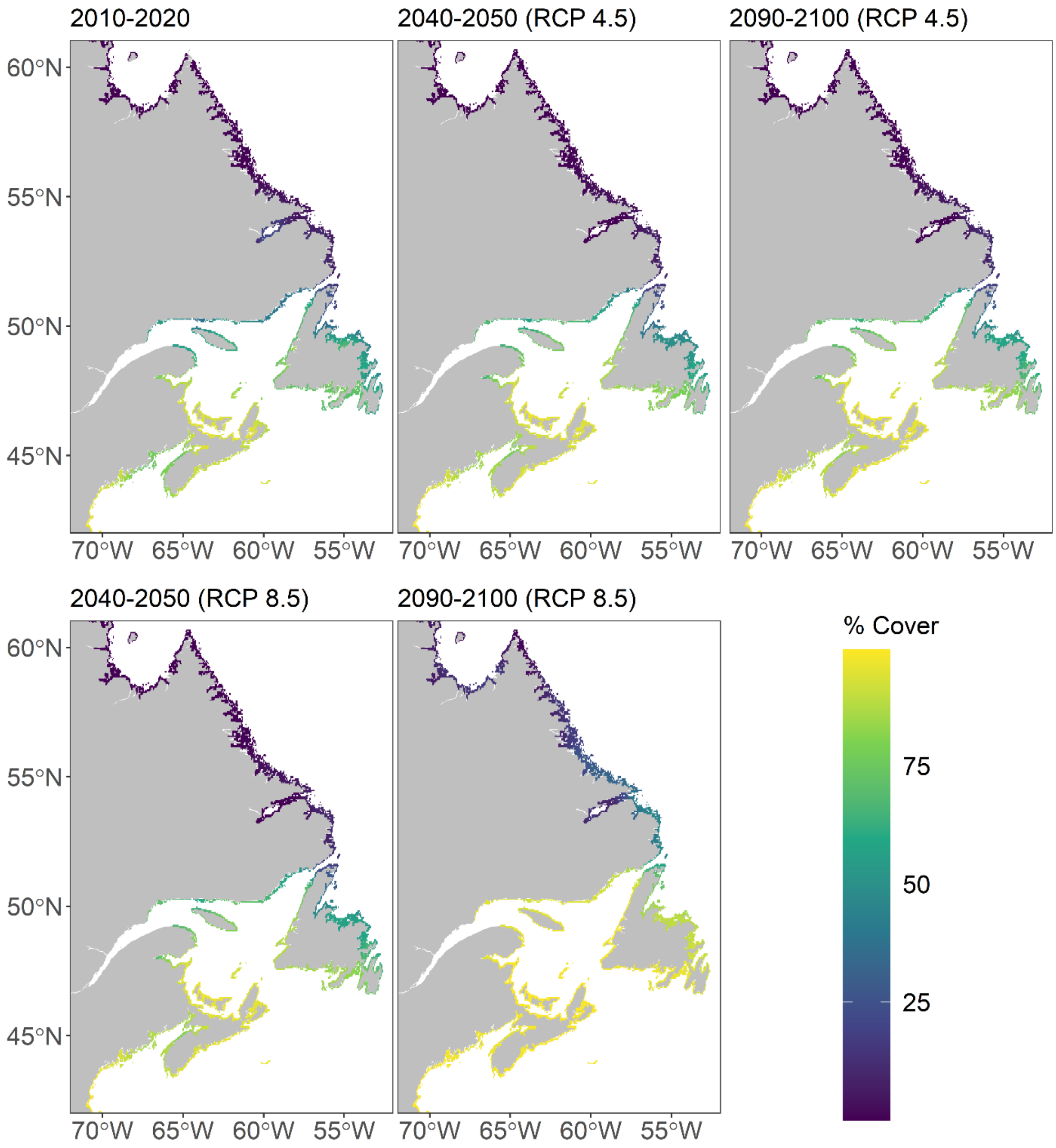

Figure 3.6 Projections of peak percent cover of *M. membranacea* on *S. latissima* in the NWA by the Norway-based SDM for present-day (2010-2020) and future SST scenarios. RCP is the Representative Concentration Pathway under which SST has been predicted for each future time period.

3.5 Discussion

Using SDMs, I projected the present and future abundance of the invasive bryozoan *M. membranacea* in the northwest Atlantic Ocean (NWA). I found that future peak percent cover of the bryozoan will depend on emission scenario, and may be magnified if an additional invasion occurs from a source population adapted to colder temperatures than in the NWA.

3.5.1 Projections of peak percent cover of *M. membranacea* in the NWA

There were large differences in projections of future peak percent cover of *M. membranacea* depending on the employed future climate change scenario. Under the likely future climate pathway of RCP 4.5, the abundance of *M. membranacea* was predicted to show modest increases by 2090-2100 compared to present-day in most areas. The largest increases were forecasted for areas where present-day cover of *M. membranacea* is intermediate (e.g. in Cape Breton Island, Nova Scotia, where cover is 13- 40% depending on kelp substrate) and no area in the NWA was predicted to reach percent cover levels above present-day maxima. Peak cover of *M. membranacea* was projected to increase approximately twice as rapidly under a worst-case emissions scenario (RCP 8.5), as projected cover by mid-century was very similar to end-of-century projections under RCP 4.5. By the end of the century under RCP 8.5, large increases in percent cover were predicted; for example, cover on *S. latissima* was expected to increase from up to 35% in present-day to over 50% in 2090-2100 in some areas of the Gulf of Maine and Maritime provinces. This increase in cover could considerably exacerbate damage to kelp beds in these locations, as kelp defoliation rapidly intensifies as peak cover of *M. membranacea* increases from 25 to 50% (Scheibling & Gagnon 2009).

Increasing habitat suitability for invasive species in the Arctic has been projected under climate change, particularly for ship-mediated invasive species like hull-fouling organisms and organisms with a planktonic stage amenable to ballast water transport (Ware et al. 2016, Goldsmit et al. 2018, Holbech & Pedersen 2018); *M. membranacea* has both of the above characteristics. There is a particularly high risk of spread of ship-mediated marine invasive species to the Arctic due to the projected increase in shipping activity in the area (Miller & Ruiz 2014), emphasising the need for predictions of suitable habitat for such invasive species and their potential impacts in the region. *M. membranacea* has not been recorded to date on the Atlantic coast of Labrador (LB) or in Ungava Bay (UB), the Arctic regions included in my SDM domain, but I predicted the bryozoan will occur there at low peak cover (<8% on all kelp species) in both 2040-2050 and 2090-2100 under RCP 4.5. Goldsmit et al. (2018) also predicted that *M. membranacea* could occur on the Atlantic coast of LB and in UB by 2045-2050 under RCP 4.5, supporting my prediction of the potential range expansion of the bryozoan to these areas. Projected cover was higher under the worst-case emissions scenario (RCP 8.5), with up to 20% cover on *L. digitata* on the Atlantic coast of LB and up to 10% in UB. However, although these cover levels are notably higher than those projected under RCP 4.5, they are still unlikely to cause significant damage to kelp beds. Overall, although it is possible that *M. membranacea* could spread to the Arctic under both future climate scenarios, there is little evidence that the bryozoan would threaten the kelp beds there under either scenario.

Substantial differences in SDM projections between climate scenarios, like those observed in this study, are common when projecting the response of marine ectotherms to climate change (e.g. Asch et al. 2018, van Woesik et al. 2018, Park et al. 2020), likely due to the strong dependence of these organisms on temperature (Schmidt-Nielsen 1997, Pörtner 2002). Given that considerable uncertainty exists regarding the extent of future warming under climate change (Hawkins & Sutton 2009, Hausfather & Peters 2020b, Schwalm et al. 2020), it is unclear which RCP scenario future climate will track most closely. The future abundance and impact of *M. membranacea* on kelp beds in the NWA are therefore largely dependent on the extent of ocean warming due to climate change.

My comparison of SDMs trained on data from Norway and the NWA revealed a pronounced difference in the response to temperature between populations of *M. membranacea* in the two regions. The bryozoan appears to achieve markedly higher percent cover in Norway than in the NWA under the same temperature conditions. I propose that populations of *M. membranacea* in Norway may be genetically adapted to grow at colder water temperatures than populations in the NWA. Indeed, *M. membranacea* from Norway are genetically distinct from *M. membranacea* from the NWA (Arpin 2021). Also, genetic evidence indicates that *M. membranacea* was likely introduced to the NWA from its native range in Europe (Schwaninger 1999), possibly from a single location (Arpin 2021). A source location for NWA populations that is warmer than Norway (e.g. England) may explain the better performance of *M. membranacea* at colder temperatures in Norway than in the NWA. In addition to differences in source population, genetic adaptation (Liu et al. 2020) and phenotypic plasticity (Zenni et al. 2014) can also lead to shifts in the climatic niche of invasive species compared to their native populations. It is possible that *M. membranacea* of Norwegian origin are already present in the NWA and have genetically or phenotypically altered their response to temperature (see Menon 1972). However, the existence of genetic differences between populations from the NWA and Norway makes the presence of phenotypically adapted Norwegian *M. membranacea* unlikely, and there is no evidence of genetic adaptation of the bryozoan within the NWA. I thus consider the hypothesis of a non-Scandinavian origin for current populations of the bryozoan in the NWA more plausible.

The introduction of *M. membranacea* from Norway, or elsewhere in northern Europe, to the NWA may cause the bryozoan to exhibit different population dynamics than the current strains in the region. Invasions from different source populations can increase the success of invasive species in their introduced range, by either facilitating local adaptation by increasing genetic diversity (Sakai et al. 2001) or acting as pre-adapted genotypes to novel areas (Le Roux & Wieczorek 2009, Novo et al. 2015). Accordingly, a future invasion of cold-tolerant *M. membranacea* could expand the thermal tolerance of the bryozoan in the NWA and allow it to proliferate at an accelerated rate in the region. Such an expansion of an invasive species has occurred in the region previously: the European green crab was originally introduced to the east coast of the United States from southern Europe, but range expansion to the colder waters of the Maritime Provinces was the result of a second invasion of a more cold-tolerant lineage from Norway (Roman 2006).

When projected to the NWA, the Norway-based SDM projected 40-50% higher peak cover of *M. membranacea* on *S. latissima* than that predicted by the NWA-based

SDM in most areas, under both present-day and future temperature conditions. Such coverage could jeopardize the viability of kelp populations throughout the region, except possibly the Atlantic coast of LB and UB. However, by the end of the century, severe negative impacts on kelp populations on the Atlantic coast of LB may also occur, as the Norway-based SDM predicted up to 50% peak cover on the Atlantic coast of LB under RCP 8.5. Studies currently predict stable or increasing populations of Arctic kelp under climate change based on environmental conditions (Assis et al. 2018a, Filbee-Dexter et al. 2019). However, high cover of *M. membranacea* in the Arctic under a potential invasion of populations from Norway underscores the importance of considering the impact of invasive (Reside et al. 2014) or other antagonistic species (Davis et al. 2021) when predicting climate refugia. Overall, given the ever increasing risk of biological invasions due to global shipping (Sardain et al. 2019) and the lack of intra-regional ballast water regulations in the NWA (Scriven et al. 2015), an invasion of Norwegian *M. membranacea* in the NWA is possible, could easily spread throughout the region from its site of introduction, and could have unexpectedly detrimental consequences for kelp bed ecosystems.

3.5.2 SDM performance and limitations

The SDM for peak percent cover of *M. membranacea* in the NWA performed well under 0.632+ bootstrap evaluation and produced reasonable present-day projections of percent cover, including moderate to high cover on *L. digitata* and *S. latissima* in the Gulf of Maine and Nova Scotia (Saunders & Metaxas 2008, 2009b, Scheibling & Gagnon 2009) and low percent cover for the northern Gulf of St Lawrence and Newfoundland (Caines & Gagnon 2012, Denley et al. 2019b). Negligible present-day cover predicted for the Atlantic coast of LB and UB fits with a lack of reports of *M. membranacea* presence in these areas to date. The distribution of peak cover of *M. membranacea* produced by the SDM is also broadly similar to present-day habitat suitability predicted by Lyons et al. (2020), with differences in some areas possibly because abundance and habitat suitability are generally only loosely correlated (Bean et al. 2014, Acevedo et al. 2017, Jiménez-Valverde et al. 2021).

I showed that accurate prediction of the abundance distribution of *M. membranacea* was not possible using only data available during the initial stage of its invasion. SDMs for invasive species that are calibrated in the early stages of the invasion may produce inaccurate projections due to an incomplete representation of the environmental niche of the species by early-stage training data (Václavík & Meentemeyer 2012) or a change in the niche of the species over time due to phenotypic or genetic adaptation to its invaded environment (Gallien et al. 2010, Jiménez-Valverde & Lobo 2011). For *M. membranacea*, the late-stage model accurately predicted early-stage observations, indicating that the latter was not the case. Instead, it is likely that the paucity of sites in the early-stage data (n =2, compared to n = 11 in the late-stage data) represented only a subset of the abiotic conditions habitable for the bryozoan (Jiménez-Valverde et al. 2011), decreasing the performance of the early-stage SDM. The lack of evidence for fundamental niche evolution over time in *M. membranacea* supports the validity of temporal extrapolation using the SDM for the bryozoan in the NWA. Additionally, the poor performance of the early-stage SDM reinforces the need for caution when calibrating SDMs for invasive species in the early stages of their invasion (Václavík & Meentemeyer 2012).

Although the SDM performed well in internal validation and produced plausible projections in most areas, projections of future cover in some areas may be unrealistic. For example, projections of future cover in some embayments (e.g. Bay of Fundy, Nova Scotia; Chaleur Bay, New Brunswick; Notre Dame Bay, Newfoundland) may be artificially low, as evidenced by projected decreases in cover under 2040-2050 temperature conditions. Projected decreases in cover arise because present-day (2010-2020) SST values have already surpassed those predicted for 2040-2050 by Bio-ORACLE for these embayments. Although decreases in SST are projected for some areas of the Atlantic under climate change (e.g. south of Greenland; Alexander et al. 2018), no evidence for decreases in temperature in these embayments exists. It is more likely that the ensemble of pre-2014 CMIP5 climate models used to generate the Bio-ORACLE SST projections (Assis et al. 2018b) underestimated the rapidity of climate change in these embayments, and projections of cover in these areas should be treated with caution as a result. Additionally, SDM projections of very low peak cover in some areas (e.g. LB and UB) may not guarantee the presence or persistence of *M. membranacea* at these locations, as abundance SDMs are not reliable at estimating absence (i.e. 0% cover; Young et al. 2012).

