THE USE OF POPULATION CONNECTIVITY IN THE DESIGN OF NETWORKS OF MARINE PROTECTED AREAS

by

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To my Baba, Doreen Joy Taylor. She was a teacher her entire life and continues to teach me every day. She has read the entirety of this thesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Ecological connectivity, the exchange of individuals among spatially fragmented habitats, is an important criterion in the design of networks of marine protected areas (MPAs). However, there are gaps in taxonomic and geographic application of knowledge on connectivity patterns to conservation planning. The main objectives of this thesis are to 1) quantify how connectivity has been applied to the design of MPAs and 2) apply lessons learned to the Atlantic coast of Nova Scotia by comparing different methods for estimating and prioritizing connectivity for management. 11% of 746 MPAs from six regions with advanced systematic conservation planning considered connectivity as an ecological criterion in their design. Practical considerations for improving implementation include considering whether to prioritize connectivity, identifying the role of a MPA in supporting connectivity, identifying the appropriate temporal and spatial scale, and improving regional patterns of connectivity. Dispersal for species with a short propagule duration could be adequately estimated with average current velocity. At the spatial scale of management units (10s of km), binning current speed by direction produced dispersal area estimates comparable to those from a biophysical model, therefore providing a lower cost and resource intensive tool. In-silico habitat fragmentation of kelp reinforced that most kelp patches are sustained by self-recruitment. Negative impacts of habitat fragmentation were no greater than the impacts of habitat loss alone, except when a critical threshold of habitat loss was surpassed (70-80 %). Priority areas for protection of kelp, that also minimized connectivity of an invasive biological threat, tended to be large, upstream patches. The priority of kelp patches also varied when testing different connectivity objectives, supporting that the role of an area in supporting connectivity is an important consideration. These results indicate that connectivity should always be considered in the design of MPAs, but the way in which information on dispersal patterns is incorporated will depend on the species of interest, investment of time and resources, and having a diverse toolkit. This thesis provides new insights into how and when to prioritize connectivity in the design of MPAs with the goal to help future proof MPAs through connectivity pathways and hubs.

LIST OF ABBREVIATIONS AND SYMBOLS USED

BLM = boundary length modifier

CBD = convention on biological diversity

CMR = commonwealth marine reserve

CPD = competent propagule duration

FPF = feature penalty factor

FVCOM = finite volume community ocean model

GBR = great barrier reef

IUCN = International Union for Conservation of Nature

MCZ = marine conservation zone

MPA = marine protected area

MPAn = marine protected area network

NCMPA = nature conservation marine protected area

PCoA = principal coordinates analysis

PD = planktonic duration

PU = planning unit

SMCA = state marine conservation area

SMR = state marine reserves or reserve

UK = United Kingdom

WDPA = world database on protected areas

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CHAPTER 1

INTRODUCTION

1.1 Background

Ocean ecosystems are facing increasing pressures from a combination of stressors such as increasing temperature, ocean acidification and sea level rise (Boyd & Hutchins, 2012). Additionally, humans obtain many direct benefits from oceans, such as fisheries and mineral extraction, as well as indirect benefits, such as carbon storage (Boyd & Hutchins, 2012; Roberts et al., 2003). Of the various spatial management interventions available to safeguard marine ecosystems from detrimental anthropogenic impacts, marine protected areas (MPAs) provide the most widely utilized tool. A MPA is a clearly defined geographical space, recognized, dedicated, and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (IUCN-WCPA 2008). The designation of MPAs should depend on biological, social, and economic criteria. However, economic considerations often take priority, which can substantially decrease the efficacy of the reserves to preserve ecosystems (Roberts et al., 2003).

Population connectivity defines the extent to which spatially distinct populations are linked by the dispersal of propagules, juveniles and adults (Palumbi, 2003). Although population connectivity is an ecological criterion particularly relevant for networks of MPAs (MPAn), its use in designing MPAs globally has been limited (Leslie 2005, Magris et al. 2014). Other ecological selection criteria, such as representativity, often take priority and are used more frequently (Barr & Possingham, 2013; Margules & Pressey, 2007). However, there are instances where population connectivity can be pivotal in the decision-making process, particularly for MPAs with limited self-recruitment or where the area identified to maintain a viable population exceeds the size of the area proposed to receive protection (Marti-Puig et al., 2013). Prioritizing connectivity is also vital to enhance resilience under present and future ocean conditions (Palumbi 2003, Álvarez-Romero et al. 2018). By prioritizing connectivity, there is potential for both economic and social benefits to occur (e.g. spillover of adults).

Patterns of population connectivity are highly variable across taxa, because of a diversity of life history characteristics and interactions with the oceanic environment. The ecological process of connectivity encompasses many biological and physical parameters, making it difficult to estimate without complex tools. Population connectivity is governed by the combined effects of: reproduction, spawning, fertilization (in dioecious broadcast spawners), physical transport, larval behaviour, larval survival, larval settlement, recruitment, and post-larval survival (Pineda et al. 2007). The ecological and evolutionary significance of connections is dependent on survival until reproduction, often referred to as reproductive population connectivity (Pineda et al. 2007). Larval swimming ability, mortality, timing of spawning, and pelagic propagule duration are some life history characteristics that need to be parameterized when estimating species-specific measures of population connectivity (Metaxas and Saunders 2009a). As a result, measurement of connectivity can occur over spatial and temporal scales ranging from metres and hours to hundreds of kilometres and months (Cowen et al. 2006).

There are a wide range of methods (e.g. biophysical models, genetics, microchemistry) used to measure connectivity (Botsford et al., 2009; Burgess et al., 2012; Thorrold et al., 2002). Their relevance to a particular scenario, whether that be management or research focussed, is dependent on the species or ecosystem of interest, resource and time availability, spatial scale of the system of interest, as well as the overarching objectives. However, it is postulated that the aforementioned methods are rarely used by management agencies or applied to reserve design, and are instead traded for simpler rules of thumb, such as size and spacing. However, simple guidelines are likely to oversimplify dispersal patterns for many benthic invertebrates and habitat forming species, which have a planktonic propagule phase capable of dispersing much further than their adult counterparts (Cowen and Sponaugle 2009). Even more so, coastal ecosystems offer additional challenges to understanding dispersal and connectivity because of a paucity of baseline knowledge on the distribution of species and habitats, complex physical oceanography, and complicated stakeholder relationships.

Research is focussing on improving ways to incorporate connectivity through space and time in spatial conservation planning tools, such as Marxan, and newly developed Marxan Connect. Marxan takes input on the spatial distribution of features to protect and calculates a best-case scenario for a MPAn design using a heuristic algorithm (Ball et al. 2009). Marxan Connect is a pre-processing tool for Marxan that uses connectivity matrices or habitat landscapes as input to produce spatial layers or spatial dependencies that represent connectivity features or strengths between management units (Daigle et al. 2020). The combination of these two spatial planning tools will make it more feasible to include connectivity in spatial management.

1.2 Objectives

The overall objective of this thesis is to explore the use of population connectivity in the design of networks of MPAs, particularly in coastal ecosystems. Specifically, I focus on bridging the gap between connectivity research for the purpose of scientific inquiry and its application to systematic conservation planning. To achieve this, I first quantify the extent to which connectivity has been incorporated into the design of MPAs and MPAn to-date. Then, I apply the lessons learned from the primary and management literature review to the Atlantic coast of Nova Scotia, a region where our understanding of connectivity patterns is limited and a network of MPAs are currently under consultation for designation. This thesis is arranged into 6 chapters, including this Introduction (**Chapter 1**). **Chapters 2-3** have been published as independent manuscripts in the primary literature. In **Chapter 2**, I synthesize the current knowledge on the use of connectivity in the design of MPAs and MPAn and propose a framework to aid in the incorporation of connectivity in the design of MPAn. In **Chapters 3-5**, I apply this framework to the Atlantic Coast of Nova Scotia, focussing on subtidal kelp bed ecosystems. In **Chapter 3**, I compare three approaches for estimating dispersal and connectivity that differ in the complexity of estimating ocean currents: current speed depth-averaged over time (1D); current velocity decomposed into along-shore and cross-shore components depth-averaged over time (2D); and spatially modelled current velocity derived from a 3D hydrodynamic model (3D), for three species with different life history characteristics. In **Chapter 4**, I tested the impact of habitat loss and habitat fragmentation on kelp habitat structure and connectivity. In **Chapter 5**, I evaluate differences in the configuration of conservation priority sites under the contrasting objectives of maximizing connectivity for poorly dispersing native kelp and minimizing the dispersal of the invasive species that smothers kelp using the decision support tool Marxan and preprocessing tool, Marxan Connect. Finally, in **Chapter 6**, I summarize the main implications of this thesis and make suggestions for future research on the topic of marine ecological connectivity.

CHAPTER 2

THE CURRENT APPLICATION OF ECOLOGICAL CONNECTIVITY IN THE DESIGN OF MARINE PROTECTED AREAS[1]

2.1 Abstract

Marine protected areas (MPAs) are an area-based conservation strategy commonly used to safeguard marine biodiversity and ecosystem services. Ecological connectivity governs the exchange of individuals among spatially fragmented habitats and is often highlighted as an important element in the design of MPAs. However, the degree to which measured or modelled representations of connectivity are applied to marine management decisions worldwide remains unclear. We reviewed the scientific and management literature to explore the application of connectivity in MPAs located in six countries or regions with advanced marine spatial planning. Only 11% of the 746 MPAs we examined considered connectivity as an ecological criterion, increasingly so since 2007. Landscape measures such as habitat linkages were used most frequently by managers and genetic and modelling approaches by scientists. Of the MPAs that considered connectivity, 71% were for state marine conservation areas or reserves in California and commonwealth marine reserves in Australia. This pattern indicates substantial geographic bias. We propose that the incorporation of connectivity in conservation planning needs to become more accessible to practitioners and provide four recommendations that together will allow scientists and managers to bridge this gap: 1. determine whether to prioritize connectivity as an ecological criterion, 2. identify the role of an MPA in supporting connectivity, 3. identify the appropriate spatial and temporal

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[1] Balbar, A. C., and A. Metaxas. 2019. The current application of ecological connectivity in the design of marine protected areas. Global Ecology and Conservation 17:e00569.

My coauthor Dr. Anna Metaxas supervised the development of the study design and analyses, and edited the manuscript.

scale of connectivity, and 4. improve regional knowledge of connectivity patterns. We also propose a framework to facilitate the communication of metrics and patterns of connectivity between scientists and practitioners to apply the best available information in the design and adaptive management of MPAs and networks of MPAs.

2.2 Introduction

Marine protected areas (MPAs) are one of the most widely utilized tools to preserve biodiversity and ecosystem services. MPAs have been shown to mitigate against biodiversity loss by promoting the persistence, recovery and growth of populations (Almany et al. 2009, Gaines et al. 2010, Speed et al. 2018). For MPAs to achieve the goal of biodiversity persistence, the protection of community composition and ecological processes governing marine ecosystems must be ensured. However, global and local threats, such as climate-change mediated shifts in temperature, ocean acidity, sea level rise, and invasive species, habitat loss, and pollution may compromise the effectiveness of MPAs (Harley et al. 2006, CBD 2008, McLeod et al. 2009, Boyd and Hutchins 2012, Blašković et al. 2017, Bruno et al. 2018, Kaplan et al. 2018). The application of ecological criteria that support the goal of biodiversity persistence offers one solution to creating more resilient MPAs in the face of accelerated anthropogenic changes. Connectivity is a fundamental ecological process in marine ecosystems that promotes both persistence and recovery of populations through the dispersal of marine life across populations, communities and ecosystems.

According to the definition provided by the International Union for the Conservation of Nature (IUCN), a MPA is “a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (Day et al. 2012). In 2010, the Convention on Biological Diversity (CBD) set a target to conserve “10% of coastal and marine areas [through] ecologically representative and well-connected systems of protected areas” by 2020 (CBD 2010). This goal underscores the importance of having direct, inferential or predictive measures of connectivity among protected areas. Grorud-Colvert et al. (2014) five types of networks of MPAs (MPAn) ranging from ad-hoc (an unplanned collection) to connectivity-based (multiple ecologically connected MPAs) and concluded that many existing MPAn do not meet the definition of a connectivity network.

Connectivity, the extent to which spatially distinct populations, communities, ecosystems, or habitats are linked by the exchange of genes, organisms (propagules, juveniles and adults), nutrients, and energy is considered an important ecological criterion in the design of true MPAn, where the whole is more than the sum of its parts (Botsford et al. 2009, Cowen and Sponaugle 2009); however, the use of connectivity in designing MPAs globally has been limited (Leslie 2005, Magris et al. 2014). Other ecological selection criteria, such as representation of species or habitats often take priority and are used more frequently (Margules and Pressey 2000, Barr and Possingham 2013). Even so, there are instances where connectivity can be pivotal in the decision-making process, particularly for MPAs with limited self-recruitment or where the size of the area required to maintain a viable population exceeds the size of the area proposed to receive protection (Marti-Puig et al. 2013). By prioritizing connectivity, there is also potential for both economic and social benefits to occur (e.g. spillover). Existing MPAn that have not incorporated larval connectivity may be ineffective in achieving persistence and protection of biodiversity (Magris et al. 2018).

Incorporating connectivity into the design of MPAs and MPAn may be challenging because of the complexity of the methods used to estimate and predict connectivity patterns (Thorrold et al. 2002, Botsford et al. 2009, Burgess et al. 2014, Bryan-Brown et al. 2017). There have been several reviews on methods to quantify connectivity and integrate it into MPAn design (Calabrese and Fagan 2004, Cowen and Sponaugle 2009, Magris et al. 2014, 2016), mainly focusing on tropical coral reef ecosystems (Almany et al. 2009, McCook et al. 2009, Jones et al. 2009). Recently, Bryan-Brown et al. (2017) summarized the patterns and trends in connectivity research and identified geographical and taxon biases. However, recommendations for integrating connectivity in the design of MPAn have not been consistently implemented by managers in practice.

There is a gap between the increasing volume in scientific research on connectivity and its integration into marine spatial planning. Managers and scientists both have long recognized the importance of this ecological criterion (Margules and Pressey 2000, Roberts et al. 2003, Steneck 2006), but managers do not have access to tools or operational frameworks that may facilitate collaboration between sectors, or they may not be familiar with the underlying ecological and physical processes mediating connections. Additionally, connectivity is not an area-based target as many other ecological criteria such as representation, making it difficult to develop quantitative objectives for marine spatial planning. Differences in the intended audience of peer-reviewed articles compared to reports in the grey literature and management plans also lead to differences in focus, style, and even the definitions of connectivity, making comparisons difficult.

Here, we review research articles published in the peer-reviewed literature and management plans of protected areas to examine whether connectivity was included in the design of MPAs and MPAn in select countries with advanced marine spatial planning. The scope of this study focuses on marine systems and does not address processes that occur at the land-sea interface. We assessed the variation in prioritizing different ecological criteria, both geographically and temporally. Combining information from management plans and peer-reviewed articles allowed us to outline differences in methods and application of connectivity between the scientific and management sectors. We provide recommendations and suggest a framework for future incorporation of empirical connectivity measurements into designing and monitoring of MPA and MPAn and identify the actors in each step. This review will add to the growing literature on connectivity by demonstrating the gap between connectivity research and application by practitioners and proposing ways to overcome this gap. Our goal is to stimulate a dialogue and collaboration between these two sectors to promote the use of the best available information on considering connectivity during the implementation of MPAs and MPAn.

2.3 Methods

2.3.1 Database acquisition

We determined the methods and metrics used in the scientific literature to measure connectivity by completing searches in the Web of Science (https://apps.webofknowledge.com) and Scopus (https://www.scopus.com). The search was completed with default search settings and the following set of search terms (* represents a wild card): ((population* OR larva* OR genetic* OR landscape* OR seascape*) connect*) AND (MPA OR “marine protected area” OR “marine reserve” OR “marine park” OR “marine sanctuary” OR “marine conservation area” OR “marine nature reserve” OR “marine management area” OR “marine national park” OR “coastal reserve” OR “marine and coastal park”) AND (monitor* OR manage* OR design OR implement OR designat*). These search terms were selected to capture studies that discussed connectivity for different designations of MPAs. The first set of search terms selected for research on connectivity, while the second set narrowed the search to articles examining connectivity in MPAs. The last set of search terms focused our efforts further on studies examining different stages of planning, i.e. prior to, during, and after designation to capture studies on planning, implementation and monitoring. The searches were completed on November 22, 2017.

The search terms returned 397 studies, excluding duplicates. An abstract review, completed through the online software covidence (https://www.covidence.org/), included 307 studies that both (1) discussed or measured demographic, genetic, or landscape connectivity and (2) discussed actionable goals for MPA design or management. Data were extracted from 186 studies, following the full text review using these two inclusion criteria. Studies were analyzed in alphabetical order to prevent systematic biases in the dataset (see details on information extracted from each paper in Table A.1).

We created a database of MPAs based on management plans, government websites and other managing agency documents. We focused on six countries or regions with advanced systematic conservation planning: Australia, California, Canada, France, Hawaii and the United Kingdom (Including England, Northern Ireland, Scotland, and Wales; hereafter focus areas). We used MPAtlas to compile an initial list of MPAs in the focus areas, and government websites to produce a comprehensive list. The final list of MPAs was confirmed with the World Database on Protected Areas (WDPA) for completeness. We used the definition of a Marine or Coastal Protected Area by the CBD Ad Hoc Technical Expert Group as our criterion for defining a MPA: “any defined area within or adjacent to the marine environment, together with its overlying water and associated flora, fauna and historical and cultural features, which have been reserved by legislation or other effective means, including custom, with the effect that its marine and/or coastal biodiversity enjoys a higher level of protection than its surroundings” (CBD 2004).

The comprehensive list, generated from management plans, included MPAs that at the time of data assembly were designated (rather than proposed only) (1) legislatively to (2) protect the ecological function, biodiversity, or an oceanographic (physical or geological) feature within an area under (3) a defined managing authority. All three conditions needed to apply for a MPA to be included. Where boundaries or designation types within the study area had changed over time, the most up-to-date regulations and rules were used. Where a new designation had been proposed but not enforced by legislation, the rules of the old designation were used. The final dataset included 746 MPAs and 9 MPAn. Only MPAs designated prior to 31 August 2017 were included in the review. Supplemental information on the information extracted from each MPA and MPAn can be found in Table A.2.

2.3.2 Database analysis

The purpose of the scientific and management literature review was to answer two questions: (1) was connectivity used as a guiding principle in the design and evaluation of MPAn, and (2) if yes, what methods and metrics of connectivity were used by scientists and managers?

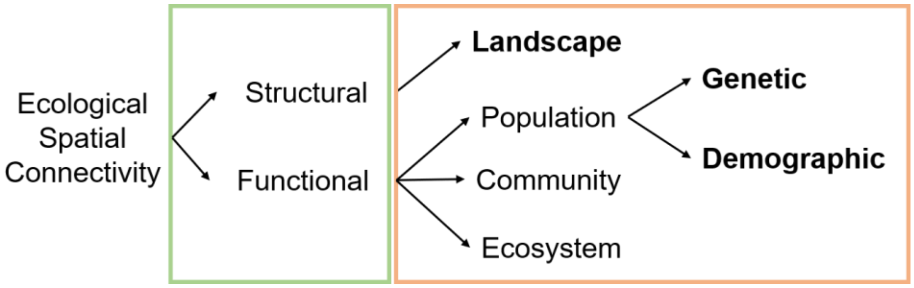

Figure 2.1: Classification of types of ecological spatial connectivity. Bolded categories are within the scope of this review.

2.3.2.1 Scientific (peer-reviewed literature) database

For the review of scientific literature, we considered studies that explicitly measured connectivity separately from those that only provided guidelines on how to incorporate connectivity in design of MPAs or MPAn (Figure 2.2). For all scientific studies, we extracted the location, studied MPA, and conclusions reached by the study. For studies that explicitly measured connectivity, we also recorded: (1) the study taxa, (2) whether the study was on design or a post-hoc evaluation of planned or existing MPAs, and (3) the methods, metrics and class of measured connectivity (landscape, demographic, and genetic; Figure 2.2). Because protection level varied across jurisdictions and IUCN criteria were not used consistently, we did not include it as a factor in the study. Additionally, the protection of the Commonwealth Marine Reserves (CMR) in Australia changed over the course of the review, with new management plans taking effect on July 1, 2018 (i.e. after we completed our research).