The impacts of biological invasions on native ecosystems are often dependent on local ecological context (de Moura Queirós et al. 2011, Thomsen et al. 2011, Hulme et al. 2013). In this study, peak percent cover of *M. membranacea* may not directly correlate with impacts on local kelp communities due to interspecific and environment-driven differences in kelp physiology. For example, all kelp species may not experience similar defoliation: *L. digitata* appears to be more resistant to damage by *M. membranacea* than

S. latissima (Krumhansl et al. 2011), which may allow *L. digitata* to persist more easily through outbreaks of the bryozoan (Saunders & Metaxas 2009b). Also, declines in abundance of kelp species more vulnerable to *M. membranacea* may allow less susceptible species to increase in abundance (Denley et al. 2019a). Thus, the same level of peak percent cover by *M. membranacea* may have different ecological implications for different kelp species, and the severity of the effect of the bryozoan may depend on the species composition of a given kelp community.

Impacts of invasive species are also affected by variability in abiotic conditions (Thomsen et al. 2011, Gutiérrez et al. 2014). For instance, kelp blades become stronger when exposed to higher wave energy (Kraemer & Chapman 1991, Thomsen et al. 2004, Wernberg & Vanderklift 2010), possibly reducing tissue weakening induced by *M. membranacea*, in turn explaining the persistence of kelp populations in some wave exposed areas of the NWA despite high cover by the bryozoan (Attridge et al. submitted). Moreover, the direct negative effect of increasing sea temperatures on kelps (Simonson et al. 2015) may worsen the impact of *M. membranacea* on kelps as the climate warms.

3.6 Conclusions

Using species distribution modelling, I showed that peak percent cover of *M. membranacea* in the NWA could increase either slightly or dramatically by the end of the century, depending on the future trajectory of ocean warming. Consequently, similarly to other ecosystems characterized by marine ectotherms, the fate of kelp beds throughout much of the NWA is largely dependent on the extent of climate change mitigation. Importantly, projected increases in the abundance *M. membranacea* may be partially underestimated in some areas (e.g. large embayments) where current temperatures have already exceeded projected trends. Kelp beds on the east coast of Labrador and Ungava Bay do not appear to be at significant risk of defoliation by *M. membranacea* over the next century, assuming the response of the bryozoan to temperature remains unchanged. However, the substantial differences in projections between populations of *M. membranacea* from Norway and NWA indicate that the bryozoan could achieve considerably higher percent cover throughout the NWA, extending into Labrador, if the former were to invade the region. This emphasises the large potential for multiple introductions to alter the impact of invasive species. An invasion of *M. membranacea* from Norway would challenge the status of the Arctic as a potential refuge for kelp under climate change, highlighting the importance of considering invasive species range shifts when predicting refugia for species of concern. Lastly, although the SDM performed well, the complex responses of kelp communities to infestation by the bryozoan and the environment limit the interpretation of the potential impacts of *M. membranacea* on kelp beds, exemplifying the need for SDMs to be interpreted in ecological context. Overall, this study provides evidence that climate change may expand the range and intensify the impact of *M. membranacea* on kelps in the NWA, indicating that the bryozoan will continue to be a significant driver of ecological change in rocky subtidal ecosystems of the region.

CHAPTER 4

CONCLUSION

Species distribution models (SDMs) are important tools for informing the management of invasive species (Gallien et al. 2010, Srivastava et al. 2019). In this thesis, I developed and employed SDMs to project the present and future distributions of the invasive bryozoan *Membranipora membranacea* in the northwest Atlantic Ocean (NWA). My results contribute valuable knowledge applicable both to the management of *M. membranacea*, but also to SDMs and their application to predictions of invasive species more broadly.

In Chapter 2, I laid the foundation for an SDM for the percent cover *M. membranacea* by thoroughly evaluating the importance of candidate predictor variables. Although previous studies had identified numerous candidate predictor variables for percent cover, their effects on the bryozoan over large spatiotemporal scales, their relative and absolute importance, and numerous details of their optimal parameterization were unknown. I found that temperature (specifically, mean temperature over the previous six months), kelp substrate, and depth were important predictors of percent cover, establishing these variables as the optimal predictors for use in an SDM for percent cover. By also examining the predictors of settler density, I not only contributed to fundamental knowledge of the environmental drivers of settlement in *M. membranacea* but also demonstrated that optimal predictors and their metrics for use in SDMs can differ depending on the life stage of the organism being modelled. This and other generalizable findings (see section 2.6) allowed me to compose a conceptual framework to guide variable selection for SDMs of other species.

Past studies have developed SDMs predicting the presence of *M. membranacea* (Goldsmit et al. 2018, Lyons et al. 2020), but models predicting the abundance and resultant impact of the bryozoan were lacking prior to this thesis. In Chapter 3, I applied the results of my variable selection analysis (Chapter 2) to construct and project SDMs for the peak percent cover of *M. membranacea* in the NWA under present and future climate scenarios. I also fit SDMs to data from the early and late stages of the invasion of the bryozoan to determine whether there was evidence of a niche shift for *M. membranacea* in the NWA over time. Lastly, I assessed the impact of a potential future invasion of the NWA by populations of the bryozoan from Norway by comparing NWA- and Norway-based SDMs. Peak percent cover in the NWA was projected to remain similar to present-day levels or to increase substantially in most areas, depending on the future climate scenario employed. Although I found no evidence of a niche shift for *M. membranacea* over time in the NWA, my results demonstrated that Norwegian populations of *M. membranacea* exhibit different responses to temperature and depth than populations in the NWA. An invasion of *M. membranacea* from Norwegian populations could potentially alter the behaviour of the bryozoan within the NWA, allowing it to achieve extremely high peak percent cover under present and future climate conditions and even to spread into eastern Labrador at levels that could negatively impact kelp populations. Overall, my results show that the threat of *M. membranacea* in the NWA may increase with future climate change (including in the Arctic under some scenarios), but the extent of this increase is dependent on the magnitude of future climate change as well as the invasion dynamics of the bryozoan.

The predictions of the distribution of *M. membranacea* can help to inform management action to mitigate the effects of the bryozoan on kelp beds in the NWA. For one, marine protected areas (MPAs) in the NWA mandated to protect kelp (e.g. Eastern Shore Islands Area of Interest; DFO 2019) should consider the current and future abundance of *M. membranacea* and its potential to negatively impact kelps in the area. MPAs could be established in areas where the present and projected impacts of *M. membranacea* on kelps are projected to remain low under climate change (e.g. eastern Newfoundland, northern Gulf of St Lawrence, Labrador and Ungava Bay; see section 3.4.2). This would allow protection of kelps from other stressors while avoiding areas impacted by the bryozoan (*sensu* Giakoumi et al. 2016). Additionally, the projected negative impacts associated with an invasion of *M. membranacea* from Norway emphasise the need for continued improvements to preventative measures (e.g. ballast water treatment; Scriven et al. 2015) and monitoring of *M. membranacea* populations (Sephton et al. 2017, DFO 2020) to detect additional invasions of the bryozoan that could change its response to environmental conditions in the NWA. However, projections of peak percent cover of *M. membranacea* must be considered jointly with the susceptibility of the local kelp community when predicting the impacts of the invasive species on kelp beds (see section 3.5.2). Therefore, continued research on the interactions between *M. membranacea*, kelp beds, and environmental conditions is necessary to fully disentangle the various context-dependent effects of the bryozoan on kelps and more accurately predict the impact of the invasive species under climate change.

APPENDIX A

CHAPTER 2

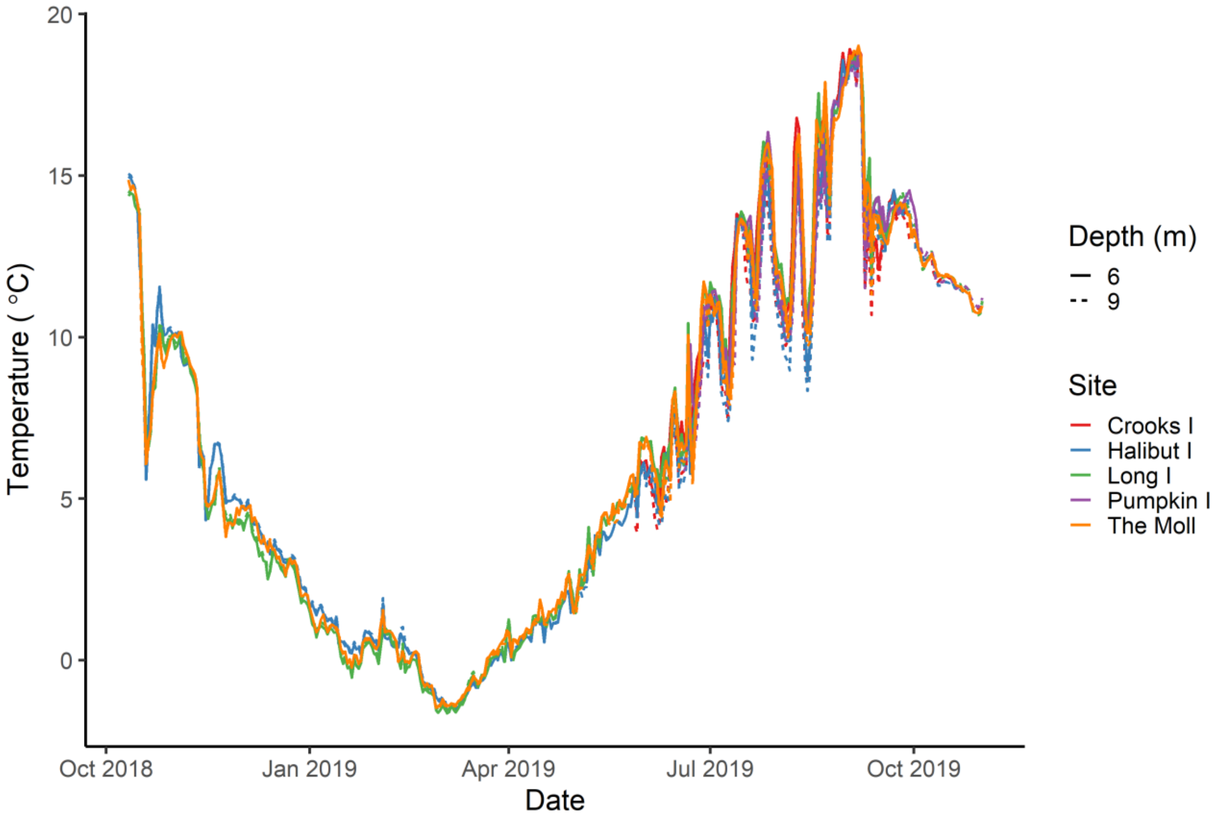

Figure A.1 Daily *in situ* temperature data from five sites in the Eastern Shore Islands from October 2018-October 2019.

Table A.l Regions (GOM = Gulf of Maine, NFLD = Newfoundland and Labrador, NS = Nova Scotia), study sites, locations, years, and kelp substrate species (AC = *A. clathratum*, LD = *L. digitata*, SL = *S. latissima*) for which data on percent cover and settler density of Membranipora membranacea were available. Sample sizes for percent cover (N (Cover)) and settler density (N (Sett)) are kelp species-specific means for each depth, site, and sampling date and are shown for the full datasets, kelp density datasets, and IST datasets respectively. Total sample sizes are shown at the bottom of the table. Cover method: method by which percent cover data were collected (blade: examining individual kelp blades; video: video transects). Sett definition: how settlers were defined in a study; see text for details.

								N (Cover)			N (Sett)			
Region	Study site	Latitude (DD)	Longitude (DD)	Year	Kelp substrate	Cover method	Sett definition	Full	Kelp density	IST	Full	Kelp density	IST	Source
GOM	Ammen Rock 1	42.89058	-68.94351	1987, 2012, 2014	SL	video[a]	NA	3	3	NA	NA	NA	NA	Witman and Lamb (2018)
	Beverly Port Marina	42.54047	-70.88256	2010, 2011	SL	blade	NA	13	NA	NA	NA	NA	NA	McCuller (2012)
	Cape Neddick	43.16700	-70.59200	1989, 1990	SL	blade	NA	3	NA	NA	NA	NA	NA	Lambert et al. (1992)
	Spring Point Marina	43.65071	-70.23037	2010, 2011	SL	blade	NA	16	NA	NA	NA	NA	NA	McCuller (2012)
	Wentworth Marina	43.05781	-70.72691	2010, 2011	SL	blade	NA	12	NA	NA	NA	NA	NA	

								N (Cover)			N (Sett)			
Region	Study site	Latitude (DD)	Longitude (DD)	Year	Kelp substrate	Cover method	Sett definition	Full	Kelp density	IST	Full	Kelp density	IST	Source
NFLD	Bird Cove	51.05528	-56.94028	2008	SL	blade	≤ 2 zooids	4	NA	NA	4	NA	NA	Caines and Gagnon (2012)
	Daniel's Harbour	50.24139	-57.58889	2008	SL	blade	≤ 2 zooids	4	NA	NA	4	NA	NA	
	Green Island Cove	51.37667	-56.60778	2008	SL	blade	≤ 2 zooids	4	NA	NA	4	NA	NA	
	Lark Harbour	49.10694	-58.35639	2008	SL	blade	≤ 2 zooids	3	NA	NA	3	NA	NA	
	Norris Point	49.50278	-57.89222	2008	SL	blade	≤ 2 zooids	2	NA	NA	3	NA	NA	
	Port au Choix	50.73222	-57.31222	2008	SL	blade	≤ 2 zooids	4	NA	NA	4	NA	NA	
	Port aux Basques	47.57861	-59.09111	2008	SL	blade	≤ 2 zooids	2	NA	NA	2	NA	NA	
	Red Bay	51.72639	-56.42889	2008	SL	blade	≤ 2 zooids	2	NA	NA	2	NA	NA	