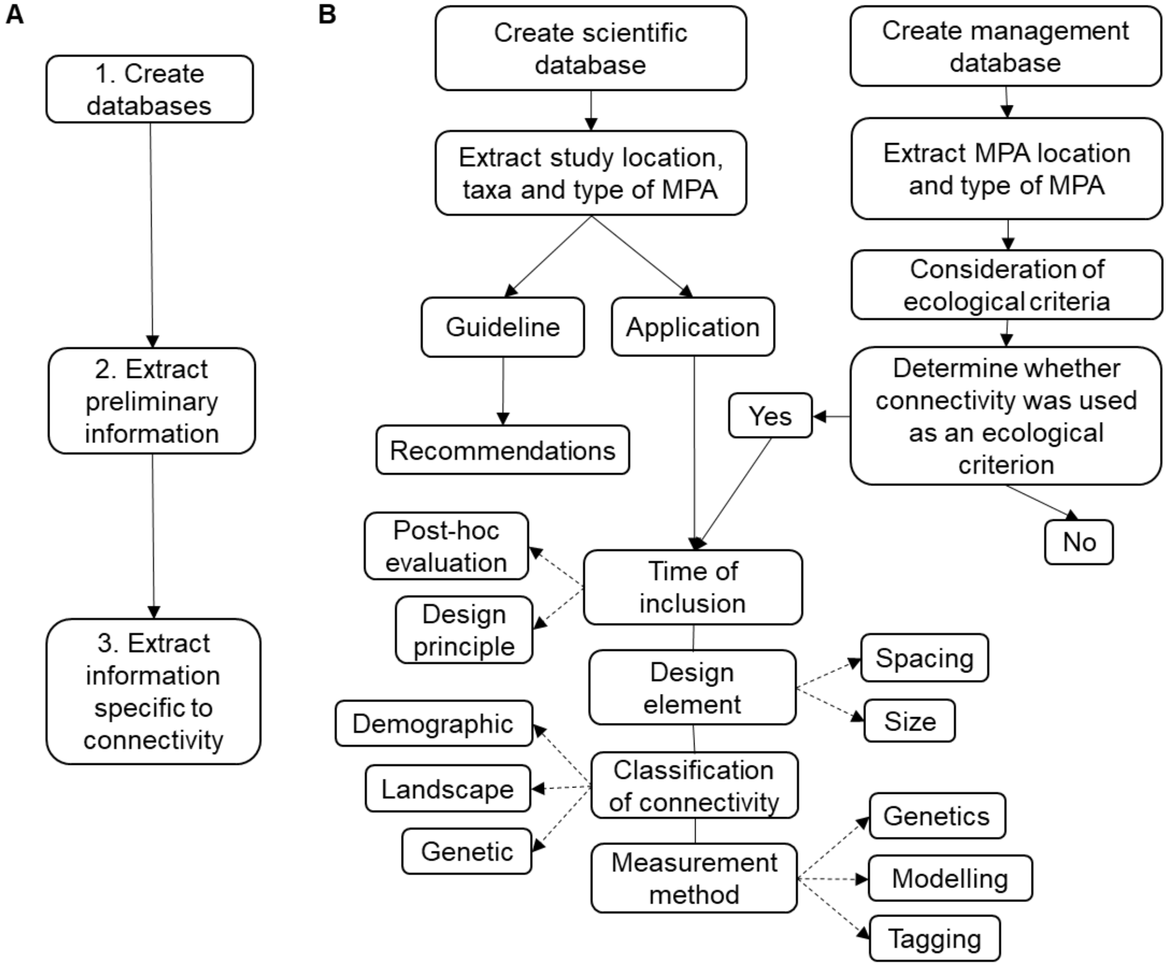

Figure 2.2: (A). Simplified and (B) detailed flowchart, depicting steps taken to extract information on the inclusion of connectivity in marine protected areas (MPAs) and marine protected area networks (MPAn) from peer-reviewed scientific and management literature. The scientific database consisted of 186 research articles and the management database consisted of management plans for 746 MPAs and 9 MPAn. See section Database acquisition and Database analysis for details.

2.3.2.2 Management database

For the review of the management literature, information on location, the category of MPA, managing authority, size of MPA, ecological selection criteria and monitoring strategies were extracted from management plans and websites of governments or other managing agencies for each MPA and MPAn. We considered individual MPAs and MPAn separately since their goals differ. We classified the ecological criteria used in site selection under 14 categories: representative features, areas of high productivity, areas of high biodiversity, biogenic habitats, nursery areas, foraging areas, spawning areas, migratory areas, species at risk, fisheries, complex or unique geomorphology, unique or rare oceanography, culturally important species, and connectivity. For MPAs that used connectivity as an ecological criterion, as well as peer-reviewed scientific articles, we classified connectivity as landscape, demographic or genetic. This allowed us to identify differences in the application of connectivity knowledge between the scientific and management sectors.

2.4. Current state of population connectivity application in research and management

2.4.1 Database summaries

2.4.1.1 Scientific literature

We identified 38 studies that only provided guidelines ("Guideline studies") and 148 studies that measured connectivity and, based on their results, made explicit MPA recommendations ("Application studies"; Table A.3). We excluded 37 studies at the full-text review stage because, although they stated that their research had MPA applications, they provided no specific recommendations.

Overall, there has been a substantial increase in the frequency of peer-reviewed publications on connectivity in MPAs since 2010 (Figure 2.3). These studies focused on a wide range of taxonomic groups but were strongly biased towards ray-finned fishes (Actinopterygii; Figure 2.4). Anthozoa were also well studied, followed by Bivalvia and Malacostraca. Of the 148 "Application studies", 34 focused on MPA design and 122 conducted post-hoc analysis of existing or prospective (area selected but no legislation in place) MPAs. Six studies had elements of analyses for both the design and post-hoc evaluation phases. The 148 studies that measured connectivity focused more often on tropical than temperate areas (Figure 2.5). There was a clear geographic bias for research on connectivity in MPAs in Australia and the United States of America (Figure 2.5).

Notable research efforts on connectivity in MPAs have also focused on the Gulf of California, some Mediterranean countries and the Coral Triangle. Overall, most countries and regions have not been the focus of scientific literature. In contrast, Figure 5 of Bryan-Brown et al. (2017) indicated that the Caribbean Sea and Northern Europe had the greatest relative research effort in studying marine population connectivity. However, we showed that there is minimal application of this research in scientific studies that evaluate connectivity in practice.

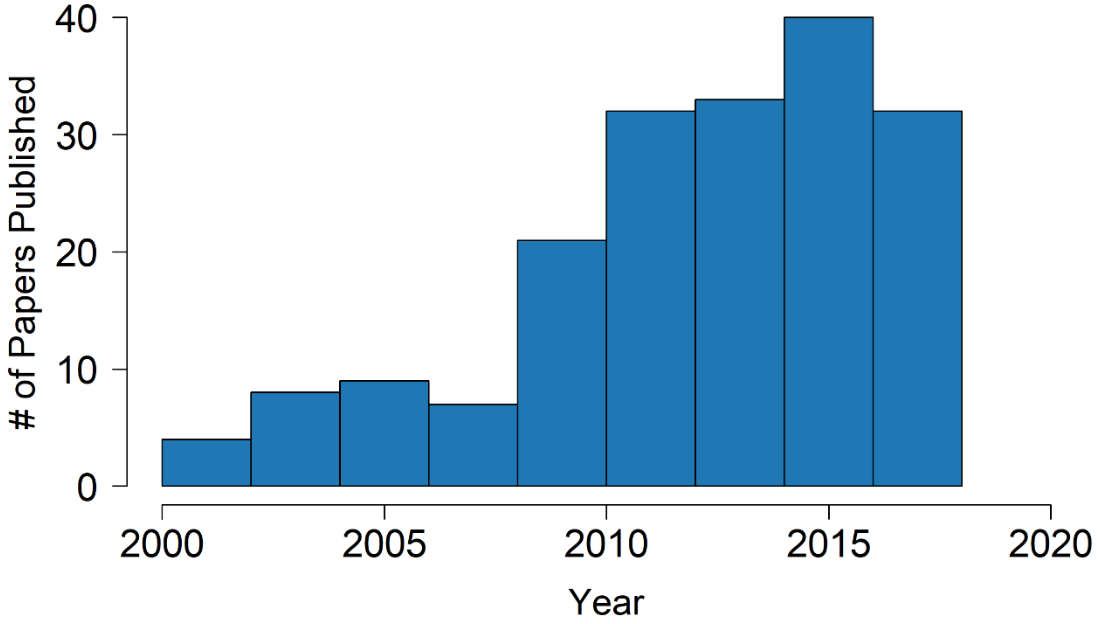

Figure 2.3: Frequency of publication in the peer-reviewed literature of research articles on the use of connectivity in marine protected areas (*n*=174). Searches using Web of Science and Scopus were completed on 23 November 2017.

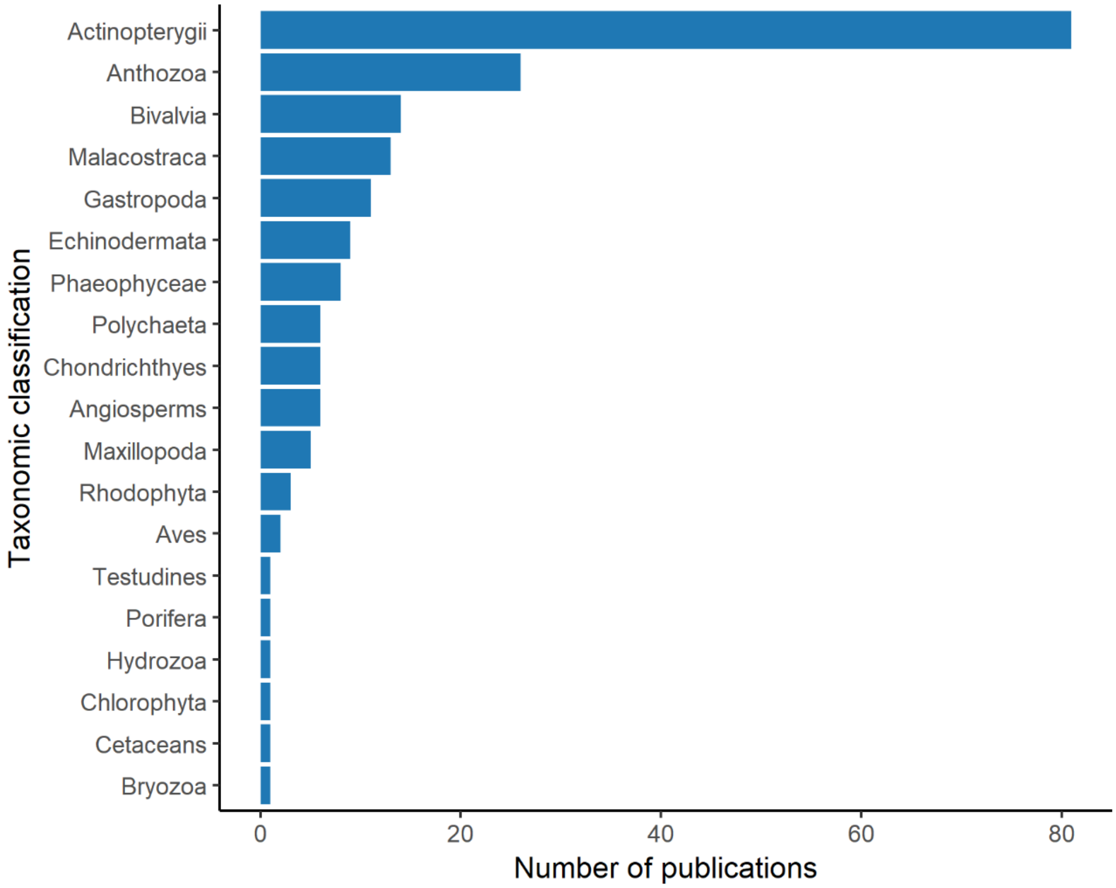

Figure 2.4: Focal taxa used in the peer-reviewed scientific literature on population connectivity in the design of marine protected areas. Taxa are shown in descending order of research effort. Note that each article may focus on more than 1 taxon (n = 140).

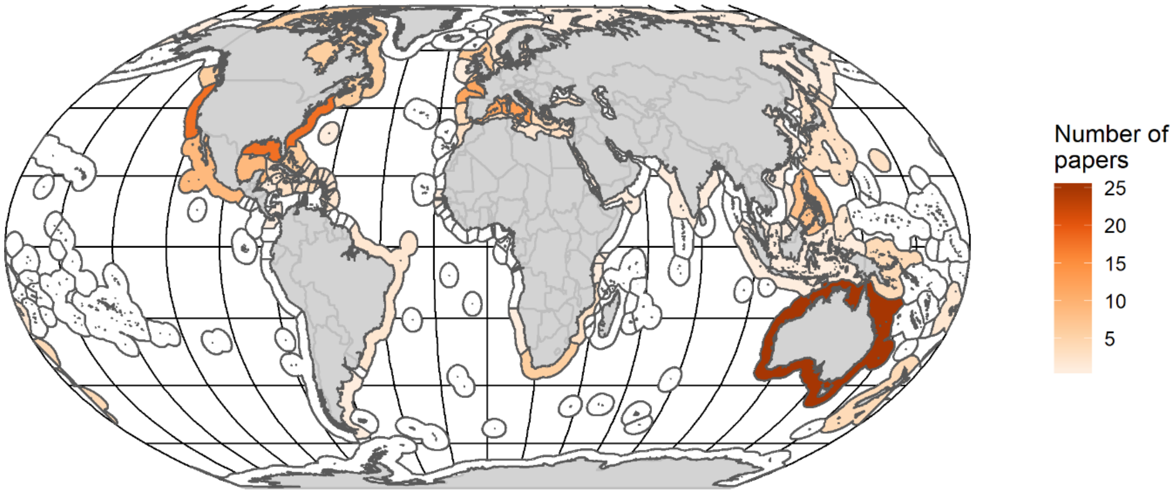

Figure 2.5: Geographic patterns in research effort on population connectivity in the design of marine protected areas by country, where colour intensity indicates the number of papers (n = 148). Six papers included in the review could not be depicted in the figure: 2 were theoretical models and 4 had an international scope.

2.4.1.2 Management literature

The review of the management literature identified 746 MPAs and 9 MPAn (Table A.4). Of the 746 individual MPAs, 80% had clearly defined selection criteria and 47.7% had a management plan, although the criteria were not always stated in the plans. There were 55 categories of MPAs, corresponding to varying levels of protection and legislation types, which reflect different conservation objectives of MPAs. Only 28.2% of analyzed MPAs used the IUCN criteria for levels of protection. Of the identified MPAs, the total area was greatest in Australia (Table 2.1), which was also where most scientific literature was based.

Representation was the most widely used ecological criterion for siting, followed by areas of high biodiversity and species at risk (Figure 2.6). Connectivity was among the least frequently used ecological criteria, followed only by culturally important species

(Figure 2.6). Conservation of biodiversity was the second most common criterion in Australia and Canada, 3rd in USA (California and Hawaii) and 4th in France and the United Kingdom (UK). Species at risk was the 2nd most common criterion in France and USA, 3rd in Australia and Canada, and not included in the top 5 criteria in the UK. Biogenic habitats were 3rd most commonly used in UK and France, 4th in Australia and the USA, and 5th in Canada. The number of ecological criteria considered for an individual MPA ranged from 1-14, with a median of 7.5 (Figure 2.7).

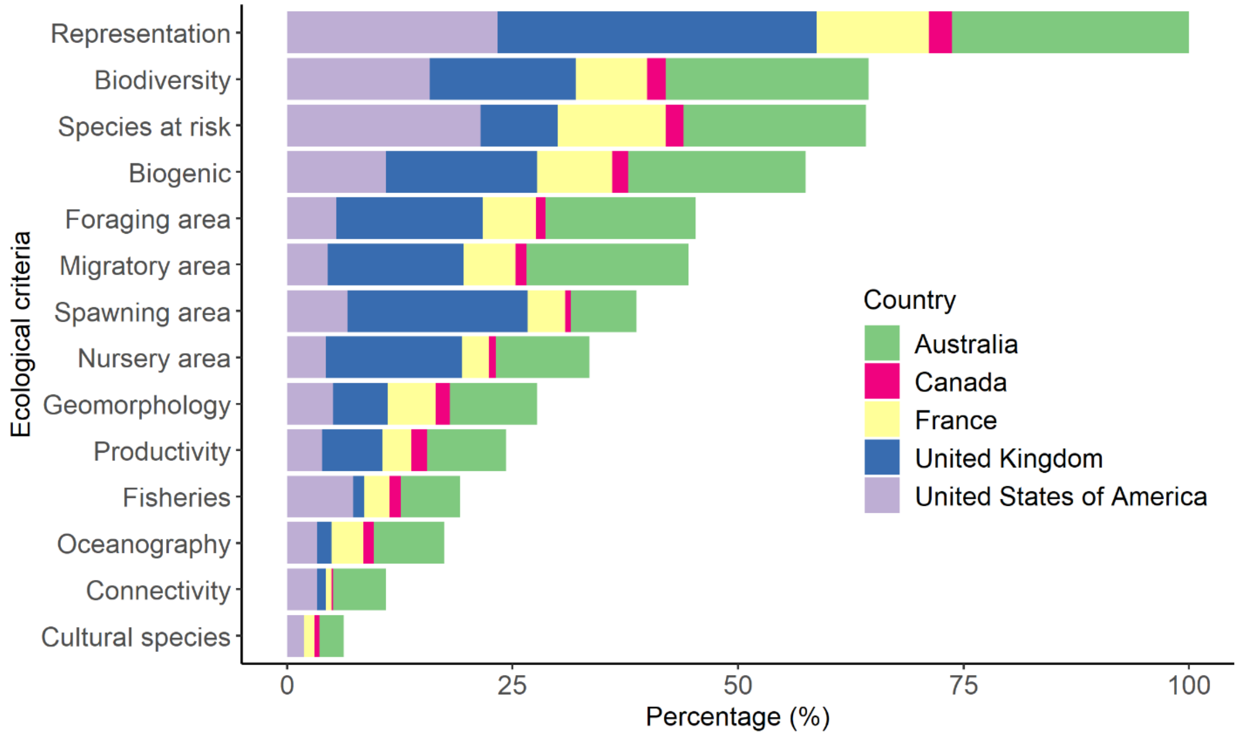

Figure 2.6: Use of 14 ecological criteria in the design of 746 marine protected areas in Australia, Canada, France, United Kingdom and the United States of America (California and Hawaii only).

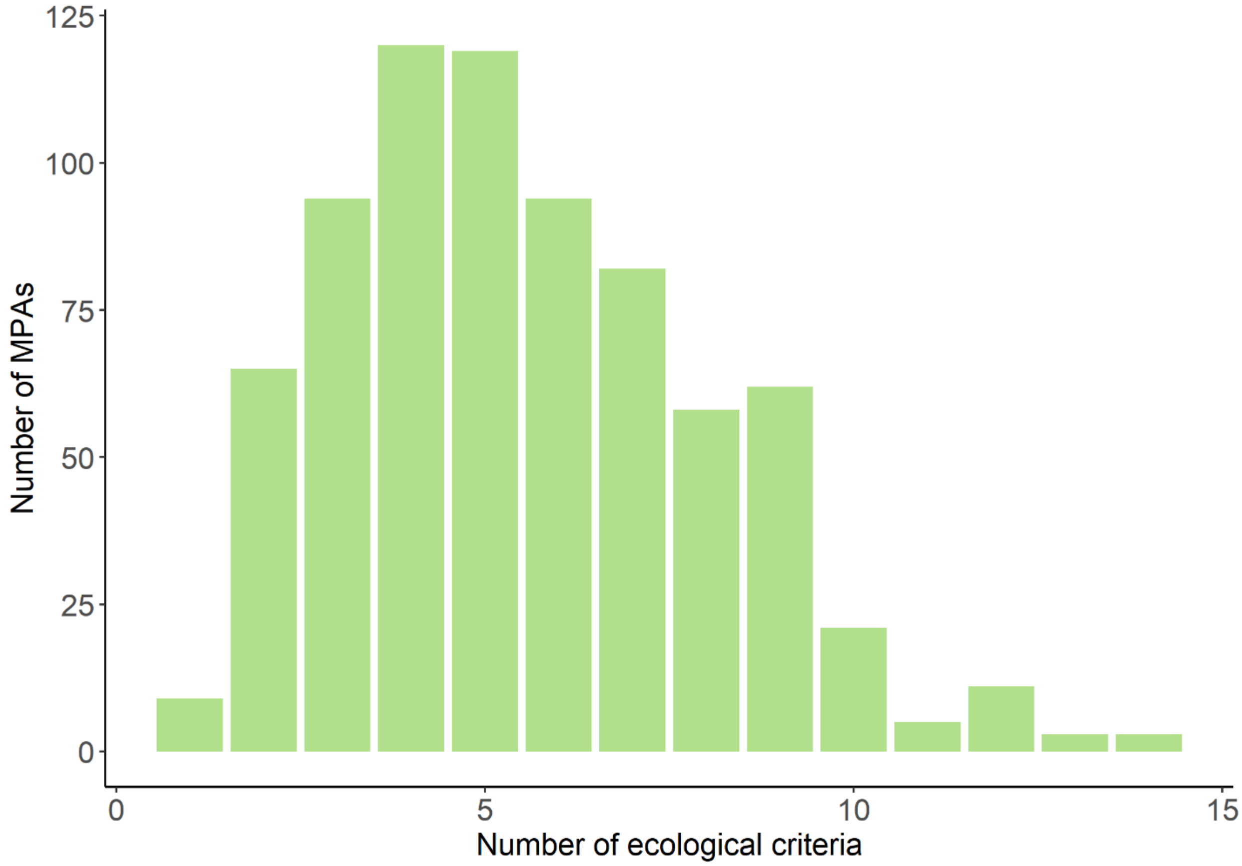

Figure 2.7: Number of ecological criteria considered in the designation of 746 marine protected areas (MPAs) in Australia, Canada, France, United Kingdom, California and Hawaii. Ecological criteria were classified into 14 categories: representative features, areas of high productivity, areas of high biodiversity, biogenic habitats, nursery areas, foraging areas, spawning areas, migratory areas, species at risk, fisheries, complex or unique geomorphology, unique or rare oceanography, culturally important species, and connectivity. Refer to Figure 2.6 for details on the use of each ecological criteria.