Region	Study site	Latitude (DD)	Longitude (DD)	Year	Kelp substrate	Cover method	Sett definition	N (Cover)			N (Sett)			Source
								Full	Kelp density	IST	Full	Kelp density	IST	
NS	Birchy Head	44.57500	-64.04167	2008	LD, SL	NA	≤ 2 zooids	NA	NA	NA	4	4	NA	Yorke and Metaxas (2012)
	Crooks Island	44.92292	-62.08627	2019	AC, LD, SL	video	NA	10	NA	NA	NA	NA	NA	This Study
	Feltzen South	44.33167	-64.28167	2008	LD, SL	blade	≤ 2 zooids	2	NA	NA	4	4	NA	Yorke and Metaxas (2012)
				2009, 2010	LD, SL	blade	≤ 2 zooids	12	NA	4	12	NA	4	Denley et al. (2014)
	Halibut Island	44.88797	-62.20700	2018	AC, LD, SL	blade	NA	3	3	NA	NA	NA	NA	This Study
				2019	AC, LD, SL	blade	< 1 cm	8	8	8	8	8	8	
	Little Duck Island	44.36667	-64.18333	1992, 1993, 1994, 1995, 1997,	SL	video	NA	36	NA	NA	NA	NA	NA	Scheibling and Gagnon (2009)

								N (Cover)			N (Sett)			
Region	Study site	Latitude (DD)	Longitude (DD)	Year	Kelp substrate	Cover method	Sett definition	Full	Kelp density	IST	Full	Kelp density	IST	Source
NS				1998, 1999										
	Long Island	44.88955	-62.30292	2019	AC, LD, SL	blade	< 1 cm	8	NA	8	8	NA	8	This Study
	Mill Cove	44.58333	-64.05000	1992, 1993, 1994, 1995	SL	video	NA	13	NA	NA	NA	NA	NA	Scheibling and Gagnon (2009)
	Paddy's Head	44.51833	-63.95056	2005, 2006	AC[b], LD, SL	blade	≤ 2 zooids	70	NA	23	57	NA	18	Saunders and Metaxas (2009b)
				2008	LD, SL	blade	≤ 2 zooids	2	NA	2	4	4	4	Yorke and Metaxas (2012)
				2012, 2013	AC, LD, SL	blade	< 1 cm	46	46	15	46	46	15	Denley and Metaxas (2017a)

								N (Cover)			N (Sett)			
Region	Study site	Latitude (DD)	Longitude (DD)	Year	Kelp substrate	Cover method	Sett definition	Full	Kelp density	IST	Full	Kelp density	IST	Source
NS	Pumpkin Island	44.82208	-62.37690	2019	AC, LD, SL	video	NA	10	NA	NA	NA	NA	NA	This Study
	Sandy Cove	44.46206	-63.70483	2005, 2006	AC^b, LD, SL	blade	≤ 2 zooids	19	NA	NA	14	NA	NA	Saunders and Metaxas (2009b)
				2008	LD, SL	NA	≤ 2 zooids	NA	NA	NA	4	4	NA	Yorke and Metaxas (2012)
				2012, 2013	AC, LD, SL	blade	< 1 cm	33	29	6	33	33	6	Denley and Metaxas (2017a)
				2015, 2016, 2017	SL	NA	< 1 cm	NA	NA	NA	20	NA	20	Denley (unpubl. data)
	Shag Rock	44.43129	-63.56631	2018	LD, SL	video	NA	4	NA	NA	NA	NA	NA	This Study
				2019	LD, SL	blade	< 1 cm	4	4	NA	4	4	NA	

								N (Cover)			N (Sett)			
Region	Study site	Latitude (DD)	Longitude (DD)	Year	Kelp substrate	Cover method	Sett definition	Full	Kelp density	IST	Full	Kelp density	IST	Source
NS	Speck Island	44.84490	-62.38682	2019	AC, LD, SL	video	NA	10	10	NA	NA	NA	NA	
	Splitnose Point	44.47735	-63.54673	2008, 2009	LD, SL	blade	NA	10	NA	NA	NA	NA	NA	Krumhansl and Scheibling (2011)
	The Lodge	44.55083	-64.01917	2005, 2006	AC^{b}, SL	blade	≤ 2 zooids	58	NA	21	45	NA	15	Saunders and Metaxas (2009b)
				2008, 2009	LD, SL	blade	NA	10	NA	4	NA	NA	NA	Krumhansl and Scheibling (2011)
				2009, 2010	LD, SL	blade	≤ 2 zooids	33	NA	22	33	1	22	Denley et al. (2014)
				2012, 2013	AC, LD, SL	blade	< 1 cm	43	43	43	43	43	43	Denley and

								N (Cover)			N (Sett)			
Region	Study site	Latitude (DD)	Longitude (DD)	Year	Kelp substrate	Cover method	Sett definition	Full	Kelp density	IST	Full	Kelp density	IST	Source
NS														Metaxas (2017a)
				2015, 2016, 2017	SL	NA	< 1 cm	NA	NA	NA	20	NA	20	Denley (unpubl. data)
	The Moll	44.92397	-62.23767	2018	AC, LD, SL	blade	NA	3	3	NA	NA	NA	NA	This Study
				2019	AC, LD, SL	blade	< 1 cm	9	9	9	9	9	9	
	Tuffin Island	44.90660	-62.15593	2018	AC, LD, SL	blade	NA	3	3	NA	NA	NA	NA	
				2019	AC, LD, SL	blade	< 1 cm	9	9	NA	9	9	NA	
	White Island	44.88707	-62.11967	2019	AC, LD, SL	blade	< 1 cm	9	9	NA	9	9	NA	
				Total				549	179	165	412	178	192	

a: Percent cover data for Ammen Rock in 2012 were collected by analyzing photos, not video

b: Only percent cover data on this species

Table A.2 Sets of top models (models with ΔAIC<7) explaining observed patterns in a) percent cover and b) settler density of *M. membranacea* in the northwest Atlantic, where SST has been separated into seasonal (day of year) and anomaly (site- or year-specific anomalies from overall mean, obtained as residuals from generalized additive models between day of the year and SST) components. REI and SST metrics are abbreviated as per Table 2.1. Marg. and Cond R^2 are the marginal and conditional R^2 values for the GLMM. Random Effect SD is the standard deviation of each random intercept.

(a)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Depth + Kelp Substrate + REI 6-Log + SST 6-M (Anomaly) + SST 6-M (Seasonal) + Kelp Substrate:SST 6-M (Seasonal)	13	643.479	-1260.959	0.000	0.577	0.569	0.756	Site = 0.577 Year = 0.152
Depth + Kelp Substrate + SST 6-M (Anomaly) + SST 6-M (Seasonal) + Kelp Substrate:SST 6-M (Seasonal)	12	642.085	-1260.170	0.788	0.389	0.543	0.750	Site = 0.596 Year = 0.162
Kelp Substrate + REI 6-Log + SST 6-M (Anomaly) + SST 6-M (Seasonal) + Kelp Substrate:SST 6-M (Seasonal)	12	639.366	-1254.732	6.227	0.026	0.560	0.751	Site = 0.569 Year = 0.192

(b)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Depth + REI Y-Log + Kelp Substrate + SST 6-I (Anomaly) + SST 6-I (Seasonal)	10	-1852.667	3725.335	0.000	0.457	0.515	0.769	Year = 0.877 Site = 0.679
Kelp Substrate + REI Y-Log + SST 6-I (Anomaly) + SST 6-I (Seasonal)	9	-1855.483	3728.966	3.631	0.074	0.513	0.769	Year = 0.868 Site = 0.701
Depth + Kelp Substrate + SST 6-I (Anomaly) + SST 6-I (Seasonal)	9	-1855.790	3729.580	4.245	0.055	0.465	0.765	Year = 0.898 Site = 0.789

A.1 Data collection: new data

I collected data from 8 previously unsurveyed sites in the Eastern Shore Islands (ESI) of Nova Scotia: Crooks Island (CR), Halibut Island (HB), Long Island (LI), The Moll (MO), Pumpkin Island (PU), Speck Island (SI), Tuffin Island (TU) and White Island (WI) (for locations, see Table A.1). Additionally, I collected data from Shag Rock (SR), a long-term study site on the southwestern shore approximately 5 km offshore of Sambro, Nova Scotia, which had anomalously high kelp cover compared to other sites in the area. I surveyed 4 sites in October 2018 (HB, MO, TU, SR), all 8 sites in the ESI in July, August and October 2019, and SR in July and October 2019.

A.1.1 Percent cover and settler density of *M. membranacea*

At HB, MO, and TU in 2018 and 2019, and LI, SR, and WI in 2019, I haphazardly collected five kelp blades of each of the three numerically dominant kelp species in Nova Scotia (*Agarum clathratum, Laminaria digitata,* and *Saccharina latissima*) between 6 and 9 m using SCUBA. I stored collected blades in plastic coolers without water and processed them within 72 hours of sampling. If blades were processed more than 72 hours after sampling, I stored them in tanks with flowing, ambient seawater to preserve them until they were processed. I visually enumerated newly settled colonies (colonies measuring <1 cm in diameter; Denley & Metaxas 2017b) on one side of each kelp blade, with the aid of an Optivisor^{TM} (up to 8x magnification) if necessary. For *L. digitata* with a basal meristem < 20 cm wide and all *A. clathratum* and *S. latissima,* I analysed one whole side of the blade. For *L. digitata* with a basal meristem > 20 cm wide, I subdivided blades widthwise into 3 equal segments and analysed 1 digitated blade in each subdivided segment. I estimated the surface area of each kelp blade from photographs using Image J and divided the number of settlers by the surface area of each kelp blade to obtain the settler density per unit area of kelp. For subdivided *L. digitata*, I divided the number of settlers on each digitated blade by the blade area to obtain settler density per unit area and averaged these densities across the 3 blades to obtain one value per kelp plant. To measure percent cover of *M. membranacea*, I divided kelp blades lengthwise into 15-cm segments on one side of the blade, starting at the proximal end. I measured the percentage of the kelp blade covered by colonies of *M. membranacea* within 25-cm^2 subsections using a grid placed in the centre of each 15-cm segment. I then averaged percent cover values across all subsections to obtain the estimated percent cover of *M. membranacea* for the entire kelp blade.

I measured percent cover of *M. membranacea* at SR in 2018, and at CR, PU, and SI in 2019, from 120-m long video transects done at 6 and 9 m depths with a handheld GoPro® Hero camera. I attached 1.5-m plumb line to the camera to keep the camera at a constant height above the seafloor and a washer attached to the bottom of the plumb line provided a scale reference for subsequent image analysis. For each video transect, I extracted and analysed video frames at ~30-second intervals in Image J using the point method (Kohler & Gill 2006). For each image, I obtained the percent cover of *M. membranacea* on each kelp species by dividing the number of points overlaying *M. membranacea* colonies on a given kelp species by the total number of points overlaying the kelp species (covered with *M. membranacea* or not). I then calculated the mean percent cover of *M. membranacea* on each kelp species across images at each depth for each site.

A.1.2 *In Situ* Temperature

I measured *in situ* temperature (IST) at 6 and 9 m depth continuously at 10-minute intervals using HOBO Pendant® temperature loggers from October 2018 to October 2019 (HB, LI, MO), May 2019 to October 2019 (CR) and June 2019 to October 2019 (PU, SR). I averaged IST across 6 and 9 m depths at each site to correspond with data on percent cover and settler density of *M. membranacea* collected from between 6 and 9 m, but also retained temperature series for 6 and 9 m to correspond with video-based measurements of percent cover at 6 and 9 m. For PU at 9 m and CR, HB, LI, and MO at both depths, IST records ended approximately one week prior to sampling of *M. membranacea* in October 2019 due to logger memory limitations. To extend the temperature series at these sites until their sampling dates, I generated a linear model based on the data from PU at 6 m to obtain an estimate of the mean rate of temperature change each day. I applied this rate of change to the other sites, which were within 25 km of PU and thus share a thermal regime (Figure A.1), for the week leading up to the sampling date.

A.1.3 Kelp Density

I measured kelp density at HB, LI and TU in October 2018 and at CR, HB, MO, LI, TU, and WI in July and October 2019. I haphazardly sampled 0.5-m^2 quadrats (n = 5-12) between 6 and 9 m in 2018 and at 6 and 9 m in 2019. I counted the number of adult *A. clathratum, L. digitata,* and *S. latissima* (>20 cm in length) within each quadrat and divided by the quadrat area to obtain kelp density per m^2 of seafloor. I then calculated the average kelp density across all quadrats at each depth.

A.2 Comparing methods for measuring percent cover of *M. membranacea*

I collected new data on percent cover of *M. membranacea* concurrently from both counts on individual kelp blades and video transects at six sites (HB, LI, MO, SR, TU, and WI), affording us the opportunity to compare percent cover data among methods using a 2-way ANOVA with fixed factors of collection methodology (2 levels: individual blade examination, video) and kelp substrate species (3 levels: *A. clathratum, L. digitata, S. latissima*). There was no significant difference in percent cover between methods for any kelp species ($F_{(2,22)} = 1.022$, $p>0.05$) or between the different methods across kelp species ($F_{(1,22)} = 0.097$, $p>0.05$).

A.3 Standardizing settler density across studies

It was necessary to standardize settler density in my dataset across studies that used different size definitions of a settler. Since mortality for newly settled colonies of *M. membranacea* is negligible (Yoshioka 1982, Denley & Metaxas 2016), I assumed I could predict the proportion of ≤2-zooid colonies (typically 0.5 - 0.9 mm in diameter; Saunders & Metaxas 2007) in the <1-cm colony size class. For observations from studies that defined settlers as colonies <1-cm (Denley & Metaxas 2017a; D. Denley unpublished data; this study), I calculated the abundance of ≤2-zooid colonies based on relationships I derived from data in Caines and Gagnon (2012) (n=26). The study enumerated multiple small size classes (≤2 zooids, and >2 zooids but ≤0.5 cm in diameter) across a wide geographic range (8 sites over a 450-km latitudinal range) over 4 months and provided monthly average IST.