Connectivity was used as an ecological criterion in 11% of MPAs. There has been an increasing number of designations that considered connectivity over time, particularly after 2007, closely mirroring the trend seen in the scientific literature (Figure 2.3, Table 2.2). This is likely related to the development of the strategic plan to “halt the loss of biodiversity” by 2010 at the 6th Convention of Parties of the CBD (CBD 2002). The frequency of designations that consider connectivity remained high (>20 every 5 years) as 2020 approaches, presumably as countries attempt to reach the Aichi Biodiversity targets.

Of the MPAs that considered connectivity, 70.7% were for state marine conservation areas (SMCA) or reserves (SMR) in California and CMRs in Australia (Table 2.2). This pattern indicates substantial geographic bias and significant differences in conservation planning and prioritization among countries. These MPAs were all part of MPAn we identified (5 in Australia and 2 in California) suggesting that MPAs designed to be part of networks are more likely to consider connectivity. Of the 9 MPAn, 8 discussed connectivity as part of their network strategy. However, empirical evidence to support that these networks are more than a collection of MPAs was not provided. Additionally, quantitative conservation objectives that address connectivity for focal species at relevant spatial and temporal scales were not stated.

Table 2.1: Number and total marine area (km^2) of marine protected areas (MPAs) and MPA networks analyzed per country

Country	**Total Marine Area (km^2)**	**Number of MPAs**	**Number of MPA networks**
Canada	184503	19	0
United States of America	1538429	174	2
Australia	3193193	196	5
United Kingdom	114001	265	1
France	42955	91	1

Table 2.2: Types and years of designation for marine protected areas that included connectivity (USA = United States of America (California and Hawaii only), UK = United Kingdom, MPA = marine protected area).

Type of MPA	Year of designation	Country	Number of MPAs
Aquatic Reserve	1998	Australia	1
Area of Interest	2017	Canada	1
Commonwealth Marine Reserve	1999	Australia	1
Commonwealth Marine Reserve	2007	Australia	13
Commonwealth Marine Reserve	2013	Australia	24
Marine Conservation Zone	2013	UK	1
Marine Conservation Zone	2016	UK	3
Marine National Monument	2006	USA	1
Marine Park	1990	Australia	1
Marine Park	2005	Australia	2
Marine Park	2016	Australia	2
Nation Wildlife Refuge	1972	USA	1
National Marine Sanctuary	1992	USA	1
National Wildlife Refuge	1972	USA	1
National Wildlife Refuge	1988	USA	1
Nature Conservation Marine Protected Area	2014	UK	2
No take zone	2008	UK	1
Parc National	1963	France	1
Parc National	2012	France	1
Parc Naturel Marin	2011	France	1
Parc Naturel Marin	2012	France	1
Parc Naturel Marin	2016	France	1
State Marine Conservation Area	2007	USA	2
State Marine Conservation Area	2010	USA	2
State Marine Conservation Area	2012	USA	5
State Marine Reserve	2007	USA	3
State Marine Reserve	2010	USA	7
State Marine Reserve	2012	USA	1

Table 2.3: Examples of population connectivity metrics used in the management literature

Connectivity metric	Example description	Example MPA	Category of MPA
Habitat linkage	Provides linkage to other similar habitats	Runswick Bay, England	Marine Conservation Zone
Larval exchange	Site protected for its role in larval exchange with other marine habitats	San Elijo Lagoon, California, USA	State Marine Conservation Area
Retention	Larval retention zone of regional importance for many fish and invertebrate species	Point Reyes, California, USA	State Marine Reserve
Source	Area considered to be a larval source	Big River Estuary, California, USA	State Marine Conservation Area
Spillover	Increase supply of large adult and larval fish that can disperse to other areas for fisheries harvest outside MPA	Asilomar, California, USA	State Marine Reserve
Stepping stone	An important biological stepping stone facilitating the transport of biological material	Cook Island, Australia	Aquatic Reserve

2.5 Methods and metrics used to incorporate connectivity into MPA design

There is no scientific consensus on the most appropriate method to measure connectivity or on the metrics to include in the design process of MPAs. Four methods of measuring connectivity were identified by Bryan-Brown et al. (2017): modelling, tagging, genetics and simple observation. Modelling approaches require complex and specific input, such as fecundity or survival, to calculate metrics such as local retention and evaluate population persistence in MPAn (Burgess et al. 2012). Genetic approaches are expensive and time-consuming, but provide detailed metrics of genetic structure and diversity of metapopulations on scales of 1 km – 100 km (Beltrán et al. 2017). Both these methods rely on data that may not be available for many MPAn designs or post-hoc evaluations carried out by practitioners.

Depending on the method used to collect connectivity data, various metrics can be used to elucidate connectivity patterns. These metrics can be based on genetics, network analysis, parentage analysis, gradients in biomass and morphometrics, among others (Bode et al. 2012, Schill et al. 2015, Buchholz-Sørensen and Vella 2016, Williamson et al. 2016, Teschima et al. 2016). Some of these metrics can only be calculated using certain approaches (e.g. genetic methods to calculate genetic diversity, or connectivity matrices to calculate network metrics such as betweenness centrality). Metrics can also be calculated from proximity of habitats (Euclidean distance) or inferring source populations based on circulation patterns and residence times. Metrics such as local retention, betweenness centrality and outflow are particularly useful to incorporate in MPA design (Burgess et al. 2014, Magris et al. 2018). Local retention, the proportion of reproductive output that recruits back in the donor population, provides details on replacement and therefore persistence of a population. However, Burgess et al. (2014) identified that self-persistence, the proportion of total recruitment to a population that was produced at that population is often used instead, although it provides no information on persistence.

In the scientific literature, demographic connectivity was studied most often, followed closely by genetic connectivity (Figure 2.8). This is largely different than efforts in the management literature (Table 2.3), where landscape connectivity, such as habitat connections, was used most frequently, followed closely by demographic measures (Figure 2.8). Genetic measures were discussed in the management plan of only three MPAs (3.8%; Figure 2.8). Recommendations to overcome these differences are discussed in section 2.6. Below we summarize the approaches used by scientists and managers, respectively, to measure and apply connectivity.

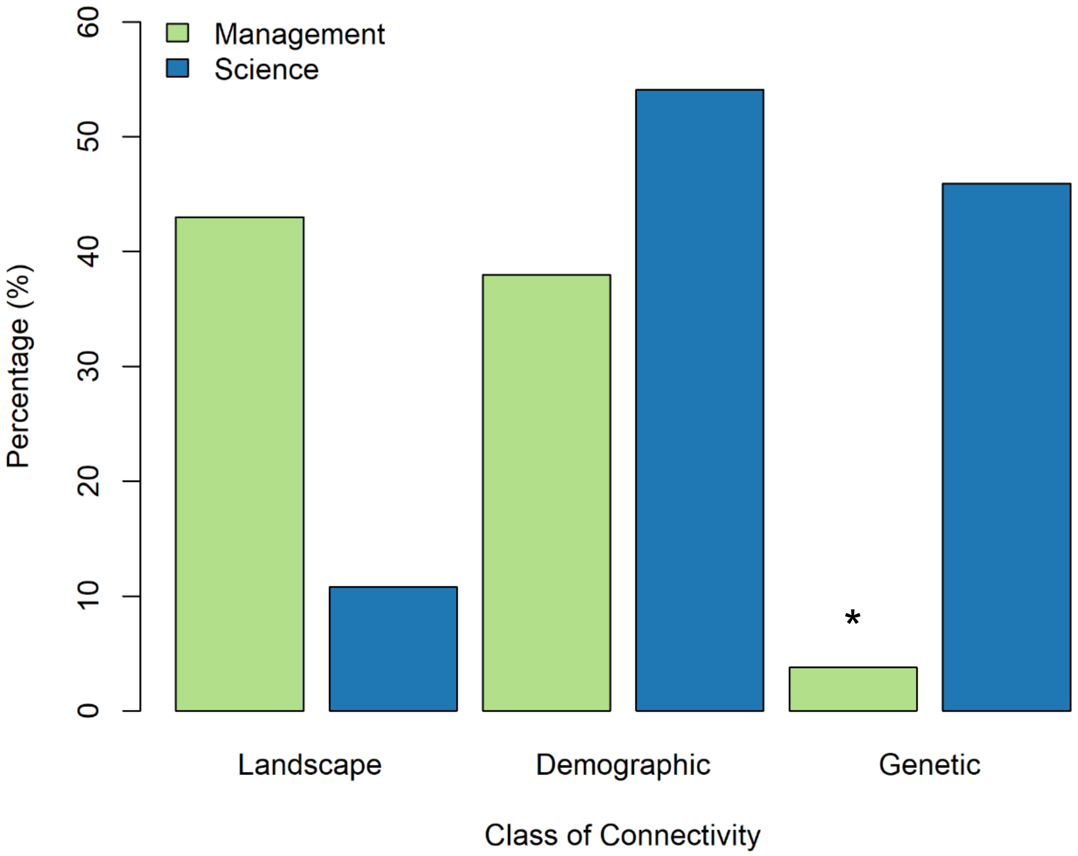

Figure 2.8: Class of connectivity used in the scientific literature (*n*=148) and management plans (*n*=82). Note that interdisciplinary studies may have considered more than one class of connectivity. *Genetic connectivity in the management literature was discussed only as a summary of known information for that region.

2.5.1 Demographic approaches

In the scientific literature, individual-based modelling approaches yielding dispersal trajectories, connectivity matrices (i.e. source distribution matrix) and dispersal kernels were commonly used (Rossi et al. 2014, Puckett and Eggleston 2016, Ross et al. 2017, Storlazzi et al. 2017). Some studies tailored metrics to taxa with different spawning and larval traits and further combined them in a multi-species approach (Holstein et al. 2014, Schill et al. 2015). Fifteen studies used tagging methods to calculate connectivity metrics (six with electronic tags and nine with natural passive tags), 13 for fish, one for molluscs and one for arthropods. Natural or artificial markers were used to delineate natal origin of captured or recaptured larvae, juveniles and adults in existing MPAs (Di Franco et al. 2012b, Gomes et al. 2016, Lazartigues et al. 2016), whereas electronic tags were used to track movement of adults within and among MPAs with acoustic telemetry being particularly useful for large predators (Espinoza et al. 2015, Ponchon et al. 2017).

In the management literature, demographic connectivity was identified through stepping stones, sources, retention zones and areas that provide spillover to adjacent protected or unprotected areas (Table 2.3). The Big River Estuary, Ten Mile Estuary and Navarro River Estuary SMCA's in California and the North-west Orkney and Turbot Bank nature conservation marine protected area (NCMPA's) in the UK were identified as larval sources. The Asilomar SMR, Calanques National Park, Golfe du Lion Natural Marine Park, Fylde marine conservation zone (MCZ) and Lamlash Bay no-take zone benefit adjacent fished areas through spillover of adults.

2.5.2 Landscape or seascape approaches

In the scientific literature, habitat modelling was used in scenarios with limited data on spatial distribution that can still provide some information on habitat linkages to managers (Anadón et al. 2011, Engelhard et al. 2017). For example, in the Baltic Sea, analysis of ecological coherence (representation and connectivity) using landscape measures was used to evaluate existing MPAn in areas where modelling or genetic data were not available (Sundblad et al. 2011, Jacobi et al. 2012). Landscape surrogates, such as patterns of reproductive output or the protection of high-density and extensive habitat provided details on larval subsidy when empirical evidence was limited (Shackell et al. 2013, Schmiing et al. 2017), and was proposed to increase fishery harvests (Bode et al. 2012).

In the management literature, landscape connectivity often related to habitat linkages. For the 5 networks of CMR and the Coral Sea CMR in Australia that cover the offshore regions, management plans discussed connecting habitat to coastal Marine Parks (Director of National Parks 2013, 2017a, 2017b, 2017c, 2017d, 2017e). Similarly, the

Western Channel MCZ was deemed important for connecting both offshore MPAs within the UK and to MPAs in France's exclusive economic zone (JNCC 2016a). The Hartland Point to Tintagel MCZ is considered critical for connectivity of habitats in the area, contributing to the protection of large intertidal habitats (JNCC 2016b).

2.5.3 Genetic approaches

Genetic methods for measuring connectivity have become increasingly more common since 2005 (Bryan-Brown et al. 2017). In the scientific literature, 68 of 148 studies utilized genetic approaches, 16.2% to inform the design of new MPAs and 95.6% in post hoc analyses for existing MPAs (8 studies had elements of design and post-hoc). Genetic metrics of isolation by distance, gene flow, population structure and haplotype diversity by genetic clustering have been used to discern connectivity patterns in MPAs (Matias et al. 2013, Wright et al. 2015, Sandoval-Castillo and Beheregaray 2015, Cossu et al. 2017, Holland et al. 2017). There are multiple types of genetic approaches that can address different scientific questions related to dispersal, source or origin of individuals and population structure (Manel et al. 2005). For example, many papers asserted that populations with measurable genetic structure at fine spatial scales (≤100 km) require small, moderately spaced MPAs to increase genetic connectivity through stepping stones (Shanks et al. 2003, McCook et al. 2010, Wright et al. 2015). Further details on the calculation of genetic connectivity metrics or an overview of genetic assignment methods can be found in (Manel et al. 2005, Selkoe et al. 2016, Bryan-Brown et al. 2017).

Genetic methods were not discussed with respect to design in the management literature. However, the management plans of three MPAs in Hawaii (Papahānaumokuākea Marine National Monument, Midway Atoll National Wildlife Refuge, and the Hawaiian Islands Humpback Whale National Marine Sanctuary) summarized genetic connectivity measurements as part of ongoing research, highlighting the advantages of a holistic view of the ecological structure in protecting resources in these areas (*Papahānaumokuākea Marine National Monument Management Plan* 2008, Chow et al. 2015). For the Humpback Whale National Marine Sanctuary, a summary of completed connectivity research suggests that species are well-connected between Ni'ihau, Kaua'i and the Northwestern Hawaiian Islands (Toonen et al. 2011).

2.5.4 Connectivity surrogates

In cases where quantitative approaches are not feasible, rules of thumb can be used instead; however, these are less reliable than the approaches discussed above. These rules may be informed by ecological life history characteristics, such as planktonic larval duration of focal species, and environmental characteristics, such as magnitude and direction of currents or temperature (Burt et al. 2014, D'Aloia et al. 2017, Smith and Metaxas 2018, but see Bode et al. 2016). Oftentimes, surrogates for connectivity are used to determine size and spacing of reserves, stepping stones and clustering (Airamé et al. 2003, Moffitt et al. 2011). However, Bode et al. (2016) suggest that using quantitative rules of thumb, ranking habitat patches and using subsets of data (e.g. self-recruiting proportion) are inadequate methods for incorporating connectivity into MPA design. Since these approaches measure an explicit demographic process, they require a post-hoc assessment to evaluate persistence (e.g. population viability analysis) (Bode et al. 2016).

Rules of thumb should not be used in place of empirical or derived measures of connectivity because they rarely elucidate species-specific patterns or represent the entire process of connectivity. The process of connectivity comprises various ecological events including reproductive output, dispersal, settlement, post-settlement survival (recruitment) and reproduction (reproductive population connectivity) (Pineda et al. 2007). Species-specific differences in the characteristics that are incorporated into rules of thumb (e.g. pelagic duration, home range, and reproductive timing) may prevent the application of these rules at the network scale because size and spacing guidelines may produce contrasting results for different species. Lastly, most rules of thumb to guide size and spacing of MPAs have been developed for well-studied taxa such as fish and coral reef ecosystems, respectively, and practitioners should exercise caution when considering these guidelines in ecosystems with different spatial structures (e.g. temperate or polar systems).

2.5.5 Combining approaches

All approaches that quantify connectivity have limitations. For example, biophysical models are limited in resolution and scale because of computational constraints. It is difficult to select a scale that is both accurate in representing dispersal dynamics and computationally efficient, because the physical processes affecting larval transport vary from large- (e.g. gyre movement) to small-scale processes (e.g. eddies). Genetic approaches, more specifically assignment tests, assume that all potential source populations are sampled and in Hardy-Weinberg equilibrium (Manel et al. 2005). Tagging methods have only been applied to larger organisms, mainly fish. Whenever connectivity is estimated, empirical data are needed to test the assumptions of models and validate their outputs. A robust assessment of connectivity should compare outcomes from multiple metrics and approaches. To address this, cross-validating studies using multiple methods to measure connectivity patterns have been proposed for a single system (Palumbi 2003, McCook et al. 2009).

2.6 Recommendations for incorporating connectivity in the design of MPAs

The scientific literature contains numerous suggestions on how to incorporate population connectivity into the design and adaptive management of specific MPAs and MPAn. There are examples of MPAs implementing these suggestions in the design and post-hoc evaluations of management decisions. The inclusion and prioritization of connectivity in the design of MPAs depends on conservation objectives but is particularly relevant for MPAn. Conservation objectives for which connectivity is important include biodiversity conservation and sustainability, population persistence, resilience, and fisheries management. Applying an ecosystem-based management approach is particularly important for species that use different ecosystems throughout their life cycle. Many studies promoted connectivity as a means for achieving demographic persistence through MPAs and MPAns (Margules and Pressey 2000, Sala et al. 2002, Botsford et al. 2009, Bode et al. 2016), particularly in the face of climate change (Magris et al. 2014).

Current levels of area, number, and protection level of MPAs may be insufficient to ensure connectivity. Priority sites for future MPA designation should be informed by data on individual passive and active dispersal that ensure connectivity and should attempt to improve persistence of populations or species that are protected by MPAs. In certain cases, additional MPAs will need to be placed in areas recognized as being important for protecting genetic diversity, maintaining health of spawning stocks and creating stepping stones between existing MPAs (Pujolar et al. 2013, Crochelet et al. 2016, Zeng et al. 2017). Additionally, some existing MPAn may not be optimally sited initially for promoting or ensuring significant ecological connections among populations (Froukh and Kochzius 2007, Guizien et al. 2012, Feng et al. 2016, Engelhard et al. 2017). Therefore, changes to current MPAn such as re-zoning, relocating or protecting adjacent habitats, have been proposed to improve connectivity (Guizien et al. 2012, Bors et al. 2012, Nakajima et al. 2017).

Here, we provide four recommendations on the incorporation of connectivity in the design of MPA(n).

2.6.1 Determine whether to prioritize connectivity as an ecological criterion

Connectivity should always be *considered* in the design of a MPA or MPAn but may not always be *implemented* due to logistical and data restraints or because its relative contribution to the effectiveness of the design may be low relative to other ecological or socio-economic criteria. Therefore, the first step is determining *whether* connectivity should be incorporated as a conservation feature. For certain habitats, species and metapopulation structures, connectivity should be prioritized. For example, landscape connections and fragmented habitats may depend on connectivity to maintain persistence by immigration to locally extinct or declining patches. Puckett and Eggleston (2016) found that a network of no-harvest oyster reserves in North Carolina was not self-persistent due to limited local retention and inter-reserve connectivity. Ensuring connectivity of threatened species with a mobile life history stage, whether larval, juvenile, or adult, is imperative for recovery, persistence of ontogenetic migrations, ecosystem connections, and fisheries. Populations exhibiting population genetic structure through subpopulations or dispersal barriers also benefit from connectivity considerations. For example, understanding subpopulation connections can allow for the prioritization of local connectivity of genetically similar populations. Froukh and Kochzius (2007) suggested that for the Fourline wrasse (*Larabicus quadrilineatus*) in the Gulf of Aqaba, the northern and southern subpopulations should be managed as two separate stocks.

There are also cases where the consideration of connectivity may be less important but depends on the conservation objective. In most cases, a feature that is only found in a single area or population would not need to be connected to adjacent areas. For example, the objective of the Basin Head MPA in New Brunswick, Canada, is to protect the asexual reproductive form of Irish moss, only found in that one area, that relies on the byssal threads of mussels as a substrate for attachment (DFO 2011). Therefore, the protection of this species depends on the maintenance of mussel beds of *Mytilus edulis* in the area, which has different dispersal and reproductive characteristics. Connectivity should be actively minimized to avoid the spread of invasive species and pollutants, but there are multiple ways of meeting this objective. In a port with a large number of invasive species or area with high agricultural runoff, one approach might be to isolate these areas, by placing MPAs far away. Alternatively, protecting healthy ecosystems nearby is a different strategy and may combat negative connectivity vectors (e.g. by outcompeting invasive species).

Alongside other important aspects of design, such as size, habitat quality, and level of protection, connectivity can increase effectiveness of MPAs. Magris et al. (2018) analyzed data from 288 Mediterranean fish species with different ranges and supported that species, particularly those with small ranges, benefited from the integration of representation and connectivity. When comparing connectivity and habitat quality, Berglund et al. (2012) argued that connectivity should be prioritized over habitat extent and quality; this suggestion is directly contradicted by Cabral et al. (2016), who argued that siting MPAs using connectivity metrics (source, sink, centrality) rarely produced optimal results over coupling habitat extent and quality, and suggested that habitat characteristics should be prioritized in spatial planning. However, it is not beneficial necessarily to prioritize these two ecological measures relative to one another because both are required to ensure metapopulation persistence. It is important to note that connectivity considerations should not replace the use of other ecological indicators, but rather complement them (Magris et al. 2018).