First, I combined abundance across the two size classes measured by Caines and Gagnon (2012) for each observation to obtain the density of colonies ≤0.5cm (Eq. A.1).

$$\text{Colonies } \leq 0.5cm = \text{Colonies } \leq 2\ zooid\ rows + 0.5cm \leq \text{Colonies } > 2\ zooid\ rows \quad \text{(A.1)}$$

I then estimated the growth rate (GR, in cm day^{-1}) for ≤0.5-cm colonies based on the monthly average temperature (T), using the field-based equation for size- and temperature-specific growth from Saunders and Metaxas (2009a; Eq. A.2).

$$\log(\mathrm{GR}) = -1.665 + 0.719 \cdot \log(0.5\ cm) + 0.072\ (\mathrm{T}) \quad \text{(A.2)}$$

This estimate assumes a relatively constant temperature (i.e. colony growth rate) and settlement rate over the period in which a 2-zooid colony matures into a 1-cm colony. By dividing 0.5 cm (the amount that a 0.5-cm colony would need to grow to reach 1 cm in diameter) by GR, I estimated the number of days that colonies would spend in the 0.5- to 1-cm size class ("residence time", RT; Eq. A.3).

$$\mathrm{RT} = \frac{0.5\ cm}{\mathrm{GR}} \quad \text{(A.3)}$$

I calculated the approximate age of the ≤2-zooid colonies using a linear model derived from temperature-dependent age estimates presented in Saunders and Metaxas (2007) (Eq. A.4) and obtain an estimated settlement rate (STR, colonies day^{-1}) for each observation by dividing the number of ≤2-zooid colonies by their estimated age (Eq. A.5).

$$\log(\mathrm{Age}) = 2.66 - 1.92 \cdot \log(\mathrm{T}) \quad \text{(A.4)}$$

$$\text{STR} = \frac{\text{Colonies} \leq 2 \text{ zooid rows}}{\text{Age}} \qquad (\text{A.5})$$

I multiplied the residence time by the settlement rate to obtain an estimate of the density of colonies between 0.5 and 1 cm in diameter, and added the density of ≤0.5-cm colonies to estimate the density of colonies <1 cm (Eq. A.6).

$$\text{Colonies} < 1 \text{ cm} = \text{Colonies} \leq 0.5 \text{ cm} \; + \; \text{RT} \cdot \text{STR} \qquad (\text{A.6})$$

Lastly, I fit a linear regression model predicting the abundance of colonies ≤2 zooids from the estimated abundance of colonies <1 cm (both log-transformed to satisfy the assumptions of normality and homogeneity of variance; intercept forced through the origin; Figure A.2). This model only holds for the range of temperatures (3.3 – 17.6°C) and settler densities (0-2663 settlers m^{-2} kelp) measured by Caines and Gagnon (2012); however, these ranges are encompass those measured by studies in Nova Scotia from May-November (e.g. IST: 5.0 – 17.3°C, settler density: 0 -1927 settlers m 2 kelp; Saunders & Metaxas 2009b), supporting my application of this model to convert observations of colonies <1 cm to colonies ≤2 zooids in my compiled dataset.

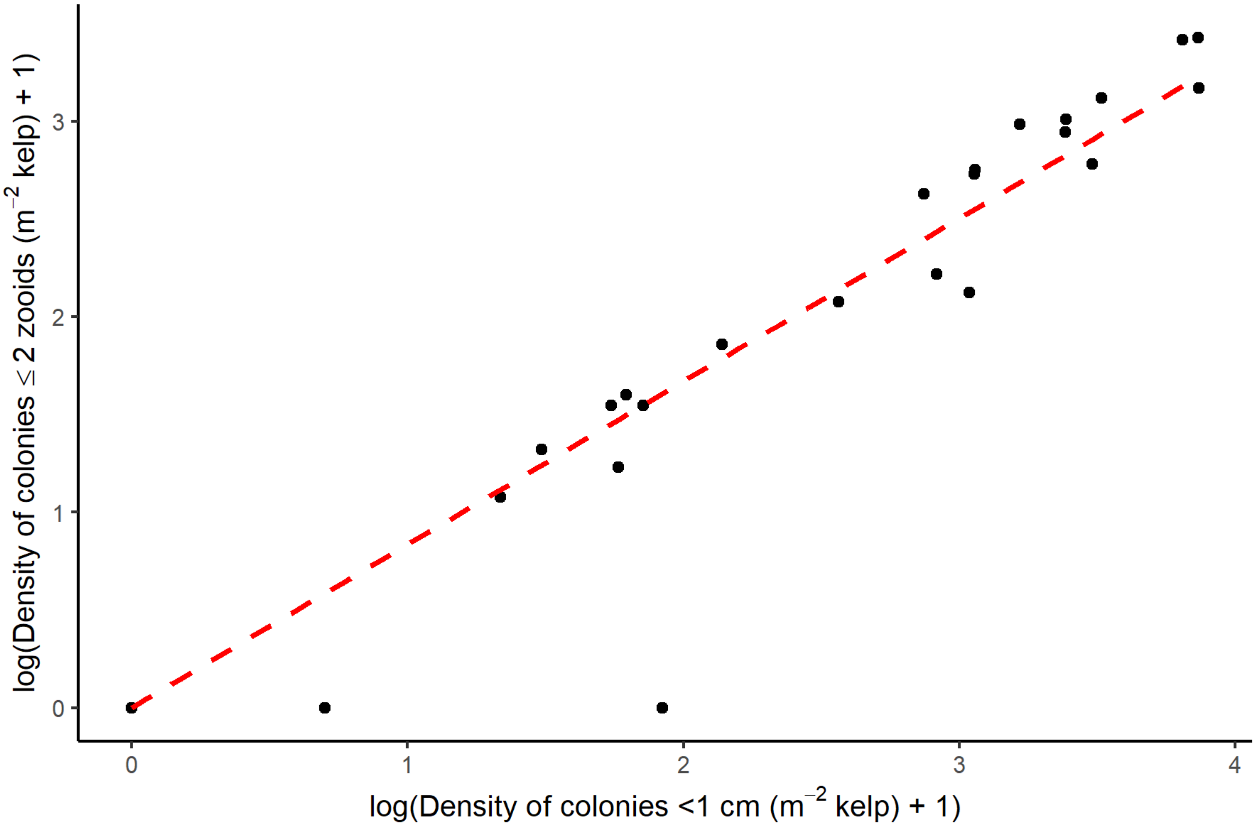

Figure A.2 Density of colonies with ≤2 zooids as a function of the estimated number of colonies <1 cm in diameter (see Appendix A.3 for details), with the regression line (dashed red line) forced through the origin. Data were log(x+1)-transformed to satisfy model assumptions. Data from Caines and Gagnon (2012). [log(Density of ≤2-zooid colonies +1) = log(0.8348(Density of <1-cm colonies) + 1), adj. $r^2 = 0.97$, $p< 2.2\cdot10^{-16}$]

A.4 Approximation of annual growth period of *M. membranacea*

I considered *M. membranacea* to be an annual species because less than 1% of colonies overwinter (D. Denley unpublished data; M. Saunders unpublished data), and the bryozoan exhibits slow growth and minimal reproductive output over winter (Saunders & Metaxas 2009a, Denley & Metaxas 2017a). I chose May as the beginning of the growing season because the onset of reproduction (Denley & Metaxas 2017a) and subsequent settlement of *M. membranacea* (Saunders & Metaxas 2007) have been shown to occur as early as May, and thus the growth of new colonies can also begin. I chose November as the end of the growing season because 1) the reproductive season ends (Denley & Metaxas 2017a), causing abundances of competent larvae to decrease substantially (Saunders & Metaxas 2010); 2) the latest recorded seasonal peaks in settler density (Saunders & Metaxas 2009b) and percent cover (Scheibling & Gagnon 2009, Saunders & Metaxas 2009b) in the northwest Atlantic both occurred in November; and 3) seasonal recession of *M. membranacea* colonies due to partial mortality also begins in November (Denley & Metaxas 2016).

A.5 Comparing methods for measuring wave exposure

To determine the accuracy of relative exposure index (REI) as a wave exposure metric, I measured wave exposure *in situ* at 5 sites (HB, CR, PU, MO, and LI) using HOBO Pendant G® Acceleration Loggers housed in Underwater Relative Swell Kinetics Instrument (URSKI) floats, after Figurski et al. (2011). I deployed these instruments, which measure bottom orbital velocity (u_b) generated by waves, for approximately 1 week in July 2019 at HB, CR, PU, and MO and in late September/early October 2019 at HB, CR, PU, MO, and LI. I chose these two deployment periods to represent relatively calm (July) and stormy (September/October) times of year to test the relationship between *in situ* and REI-based exposure under a range of conditions. I calculated mean u_b in the horizontal dimensions over each sampling period at each site after Figurski et al. (2011).

I explored the relationship between mean u_b over each deployment period and REI averaged over a one-month window centered at the URSKI deployment period at each site using simple linear regression. I averaged REI values over the one-month window because preliminary analyses indicated that it is not possible to generate an accurate estimate of REI for periods of 1 week using hourly wind data, due to an insufficient number of observations.

There was a significant linear relationship between REI and u_b ($p<0.05$, $R^2 = 0.62$); however, the relationship was significant only when data from PU were not included (Figure A.4). Mean u_b values for PU were substantially lower than expected given the REI values calculated for the site (Figure A.4), likely due to the presence of underwater ridges on the exposed side of the site which may attenuate wave energy but were not accounted for in calculations of fetch for REI. This example highlights a limitation of REI as a representation of *in situ* wave exposure and emphasises that *in situ* measures of wave exposure are preferable when it is possible to collect such data.

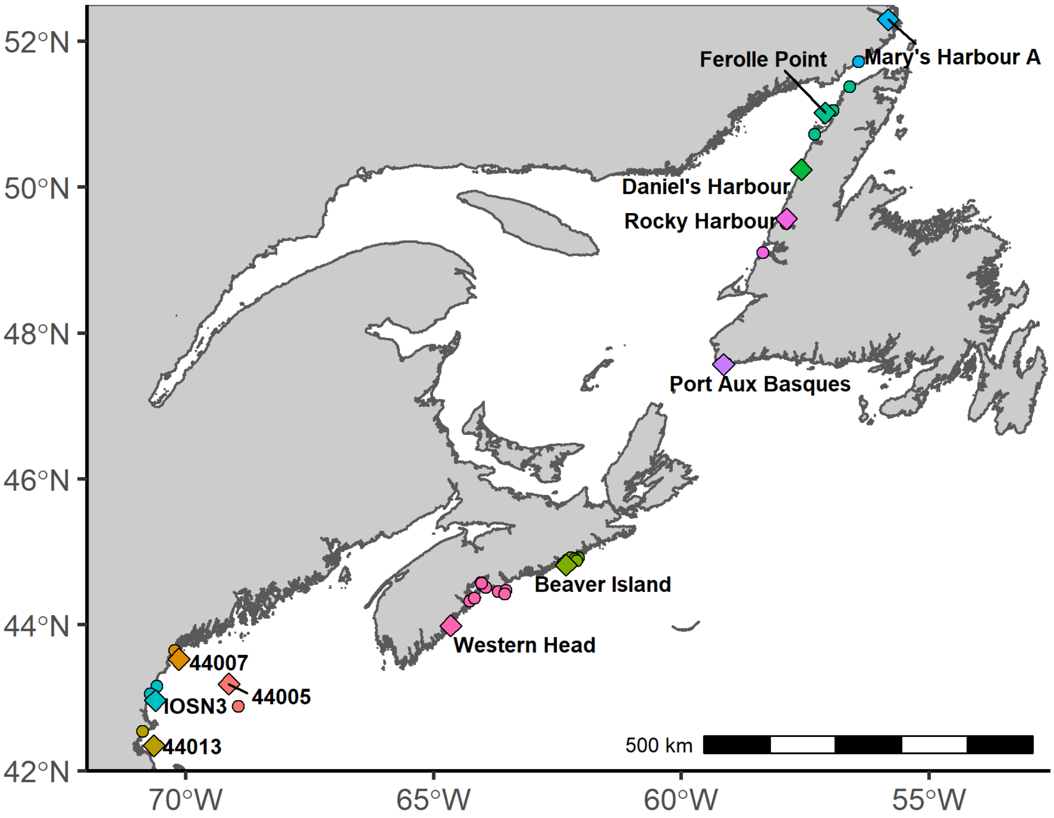

Figure A.3 Map of weather stations (labelled, diamond-shaped points) and study sites (round points). The color of each point corresponds to the weather station from which wind data were used to calculate REI. Weather station names/codes correspond to the station information found on Environment and Natural Resources Canada's Historical Climate Database (http://climate.weather.gc.ca) for Canadian stations and NOAA's National Data Buoy Center (https://www.ndbc.noaa.gov) for stations in the Gulf of Maine.