The importance of incorporating connectivity in MPA design highlights the need for tools that can be used by managers to evaluate the role of connectivity in marine spatial planning. White et al. (2014b) suggested an independent assessment to deduce the improvement gained by incorporating scientific knowledge on connectivity patterns into MPA design, and new tools becoming accessible to managers may prove useful. The R toolbox ‘best MPA’ aims to explore alternative MPA network designs and assess trade-offs of different ecological decisions (Daigle et al. 2015). The widely used spatial planning tool, Marxan, also allows for connectivity to be incorporated as a discrete feature or by replacing the boundary length modifier with connectivity values. Connectivity data can also be imported into Zonation, another spatial planning tool, to optimize for connections through corridors or apply penalties based on boundary lengths (Di Minin et al. 2014). A newly developed tool, Marxan Connect, provides a graphical user interface to incorporate connectivity matrices and landscape connectivity data into Marxan (http://marxanconnect.ca/). Simpler tools, such as a decision tree, can allow managers to incorporate size and spacing into MPAn planning, if data on connectivity are limited (Burt et al. 2014, D’Aloia et al. 2017, Smith and Metaxas 2018) (See section 2.8.1.3 for more information on applying connectivity data into MPA design using spatial planning tools).

While there is clear evidence to support that connectivity in some cases improves the efficiency of designing MPAn (Magris et al. 2018), we acknowledge the current challenges and setbacks that may prevent its inclusion such as: data unavailability, competing social and economic goals, and time and funding constraints. Nonetheless, assuming connectivity objectives are met incidentally by inflating representation targets should only be considered as a last resort. Spatial planning tools are widely utilized, and their algorithms are designed to meet area-based targets and, therefore, do not select for well-connected areas, even when the ‘clumping’ factor is increased. Including landscape metrics of least cost path or Euclidean distance, which do not require any additional ecological data, can provide useful information about the proximity of populations to one another.

2.6.2 Identify the role of a MPA in supporting connectivity

When incorporating connectivity into the design of MPAn, it is essential to identify the role that each MPA plays in supporting connectivity. For example, the existence of source and self-replenishing populations enhance connectivity and persistence of a MPAn, whereas other MPAs in a network may be stepping stones or corridors that connect widely distributed species. In post-hoc connectivity evaluations of existing networks, MPAs containing these source populations, self-replenishing populations and central populations are often considered essential to the network (Christie et al. 2010b, Berumen et al. 2012, Pusack et al. 2014, Gomes et al. 2016, Jahnke et al. 2017, Magris et al. 2018).

Transport of individuals across dispersal barriers can be facilitated by centrally located MPAs, increasing the efficacy of the latter (e.g. Ross et al. 2017). However, centrality is not always the best connectivity metric to optimize. Burgess et al. (2014) proposed that optimizing for local retention and therefore persistence is generally more advantageous. For example, the network of Mediterranean MPAs is not fully connected for the dusky grouper (*E. marginatus*), but single MPAs with high betweenness centrality values may be important for connectivity of the entire system (Andrello et al. 2013). Therefore, considering centrality measures is important for identifying connectivity hotspots, but other metrics are better suited for decisions on the scale of the network.

Incorporating connectivity need not only provide benefits to the network, but also to surrounding unprotected areas, for example in fisheries, through export and overall population maintenance and growth. A passive drifter experiment at Riley's Hump in the Tortugas Ecological Reserve South indicated that the MPA may be a source of recruits for mutton snapper to the Florida Keys and southeast Florida and, therefore, may be acting as a fisheries reserve (Domeier 2004). Export to surrounding areas depends greatly on the location and size of a single MPA. *E. marginatus, Pagellus erythrinus* and *Scorpaena porcus* benefit from the protection of the Medes Island MPA, which encompasses a known spawning area for these species (López-Sanz et al. 2011).

2.6.3 Identify appropriate spatial and temporal scales

If connectivity is to be implemented in the design of a MPAn, management units should be scaled based on realistic connectivity patterns. For example, white seabream (*Diplodus sargus*) and dusky grouper (*E. marginatus*) have two separate subpopulations in the area surrounding Sicily, concordant with oceanographic currents, suggesting that management units should represent these geographic differences (González-Wangüemert et al. 2012, Buchholz-Sørensen and Vella 2016). In the western North Pacific, two genetic clusters of the neon damselfish (*Pomacentrus coelestis*) with minimal gene flow between them have been identified, possibly requiring separate MPAn for their management (Liu et al. 2011).

Dispersal is a key factor in determining the spatial scale of the management unit and varies among target species. Species with short dispersal distances and low representation in networks may be more vulnerable to stressors, whereas species with long-range dispersal, such as grey reef sharks, may require larger protection areas, and still spend substantial periods in unprotected areas (White et al. 2017, Gallego et al. 2017). On the west coast of North America, the brown rockfish, which exhibits high dispersal potential, was found to have low realized dispersal based on genetic divergence. It was recommended that a regional, rather than coast-wide scale be considered for MPAn design and that MPAs should be distributed with close spacing across the entire species range as a buffer against environmental variability and fragmentation (Buonaccorsi et al. 2005).

The relevant spatial scale for management should be determined on a case-by-case basis, depending on the potential and, if known, realized dispersal of focal species on ecologically relevant scales (10s -1000s kms). Miyake et al. (2011) suggested measuring dispersal from each larval source to adequately understand the variance in dispersal potential and suggested that in coastal systems a scale of 80 km is necessary to capture larval dispersal. In Central America, genetic analyses identified connectivity at spatial scales beyond international boundaries for spiny lobster; recruitment to the Mesoamerican Barrier Reef likely occurs from source populations outside national boundaries (Truelove et al. 2015a). Considering spatial scales that encapsulate multiple habitats and ecosystems is essential for protecting species that move between habitats (Weeks 2017).

Patterns of connectivity may also vary over time, highlighting the need for measurements at local spatial scales over multi-year time scales. For example, connectivity of reef fish between nodes in a MPAn varied by species and over time in Kimbe Bay, Papua New Guinea (Berumen et al. 2012). In California, the Garibaldi damselfish (*Hypsypops rubicundus)* exhibited a source-sink metapopulation on a bi-weekly time scale, but the pattern was not maintained at interannual time scales (Cook et al. 2014). Therefore, managers should caution against applying conservation strategies based on connectivity measures from a single point in time as they may not capture the full variation in dispersal patterns (Berumen et al. 2012, Soria et al. 2014, Pusack et al. 2014).

2.6.4 Improve regional knowledge of patterns of connectivity

Increasing the taxonomic and geographic resolution of patterns in connectivity is needed for both scientific and management applications. For example, understanding the dispersal patterns of the white sea bream using otolith chemistry in Mediterranean rocky reefs led to a body of work on the connectivity of this important coastal species (Di Franco et al. 2012b). This knowledge, in combination with connectivity patterns from other fish species, can be used to determine optimal size and spacing constraints to maintain connectivity in a MPAn. In Fijian reefs, large differences in population connectivity among species highlighted the need for management with more than a single unit (Drew and Barber 2012). Coupled biophysical models have been used to quantify larval dispersal and determine potential population connectivity in shallow and coastal waters (Treml et al. 2012, Guizien et al. 2012), but this approach is not feasible in the deep sea. Hilário et al. (2015) compiled data on pelagic larval duration as an indicator for dispersal distance for 93 species at 2 depth classes (eurybathic and deep) and proposed using a larval duration of 69 days to ensure a minimum dispersal for 75% of measured species. Such metrics use the best available knowledge to inform connectivity for a broad group of taxa and can be updated as more information becomes available.

2.7 Challenges and limitations of this review

The level of documentation in the management literature limited our analysis of ecological criteria. A management plan includes selection criteria deemed important for a MPA, typically developed during a consultation process. If connectivity had not been included in a management plan, we were unable to distinguish whether this was because it had not been deemed a priority or was not considered at all. Not including connectivity could be because of lack of data, limited understanding of the process, or limited resources (perhaps supported by a value of information analysis).

For practical reasons, we restricted the scope of our study to regions with advanced systematic conservation planning, likely inflating the percentage of MPAs that consider connectivity. If we had included all MPAs worldwide, this percentage would most likely be much lower. There were also ample examples in the scientific literature where connectivity for a particular MPAn was evaluated, even when connectivity was not included as an original design element.

In the design of many MPAs, there were insufficient data to make inferences about connectivity. Assessments of metapopulation connectivity over large spatial scales are essential to both establishing new MPAs and evaluating existing ones, but this information is lacking for most species (Fenberg et al. 2012). Our understanding of connectivity continues to expand, and significant advancements have been made since the 2000s. We have progressed from the need for a better understanding of the spatial and temporal scale of connectivity (Kritzer and Sale 2004) to measuring connectivity for different taxa over broad areas and time scales (Cook et al. 2014). As the field continues to progress, frameworks should be optimized to introduce new information at each step in the MPA design process and in post-hoc evaluations of existing designs.

2.8 Future approaches for prioritizing connectivity

2.8.1 Framework for including connectivity in MPA design

As new MPAs and MPAn are designated, evaluating their efficacy and determining whether they achieve conservation objectives is essential. We have identified large regional differences in the planning process and consideration of connectivity. We have also identified a distinct difference in the class of connectivity data (landscape, demographic or genetic) used by scientists and managers. The accessibility of connectivity data and the language in which it is communicated to managers by scientists poses a source of disconnect between these two sectors. Therefore, future planning processes should attempt to rectify these differences and target regional improvements based on current progress, data availability and resources. For example, the GBR has advanced MPAn design strategies and tools available for adaptive management. In contrast, Canada and many other countries with lower data availability, may be limited to less sophisticated tools, such as decision trees (Smith and Metaxas 2018). Matching the appropriate tool with data availability for regional assessments, as well as improving the accessibility of data and tools to managers, can help bridge the identified gap between science and management. Here, we propose a framework to implement connectivity during the planning phase and when evaluating the connectivity of existing MPAs and MPAn that attempts to bridge this gap (Figure 2.9). Our framework clearly identifies the information that needs to be communicated and the roles of the two players at each stage. There is no distinct entry point to the proposed framework, but in most cases, it will naturally begin with the development of conservation objectives for a MPA/MPAn.