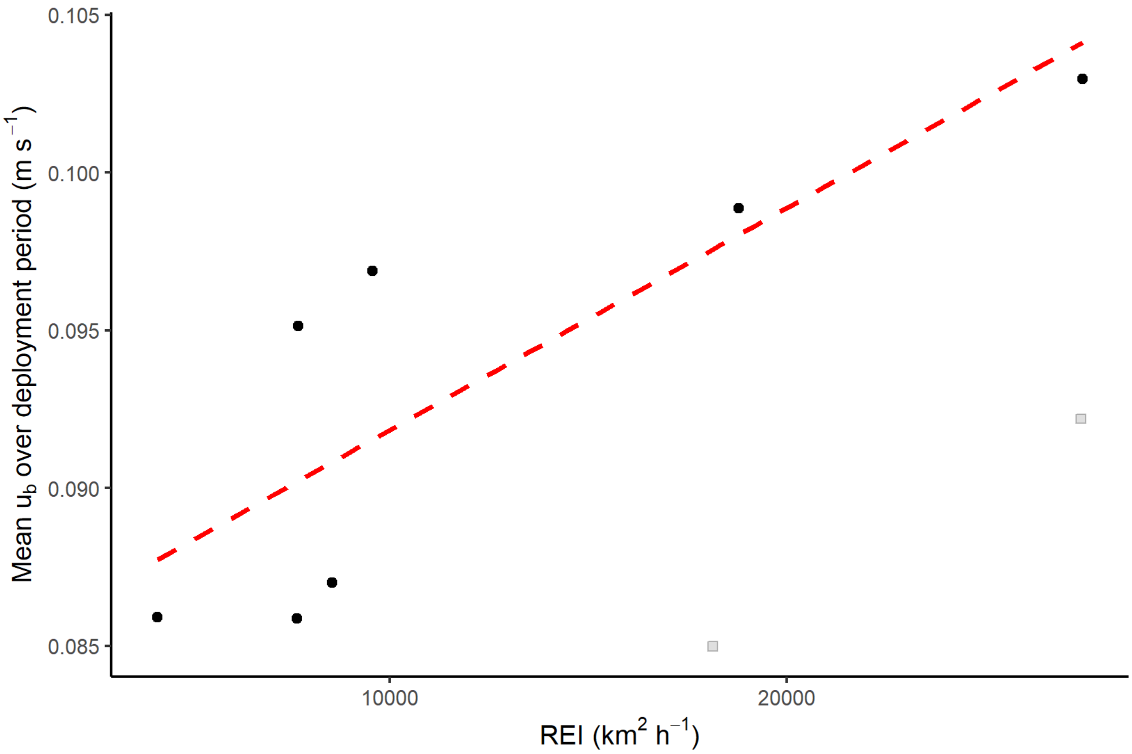

Figure A.4 Relationship of REI calculated from wind data averaged over a one-month window centered at the URSKI deployment period with mean u_b over the URSKI deployment period. Square, grey points, from PU, were considered outliers and not included when fitting the linear regression line (dashed red line).
[Mean $u_b = -0.085 + 7.026 \cdot 10^{-7}$(REI), $r^2 = 0.62$, p=0.02]

A.6 Relative and absolute importance of kelp density as a predictor of percent cover and settler density of *M. membranacea*

Kelp density was only measured in less than half of the observations of *M. membranacea* percent cover and settler density in my full dataset. Therefore, I assessed the relative importance of kelp density separately from the other predictors using the subset of the full dataset for which kelp density data were available (kelp density datasets; n = 179 for percent cover, n= 178 for settler density, Table A.1). First, I determined the optimal REI and SST metrics for the kelp density datasets as described in section 2.3.4.1. I then constructed global models consisting of depth, kelp density (Kelp_R of *L. digitata* and *S. latissima* for cover, Kelp_T for settler density), kelp substrate, the most important REI metric, and the most important SST metric as fixed effects, with an interaction between SST and kelp substrate, and site and year as random intercepts. Lastly, I created complete model sets from the global models and assessed the relative and absolute variable importance of kelp density though model averaging.

Relative kelp density was the least important predictor in explaining patterns in percent cover (Figure A.8a) and relative density of neither *L. digitata* nor *S. latissima* appeared in any model in the top model set for percent cover (Table A.3a). Similarly, total kelp density was of low relative importance in explaining patterns in settler density (Figure A.8b) and did not appear in either model in the top model set (Table A.3b).

Table A.3 Sets of top models (models with ΔAIC<7) explaining observed patterns in a) percent cover and b) settler density of *M. membranacea* in the northwest Atlantic, fit to the kelp density datasets. REI and SST metrics are abbreviated as per Table 2.1. Marg. and Cond R^2 are the marginal and conditional R^2 values for the GLMM. Random Effect SD is the standard deviation of each random intercept.

(a)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Depth + Kelp Substrate + REI 3-Log + SST 6-I + Kelp Substrate:SST 6-I	12	225.961	-427.923	0.000	0.323	0.385	0.904	Site = 1.363 Year = 0.31
Kelp Substrate + REI 3-Log + SST 6-I + Kelp Substrate:SST 6-I	11	224.521	-427.043	0.880	0.208	0.376	0.900	Site = 1.363 Year = 0.321
Depth + Kelp Substrate + SST 6-I + Kelp Substrate:SST 6-I	11	222.390	-422.780	5.142	0.025	0.414	0.790	Site = 0.823 Year = 0.264
Kelp Substrate + SST 6-I + Kelp Substrate:SST 6-I	10	220.716	-421.433	6.490	0.013	0.397	0.775	Site = 0.809 Year = 0.267

(b)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Kelp Substrate + SST 6-I + Kelp Substrate:SST 6-I	9	-722.025	1462.050	0.000	0.324	0.397	0.777	Year = 1.015 Site = 0.702
Kelp Substrate + SST 6-I	7	-726.854	1467.708	5.658	0.019	0.376	0.761	Year = 1.027 Site = 0.666

A.7 Additional R packages

Numerous R packages were used in this study in addition to those listed in the main text. Tukey tests were conducted using emmeans (Lenth 2020) and VIF and Nakagawa's R^2 values were calculated using performance (Lüdecke et al. 2020). Figures were created using ggplot2 (Wickham 2016) and cowplot (Wilke 2019), with maps being constructed using sf (Pebesma 2018), ggrepel (Slowikowski 2019), and ggspatial (Dunnington 2018). Tables were created using kableExtra (Zhu 2019) and knitr (Xie 2020). Fetch values for use in REI calculations were calculated using fetchR (Seers 2018) and sp (Pebesma & Bivand 2005). The raster package (Hijmans 2020) and ncdf4 (Pierce 2019) were used to extract SST data for study sites. The mgcv package (Wood 2004) was used to fit GAMs for separating seasonal SST and SST anomaly. Finally, data exploration and manipulation were conducted using GGally (Schloerke et al. 2018), lubridate (Grolemund & Wickham 2011), stringi (Gagolewski 2020), and tidyverse (Wickham et al. 2019).

Table A.4 Results of models comparing REI and temperature (SST or IST) metrics as predictors of percent cover and settler density in the IST datasets, for a) SST-based models and b) IST-based models of percent cover and c) SST-based models and d) IST-based models of settler density. Models of the form shown in Table 2.2 (excluding kelp density as a predictor) were fit using each REI and temperature metric. REI and temperature metrics are abbreviated as per Table 2.1. For comparison of REI metrics, six-month mean was the temperature metric in the model. For comparison of temperature metrics, the optimal REI metric was employed as the REI metric in the model. AIC, dAIC (change in AIC relative to top-ranked model) and Akaike weight were calculated for each model. REI and SST metrics are ranked in order of descending model performance.

(a)

Variable	Metric	AIC	dAIC	weight
REI	6-Log	-469.916	0.000	0.196
	3-Lin	-469.615	0.300	0.169
	6-Lin	-468.757	1.159	0.110
	Y-Lin	-468.749	1.166	0.110
	3-Log	-468.730	1.186	0.109
	Y-Log	-468.706	1.209	0.107
	3-Q	-468.406	1.509	0.092
	6-Q	-467.706	2.209	0.065
	Y-Q	-466.830	3.085	0.042
SST	3-I	-470.491	0.000	0.284
	3-M	-470.470	0.021	0.281
	6-I	-469.996	0.496	0.222
	6-M	-469.916	0.576	0.213

(b)

Variable	Metric	AIC	dAIC	weight
REI	3-Lin	-473.841	0.000	0.157
	6-Log	-473.815	0.027	0.155
	3-Q	-473.544	0.298	0.135
	Y-Lin	-473.245	0.597	0.116
	3-Log	-473.209	0.632	0.114
	Y-Log	-472.980	0.861	0.102
	6-Lin	-472.951	0.890	0.100
	6-Q	-472.345	1.497	0.074
	Y-Q	-471.427	2.414	0.047
IST	3-M	-480.485	0.000	0.495
	3-I	-480.378	0.107	0.469
	6-M	-473.841	6.644	0.018
	6-I	-473.834	6.652	0.018

(c)

Variable	Metric	AIC	dAIC	weight
REI	6-Q	1893.858	0.000	0.142
	1-Log	1894.106	0.248	0.126
	6-Lin	1894.568	0.710	0.100
	Y-Lin	1894.738	0.880	0.092
	3-Lin	1894.797	0.939	0.089
	1-Lin	1894.856	0.999	0.086
	3-Q	1895.014	1.156	0.080
	3-Log	1895.165	1.307	0.074
	6-Log	1895.378	1.520	0.067
	Y-Log	1895.481	1.623	0.063
	Y-Q	1896.284	2.426	0.042
	1-Q	1896.437	2.579	0.039
SST	3-I	1879.020	0.000	0.382
	3-M	1879.135	0.115	0.361
	1-M	1881.194	2.175	0.129
	1-I	1881.213	2.193	0.128
	6-I	1893.553	14.533	<0.001
	6-M	1894.106	15.087	<0.001

(d)

Variable	Metric	AIC	dAIC	weight
REI	6-Q	1899.394	0.000	0.161
	1-Log	1899.954	0.560	0.122
	6-Lin	1900.209	0.814	0.107
	Y-Lin	1900.566	1.171	0.090
	1-Lin	1900.603	1.208	0.088
	3-Lin	1900.697	1.303	0.084
	3-Q	1900.721	1.327	0.083
	3-Log	1901.061	1.666	0.070
	6-Log	1901.442	2.048	0.058
	Y-Log	1901.450	2.055	0.058
	Y-Q	1902.182	2.787	0.040
	1-Q	1902.280	2.885	0.038
IST	1-I	1862.247	0.000	0.640
	1-M	1863.397	1.151	0.360
	3-I	1890.235	27.989	<0.001
	3-M	1890.471	28.224	<0.001
	6-I	1899.348	37.101	<0.001
	6-M	1899.954	37.708	<0.001

Table A.5 Sets of top models (models with ΔAIC<7) based on the IST datasets explaining observed patterns in a) percent cover (SST-based models), b) percent cover (IST-based models), c) settler density (SST-based models), d) settler density (IST-based models) of *M. membranacea* in the northwest Atlantic. REI and temperature metrics are abbreviated as per Table 2.1. Marg. and Cond R^2 are the marginal and conditional R^2 values for the GLMM. Random Effect SD is the standard deviation of each random intercept.

(a)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Depth + Kelp Substrate + SST 3-I + Kelp Substrate:SST 3-I	11	246.329	-470.658	0.000	0.260	0.586	0.771	Site = 0.456 Year = 0.377
Depth + Kelp Substrate + SST 3-I	10	245.279	-470.558	0.101	0.247	0.613	0.801	Site = 0.491 Year = 0.407
Depth + Kelp Substrate + SST 3-I	9	244.269	-470.539	0.120	0.245	0.589	0.771	Site = 0.447 Year = 0.387

(b)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
IST 3-M + Kelp Substrate	8	249.782	-483.565	0.000	0.266	0.616	0.769	Site = 0.453 Year = 0.277

(c)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Depth + Kelp Substrate + SST 3-I	8	-929.949	1875.898	0.000	0.332	0.327	0.718	Year = 0.848 Site = 0.822
Kelp Substrate + SST 3-I	7	-932.036	1878.071	2.173	0.112	0.326	0.718	Year = 0.865 Site = 0.819
Depth + SST 3-I	6	-934.484	1880.968	5.070	0.026	0.265	0.713	Year = 0.922 Site = 0.874

(d)

Model	df	logLik	AIC	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Random Effect SD
Depth + IST 1-I + Kelp Substrate	8	-920.821	1857.641	0.000	0.524	0.275	0.784	Year = 1.173 Site = 0.905
Depth + IST 1-I	6	-925.361	1862.722	5.081	0.041	0.231	0.780	Year = 1.224 Site = 0.94

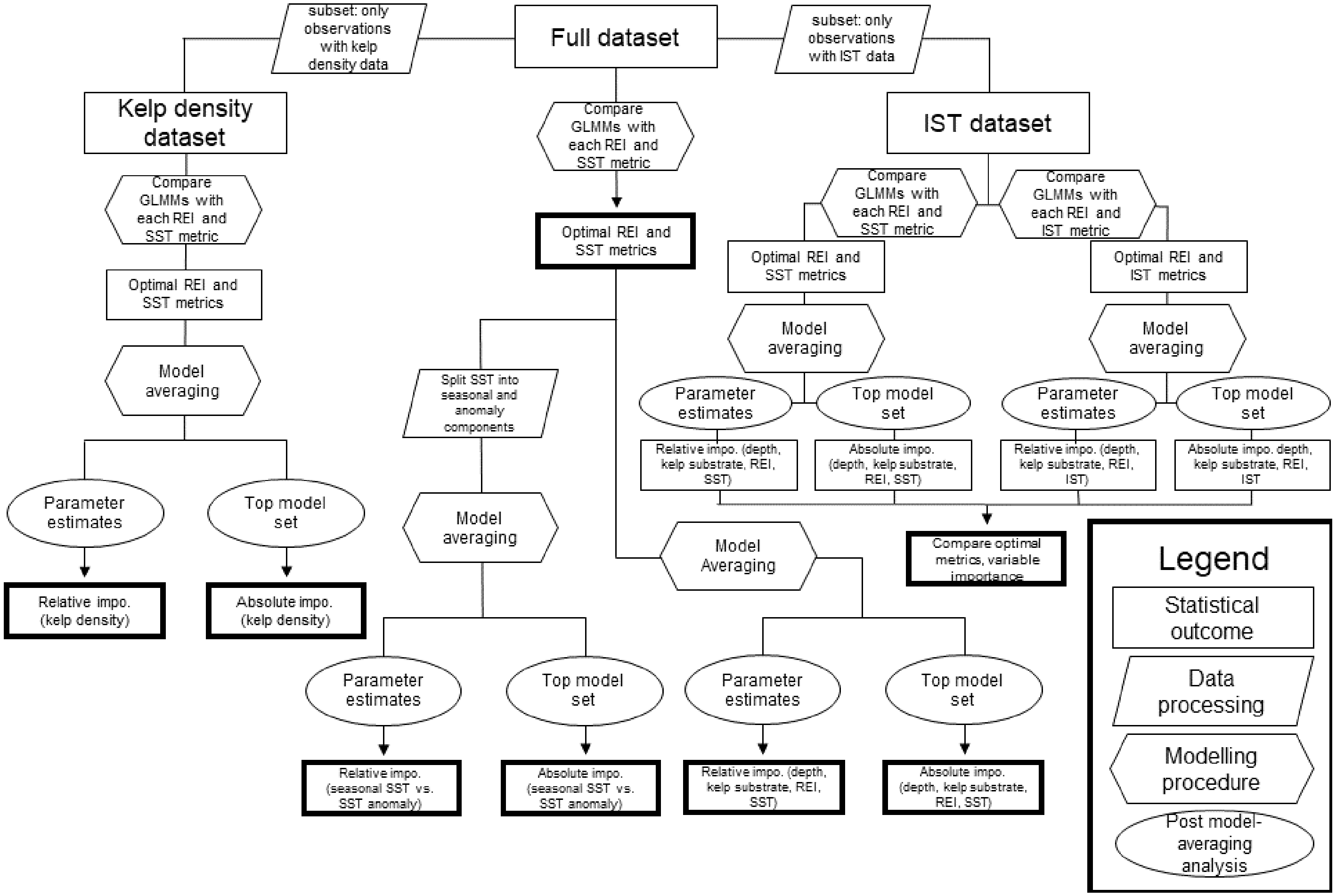

Figure A.5 Schematic of data processing and modelling procedures used to assess the importance of predictors in contributing to observed patterns in the percent cover and settler density of *M. membranacea* in the northwest Atlantic over broad spatial and temporal scales. Boxes with a dark outline represent the fulfillment of a study objective.

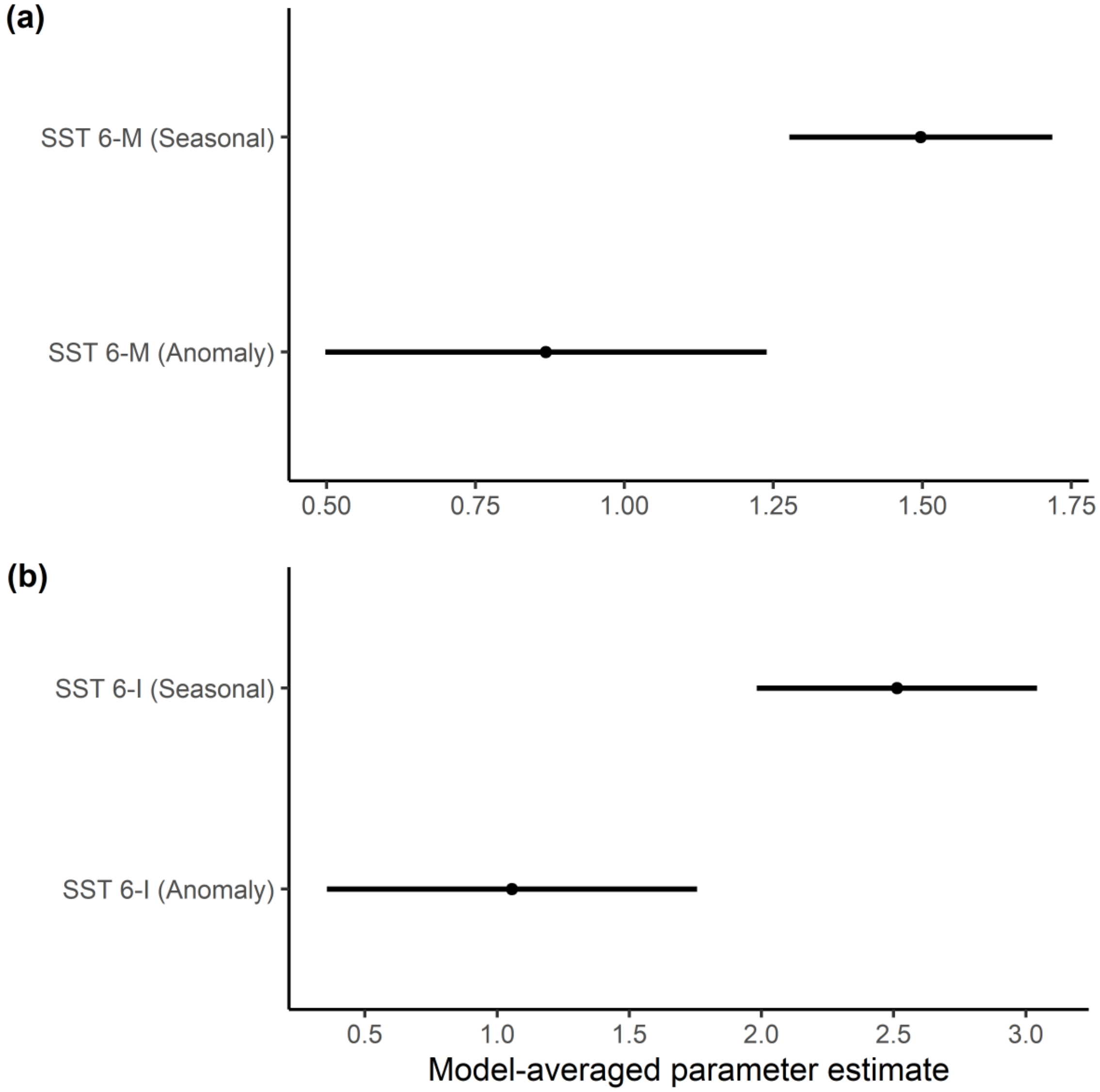

Figure A.6 Full-model averaged standardized parameter estimates for the seasonal (day of year) and anomaly (site- or year-specific anomalies from overall mean, obtained as residuals from generalized additive models between day of the year and SST) components of temperature for a) percent cover and b) settler density. SST metric names are abbreviated as per Table 2.1. Error bars represent a 95% confidence interval based on unconditional standard error.

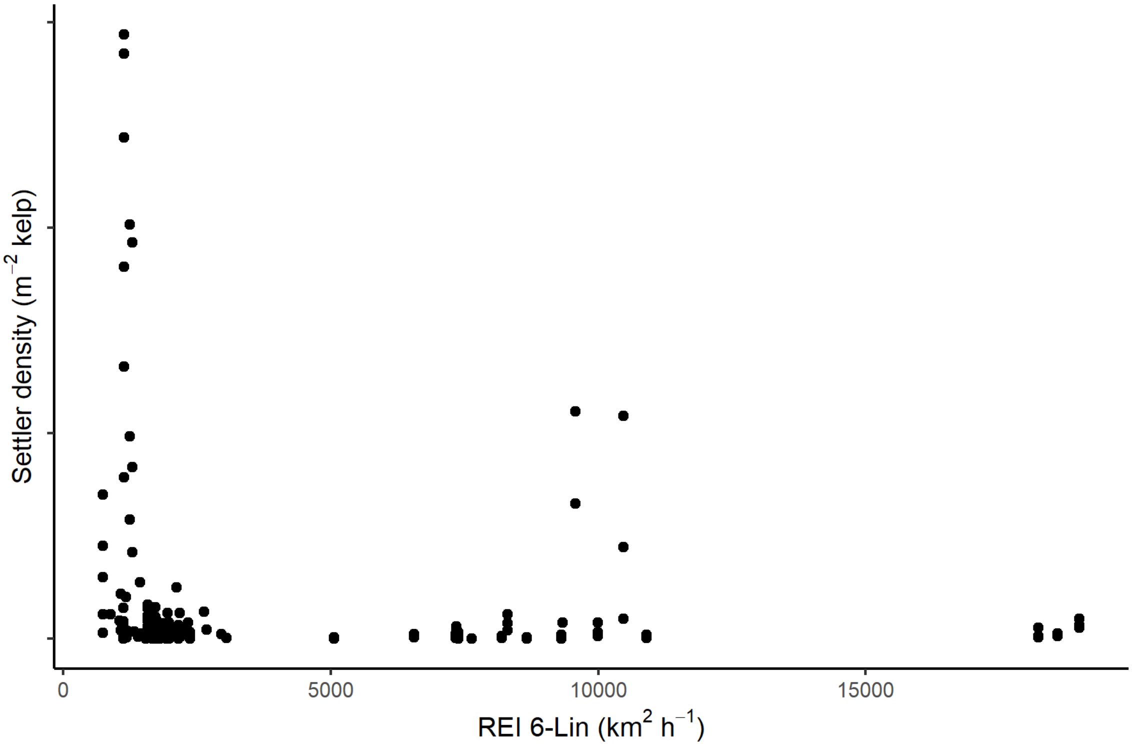

Figure A.7 Settler density (no. individuals per m^2 kelp; kelp species-specific means for each depth, site, and sampling date) as a function of six-month mean REI (relative wave exposure index calculated using wind data over the six months prior to a given observation of settler abundance) from the IST dataset.

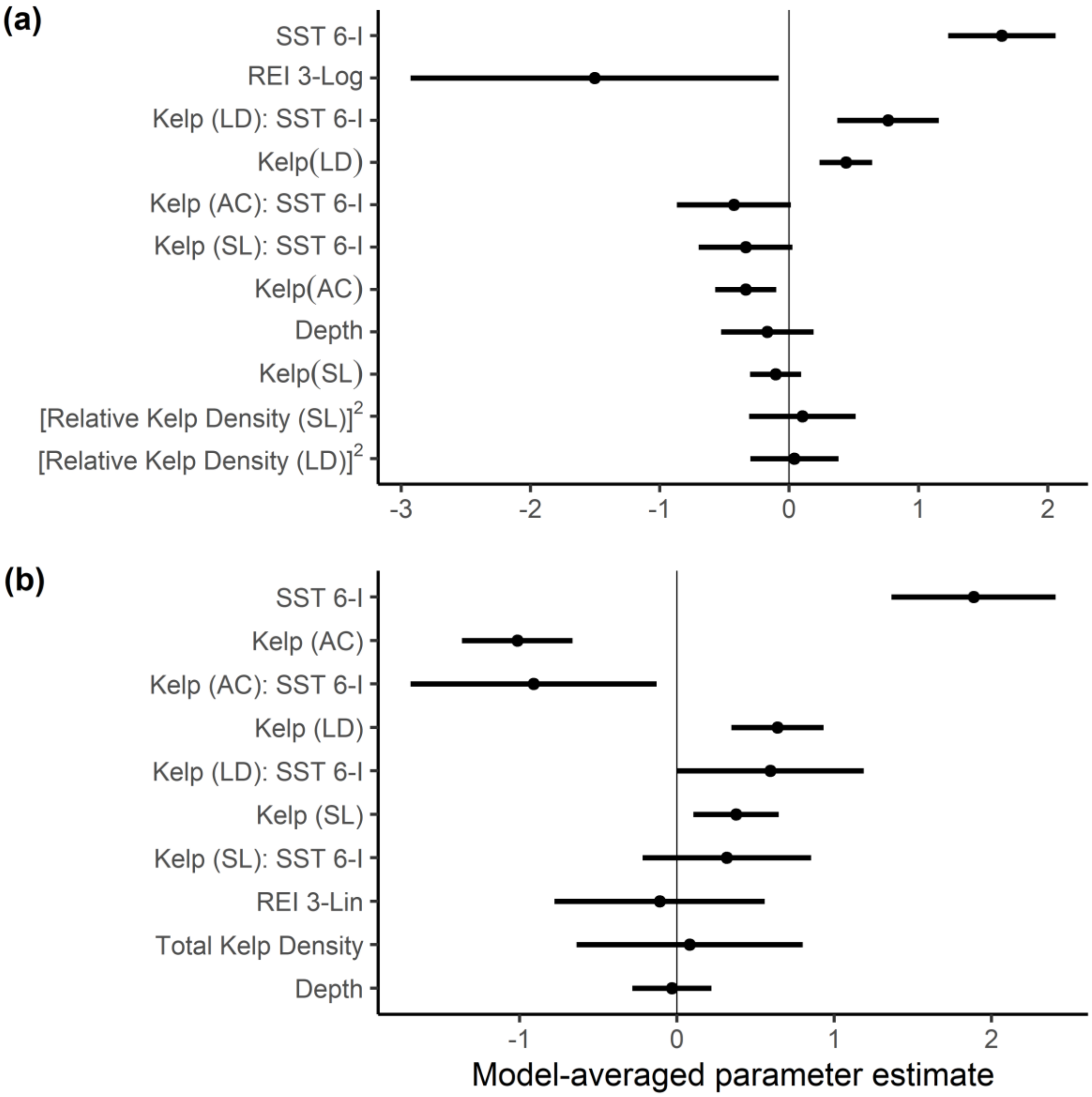

Figure A.8 Full-model averaged standardized parameter estimates for depth, kelp density, kelp substrate, REI and SST as predictors of a) percent cover and b) settler density, based on models fit to the kelp density datasets, arranged in descending order of magnitude. REI and SST metrics are abbreviated as per Table 2.1. Kelp density metrics are relative density (species-specific density divided by sum of density of 3 dominant species) of *Laminaria digitata* and *Saccharina latissima* residualized against REI for percent cover (squared; coefficients for linear components not shown) and total kelp density (sum of density of 3 dominant species) for settler density. Error bars represent a 95% confidence interval based on unconditional standard error. AC = *A. clathratum*, LD = *L. digitata,* SL = *S. latissima.*

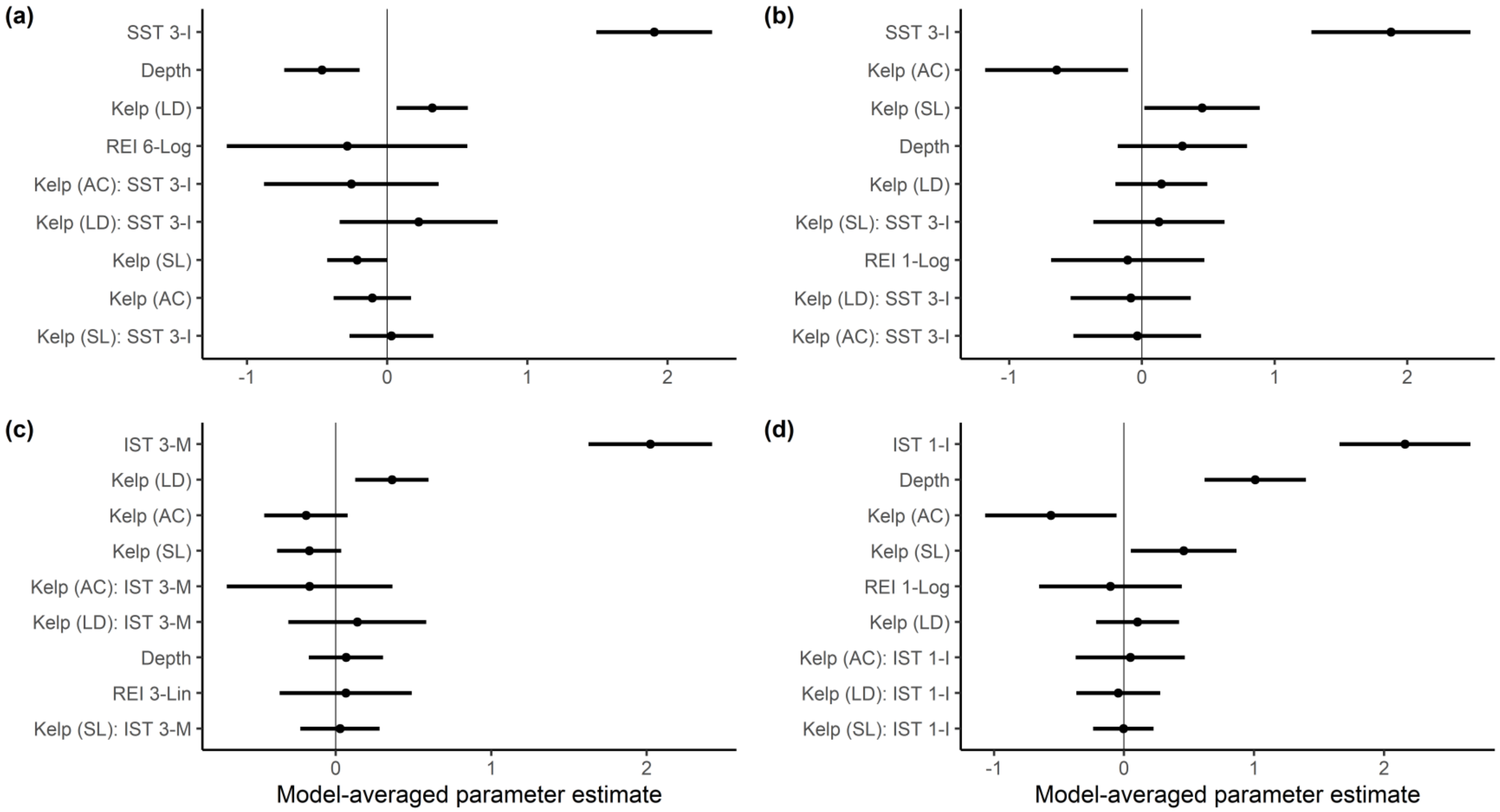

Figure A.9 Full-model averaged standardized parameter estimates for depth, kelp substrate, REI and temperature as predictors of a) percent cover (SST-based models), b) settler density (SST-based models), c) percent cover (IST-based models), and d) settler density (IST-based models), based on the IST datasets. REI and temperature metrics are abbreviated as per Table 2.1. Estimates arranged in descending order of magnitude. Error bars represent a 95% confidence interval based on unconditional standard error. AC = *Agarum clathratum,* LD = *Laminaria digitata*, SL = *Saccharina latissima.*

APPENDIX B

CHAPTER 3

B.1 Determination of time period for present-day climatology

To determine the most representative time period for present-day SST conditions in the NWA, I elected to calculate a long-term baseline temperature for the NWA and compare annual mean temperatures to the baseline. SST data from CoralTemp, which I used to parameterize and project SDMs, are only available from 1985 to present, a period not long enough to establish a long-term baseline. Therefore, for this analysis, I obtained annual SST rasters for the NWA from the NOAA Extended Reconstructed SST (ERSST) v5 dataset (Huang et al. 2017), and calculated a long-term baseline as the mean temperature across all cells between 1900 and 2000. I then used the ERSST data to calculate annual mean temperature across all cells for the range of years in my dataset (1987-2020), and subtracted the long-term baseline temperature from each annual value to obtain annual anomalies for each year. To segregate the years into groups based on their temperature anomaly, I conducted k-means clustering analysis (k = 3, starting iterations = 25; Hartigan & Wong 1979). I found that the most recent cluster of years, with the greatest positive anomaly from 20th century average temperature, was 2010-2020 (Figure B.1). Therefore, I selected 2010-2020 as the years over which to calculate present-day percent cover of *M. membranacea*.

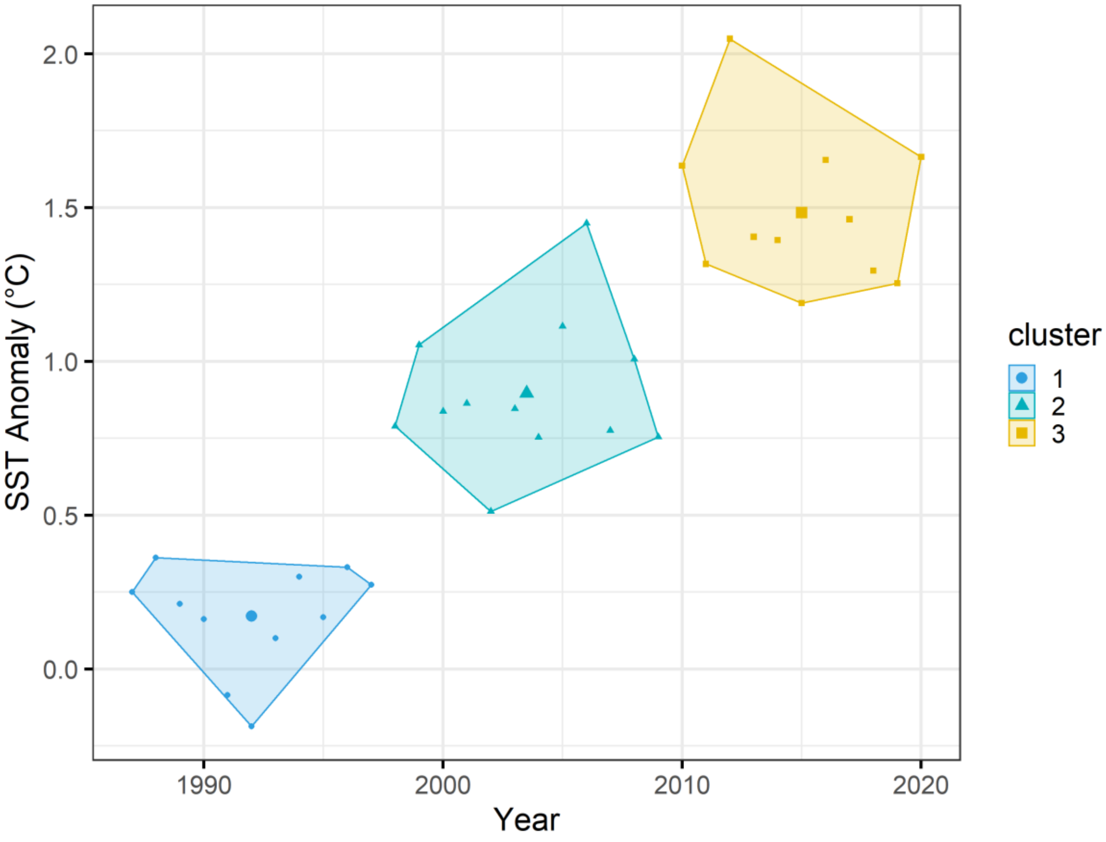

Figure B.1 Results of k-means clustering of annual sea surface temperature (SST) anomalies from mean SST from 1900-2000. Clusters 1-3 are groups of years with similar values of SST anomaly, where small points represent annual mean SST values and large points represent the cluster mean.

B.2 Salinity threshold

As *M. membranacea* is thought to be negatively impacted by low salinity (Forbord et al. 2020), and the NWA contains multiple estuarine areas, I sought to limit my SDM domain by salinity to avoid projected percent cover to areas where *M. membranacea* has not been recorded previously. I obtained present-day (2000-2014) sea surface salinity (SSS) data from Bio-ORACLE (Assis et al. 2018b) and extracted SSS at all sites in my dataset. When included as a predictor in the SDM, I found no significant relationship between salinity and percent cover, but the sites in my dataset included a narrow range of relatively high salinity (~30-32 PSU). To determine the broader range of salinity inhabited by *M. membranacea* in the NWA, I extracted SSS at monitoring sites with settlement plates inhabited by *M. membranacea* in the Gulf of St Lawrence (GoS; Fisheries and Oceans Canada 2006-2020), which has a lower average salinity than the sites in my dataset. The lowest salinity inhabited by *M. membranacea* in the GoS was 21.2 PSU. Since *M. membranacea* exhibits similar phenology and had a similar rate of spread in the GoS compared to other (more saline) areas in the NWA (Gulf of Maine and Nova Scotia; Denley et al. 2019b), there is no evidence that *M. membranacea* is negatively impacted by lower salinity levels in the GoS. Therefore, I used 21.2 PSU as the minimum salinity value for projecting my SDMs. This excluded from the domain of the SDM much of the St Lawrence Estuary in southern Quebec, and the George River Estuary in northern Quebec.

B.3 Additional R packages

In addition to those mentioned in the main text, I used several additional R packages to conduct the analyses in this study. I created tables with *sjplot* (Lüdecke 2020), *kableextra* (Zhu 2019) and *knitr* (Xie 2020). I obtained data from Bio-ORACLE using *sdmpredictors* (Bosch 2020). I used *sp* (Pebesma & Bivand 2005) and *rSDM* (Rodriguez-Sanchez 2021) to assign SST values to sites not on the raster grid. I worked with netcdf files from CoralTemp using *ncdf4* (Pierce 2019). To establish cells in contact with land, I converted the land shapefile to a raster format using *fasterize* (Ross 2020). I conducted k-means clustering analysis using *stats* (R Core Team 2020) and plotted the results using *factoextra* (Kassambara & Mundt 2020). For data management and manipulation, I used *tidyverse* (Wickham et al. 2019), *lubridate* (Grolemund & Wickham 2011), *car* (Fox & Weisberg 2019), *anytime* (Eddelbuettel 2020), and *readxl* (Wickham & Bryan 2019).

B.4 ODMAP

B.4.1 Overview

Authorship

Contact : c.pratt@dal.ca

Study link: (will include after study published)

Model objective

Model objective: Mapping and interpolation

Target output: Abundance

Focal Taxon

Focal Taxon: *Membranipora membranacea*

Location

Location: Northwest Atlantic Ocean

Scale of Analysis

Spatial extent: -72, -52, 42, 61 (xmin, xmax, ymin, ymax)

Spatial resolution: 5

Temporal extent: - 2010-2020 - 2040-2050 - 2090-2100

Temporal resolution: decadal

Boundary: rectangle

Biodiversity data

Observation type: field survey

Response data type: Abundance

Predictors

Predictor types: climatic, habitat, topographic

Hypotheses

Hypotheses: Cover of *Membranipora* has a positive, exponential relationship with temperature. Cover also depends on the species of kelp acting as its substrate, with *Laminaria digitata* hosting the highest cover, followed by *Saccharina latissima* then *Agarum clathratum*. Cover also has a negative relationship with depth, which is due to decreasing temperature with depth. These hypotheses were all supported by Chapter 2.

Assumptions

Model assumptions: - All key environmental drivers are included in the model - the species is in equilibrium with its environment - the model extrapolates in a biologically sensible manner; niche conservatism through time - predictors and abundance data were collected without error.

Algorithms

Modelling techniques: generalized linear mixed model (GLMM)

Model complexity: I conducted a thorough variable selection analysis (Chapter 2) and determined the predictors used in this study to be the optimal set of predictors for the percent cover of *M. membranacea*

Model averaging: Did not use ensemble modelling because of limited alternatives to GLMM when modelling grouped data. Alternatives that do exist are tree-based (mixed-effects random forest, gaussian process boosting) and not suitable for extrapolation

Workflow

Model workflow: - Fit GLMM according to specifications from Chapter 2 - Validate GLMM using either 0.632+ bootstrap (following Potts & Elith 2006) or external validation on test data, depending on analysis - Project GLMM to present and future climate scenarios using rasters of SST and setting depth and kelp substrate as constants

Software

Software: -I used R version 4.0.3. (R Core Team 2020) in the R Studio environment (RStudio Team 2020) for all analyses -key packages: glmmtmb (Brooks et al. 2017), raster (Hijmans 2020)

Code availability: -will be uploaded to Dryad

Data availability: -will be uploaded to Dryad

B.4.2 Data

Biodiversity data

Taxon names: *Membranipora membranacea*

Taxonomic reference system: N/A

Ecological level: populations, species

Data sources: Compiled from literature, unpublished, and original data

Sampling design: Opportunistic (determined by data availability). Nested within sites and years

Sample size: 607 (main dataset); 43 (invasion stage analysis); 118 (Norway data)

Clipping: N/A

Scaling: N/A

Cleaning: Percent cover was averaged by site, depth, kelp substrate, and sampling date

Absence data: N/A

Background data: N/A

Errors and biases: Percent cover values will have varying error rate depending on study they originated from

Data partitioning

Training data: No data partitioning was applied

Validation data: 0.632+ bootstrap validation (n = 200 replicates) or external validation used depending on the analysis

Test data: Test data were determined by the needs of the analysis

Predictor variables

Predictor variables: maximum six-month mean sea surface temperature (SST 6-max); depth; kelp substrate

Data sources: daily SST from CoralTemp (NOAA Coral Reef Watch 2020), future SST from Bio-ORACLE (Assis et al. 2018b)

Spatial extent: -72, -52, 42, 61 (xmin, xmax, ymin, ymax)

Spatial resolution: CoralTemp: 5km; Bio-ORACLE: 9km

Coordinate reference system: “+proj=longlat +datum=WGS84 +no_defs”

Temporal extent: 1987-2020

Temporal resolution: daily

Data processing: Bio-ORACLE SST rasters downscaled to match resolution of CoralTemp data using bilinear interpolation

Errors and biases: N/A

Dimension reduction: See Chapter 2

Transfer data

Data sources: Transferred to Norwegian percent cover data compiled from multiple studies (Førde et al. 2016, Matsson et al. 2019, Forbord et al. 2020)

Spatial extent: 4.7, 19.8, 58.1, 70.1 (xmin, xmax, ymin, ymax)

Spatial resolution: 5km (CoralTemp SST)

Temporal extent: 2014-2017

Temporal resolution: daily SST

Models and scenarios: Transferred NWA model to Norway data to test performance

Data processing: N/A

Quantification of Novelty: N/A

B.4.3 Model

Variable pre-selection

Variable pre-selection: Model averaging-based approach (see Chapter 2)

Multicollinearity

Multicollinearity: Tested for collinearity using VIF and Pearson correlation

Model settings

GLMM: REML (FALSE), ziformula (~.), formula (percent_cover ~ depth + kelp_substrate + six_month_mean_sst + kelp_substrate*six_month_mean_sst + (1|site) + (1|year)), family (beta_family(link="logit"))

Model settings (extrapolation): N/A

Model estimates

Coefficients: Extracted from glmmTMB output in R

Parameter uncertainty: Standard error of model-averaged parameter estimates (see Chapter 2)

Variable importance: Model averaged parameter estimates (see Chapter 2)

Model selection - model averaging - ensembles

Model selection: Information-theoretic approach (see Chapter 2)

Model averaging: N/A

Model ensembles: N/A

Analysis and Correction of non-independence

Spatial autocorrelation: N/A (autocorrelation not present)

Temporal autocorrelation: N/A (autocorrelation not present)

Nested data: Crossed random intercepts in GLMM to account for nesting within site and year

Threshold selection

Threshold selection: N/A

B.4.4 Assessment

Performance statistics

Performance on training data: Pearson correlation between observed and predicted values, Spearman rank correlation between observed and fitted values, Model calibration (slope and intercept of linear regression between observed and predicted values), RMSE, Average error

Performance on validation data: All statistics estimated via 0.632+ bootstrap for main model validation (section 3.3.4.2)

Performance on test data: All statistics estimated via test data for comparison to Norwegian percent cover data (section 3.3.4.5)

Plausibility check

Response shapes: Response plots (see Chapter 2)

Expert judgement: Map display

B.4.5 Prediction

Prediction output

Prediction unit: peak percent cover of *Membranipora membranacea*

Post-processing: projections clipped to raster cells in contact with land and to areas with salinity greater than or equal to 21.2 (minimum salinity where *M. membranacea* has been recorded in the NWA)

Uncertainty quantification

Algorithmic uncertainty: Standard error

Input data uncertainty: Due to varying methods, uncertainty in input data varies by data point

Parameter uncertainty: Estimates of standard error are low (+/- 10%) and do not have a substantial impact on interpretation of predictions

Scenario uncertainty: for CoralTemp, see Liu et al. (2014) and Maturi et al. (2017); for Bio-ORACLE, see Assis et al. (2018b)

Novel environments: N/A

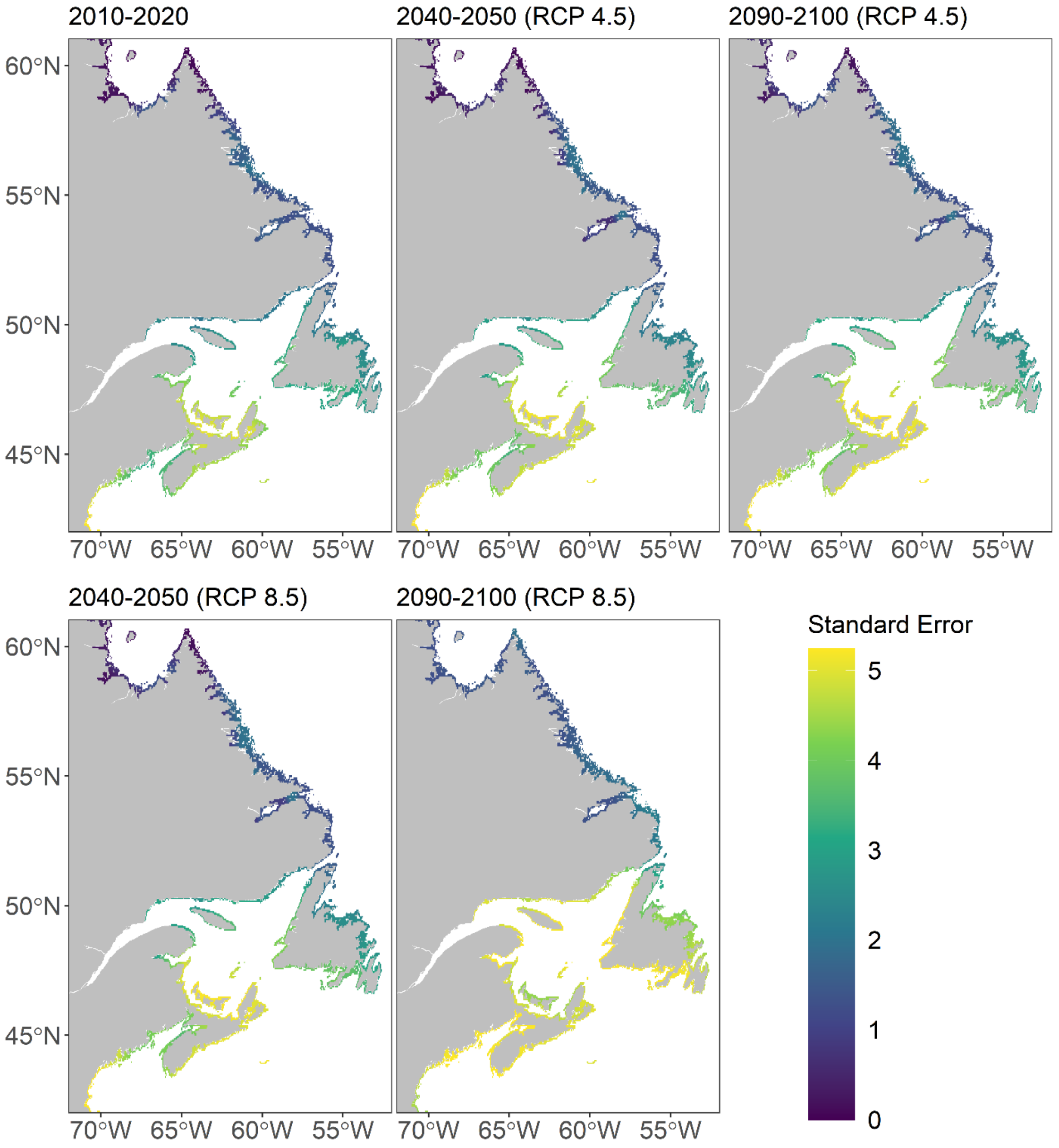

Figure B.2 Model standard error for SDM projections of peak percent cover of *M. membranacea* on *L. digitata* for present-day (2010-2020) and future SST scenarios. RCP is the Representative Concentration Pathway under which SST has been predicted for each future time period.

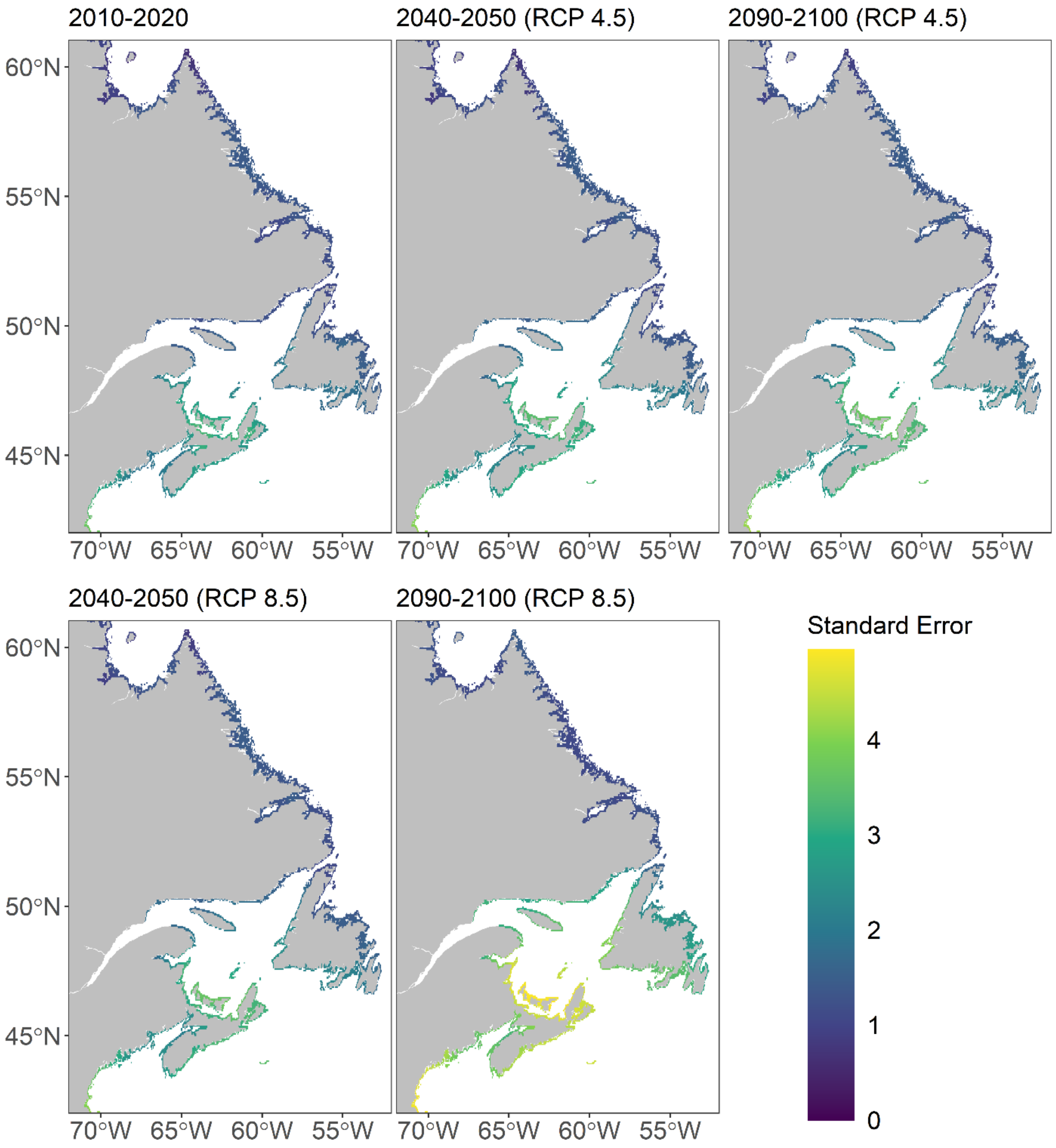

Figure B.3 Model standard error for SDM projections of peak percent cover of *M. membranacea* on *S. latissima* for present-day (2010-2020) and future SST scenarios. RCP is the Representative Concentration Pathway under which SST has been predicted for each future time period.

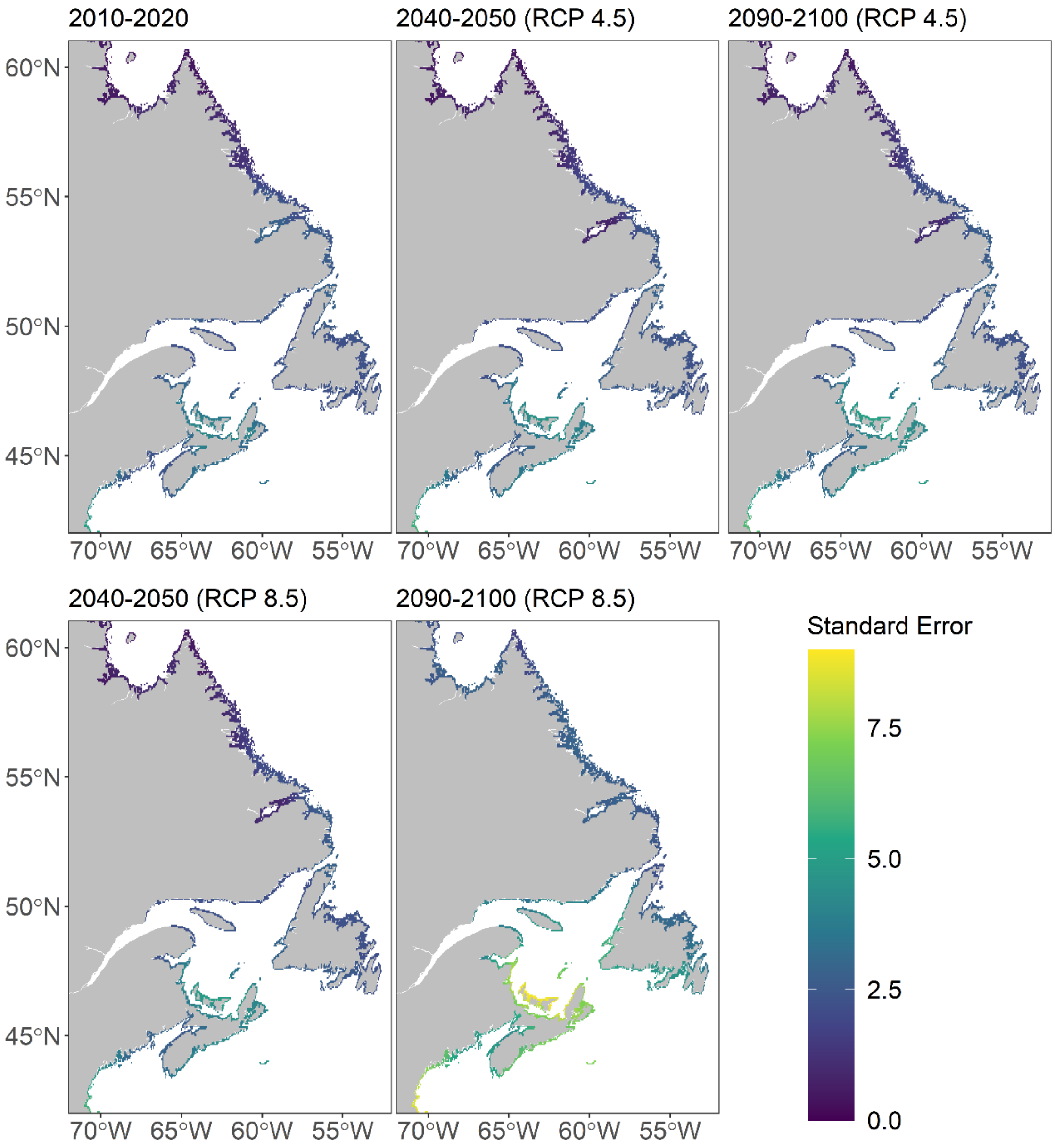

Figure B.4 Model standard error for SDM projections of peak percent cover of *M. membranacea* on *A. clathratum* for present-day (2010-2020) and future SST scenarios. RCP is the Representative Concentration Pathway under which SST has been predicted for each future time period.

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