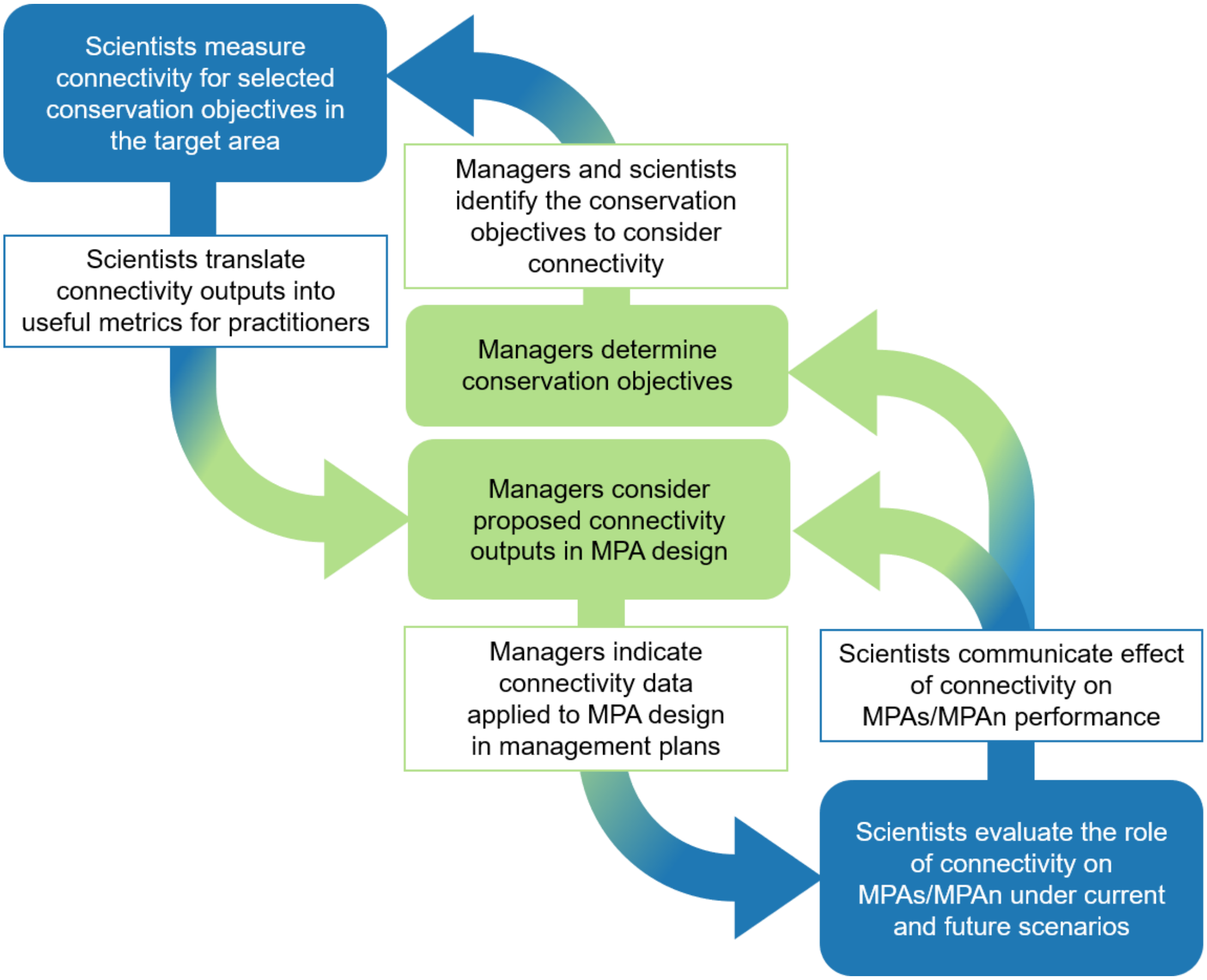

Figure 2.9: Framework outlining steps in the design and evaluation of marine protected areas (MPAs) and networks of MPAs (MPAn) where connectivity can be incorporated. Blue boxes indicate steps where scientific research and advice are pertinent and green boxes indicate steps which rely on action by practitioners. Arrows indicate the facilitation of usable information between science and management sectors. See section 7.1 for a detailed description of the framework.

2.8.1.1 Determine MPA/MPAn conservation objectives

For scientists to provide meaningful metrics of connectivity, managers must first identify conservation objectives (Figure 2.9); these are typically representation-based, ranging from the protection of habitats (e.g. biogenic, unique, pristine) to species (e.g. spawning, foraging, nursery grounds), and are informed by data on, but not limited to, the

14 ecological criteria discussed above. Managers and scientists should then collaborate to identify which conservation objectives should consider connectivity and be guided by the 4 recommendations discussed above to incorporate connectivity into the design of MPAs (section 2.6).

2.8.1.2 Evaluate and measure connectivity in the target area

Once the relevant conservation objectives and target areas have been identified, scientists can focus data collection that will allow them to calculate relevant metrics of connectivity (Figure 2.9). For example, if the objective is to protect a source population, then considerations of larval output, dispersal and home range will be useful in determining the appropriate size and spacing of planned MPAs. Alternatively, if the objective is to provide stepping stones among MPAs, then network theory centrality metrics are one approach to derive meaningful metrics of connectivity.

Scientists will collect a suite of measurements of biological (ecological and genetic), physical, and geological variables. Habitat and species distributions (whether empirical measurements or suitable distribution modelling) can form the baseline to discern connections among populations and within the landscape. In turn, these data can be acquired from surveys, allowing for the calculation of landscape metrics (e.g. Euclidean distance or least cost path). In most cases, more specific data on the life history of species (e.g. pelagic duration, spawning time, larval behaviour) or more accurate location data allows for the calculation of more complex metrics. For example, tagging or taking tissue samples of individuals from multiple populations allows for the calculation of metrics such as home range, larval origin, or genetic analyses, respectively. With the addition of ocean circulation data (at relevant spatial scales) and physical models, flow, migration and probability connectivity matrices can be generated, and a suite of network theory metrics calculated (e.g. centrality, local retention).

2.8.1.3 Interpretation and consideration of connectivity outputs in MPA design

Accurate interpretation of connectivity data is key to implementation and requires close collaboration between scientists and managers (Figure 2.9). Scientists are responsible for interpreting connectivity data and translating connectivity outputs into useful metrics for practitioners. For example, dispersal distances provide information about the spatial scale of movement at a particular life stage (most commonly propagule dispersal) and can therefore inform size and spacing of MPAs. Managers can either make MPAs large enough to incorporate self-recruitment or space MPAs near enough to ensure dispersal between adjacent MPAs. Another common form of connectivity output data is a connectivity matrix. In a connectivity matrix (p_{ij}), columns are origins, rows are destinations and the entries represent the proportion of individuals in population *i* that originated in population *j* (Cowen et al. 2007, Burgess et al. 2014). Scientists can guide managers on how to use matrices in MPA design by communicating which metrics are useful for a particular conservation question. For example, if the objective of a MPA is to provide a hub or stepping stone that facilitates movement across an entire network, then a scientist could recommend the use of betweenness centrality. Populations that have a high betweenness centrality value have the highest number of shortest paths in a network (i.e. are centrally located). Once scientists outline how to apply connectivity data to MPAs design, managers can use this information to optimize MPA/MPAn design using decision support tools.

There is a wide range of decision support tools available to managers, including decision trees (Smith and Metaxas 2018), integrative frameworks (Magris et al. 2014, D'Aloia et al. 2017) and spatial planning tools (Watts et al. 2008, Anadón et al. 2011, Di Minin et al. 2014, Hanson et al. 2019, Daigle et al. 2020) that can optimize protected area design. When some approaches are not feasible because of data (un)availability, or analytical and computational costs, frameworks and decision trees can be used to incorporate practical connectivity metrics into MPA design. Magris et al. (2014) suggested a framework for developing quantitative objectives to integrate connectivity through conservation objectives based on data requirements and the complexity of analysis. To consider species with ontogenetic movements, a framework developed by

D'Aloia et al. (2017), that considers larval, juvenile and adult movement guides managers to determine where connectivity considerations are most important (e.g. adults with seasonal migrations), and which metrics and tools to use. In addition, Smith and Metaxas (2018) developed a decision tree for incorporating size and spacing guidelines into MPAn design based on larval dispersal, and juvenile and adult movement.

In cases where spatial or landscape data are available, a variety of decision support tools are available for managers for optimization of the arrangement of MPAs with multiple conservation objectives. Marxan is a reserve selection tool that balances cost with representation targets (Ardron et al. 2010), Marxan with Zones is a Marxan extension that allows users to incorporate different zones or protection levels into spatial planning (Watts et al. 2008), and Zonae Cogito is Marxan add-on used for data management and GIS visualization (Watts et al. 2011). Connectivity can be incorporated into Marxan as a conservation feature, or by using a connectivity matrix as a cost layer and tuning the boundary length modifier. Marxan Connect, a new software program, is another useful tool that derives connectivity metrics and translates them into quantitative conservation features or connectivity strength values (Daigle et al. 2020). Zonation is another reserve selection tool that balances biodiversity features, costs, and threats. It also has the capability to import connectivity data and apply boundary length penalties, and matrix or corridor connectivity (Di Minin et al. 2014). Prioritizr is a R package designed to create and solve conservation problems as mathematical optimization problems and can be used with a variety of exact algorithm solvers (e.g. heuristics or simulated annealing). Connectivity can be incorporated into prioritizr using penalties or constraints (Hanson et al. 2019) and using outputs from Marxan Connect. Once spatial planning tools have generated reserve solutions, and economic and social criteria are considered, practitioners are responsible for indicating within management plans (i) whether connectivity was considered in MPA design, (ii) included and (iii) the reasons for the decision, and (iv) the connectivity metrics used where relevant. This can allow scientists to evaluate the contribution of including (or not) connectivity in the performance and efficacy of MPAs and MPAn post-hoc.

2.8.1.4 Evaluate the connectivity of MPAs and MPAn

Connectivity of MPAs and MPAn must be evaluated by scientists to determine their efficacy, particularly in a rapidly changing climate and when MPAs are designated incrementally (Kininmonth et al. 2011, Magris et al. 2018; Figure 2.9). Assessing the connectivity of a designated network uses many of the same approaches used to inform the design of MPAs. To evaluate whether a MPA is meeting conservation objectives related to connectivity, scientists should consider the four recommendations outlined in section 2.6. To address high level conservation objectives at the network scale, additional approaches, such as population viability analysis or metapopulation growth rate can be used to evaluate persistence.

Where post-hoc evaluations of MPA effectiveness reveal that patterns of regional connectivity should be protected to meet conservation objectives, steps should be taken to improve management of these areas. Scientists are responsible for communicating the effect of connectivity on MPA/MPAn performance and making recommendations for future MPAs (Figure 2.9). Recommendations may include adding new MPAs or adjusting boundaries or zoning of existing MPAs. Managers need to evaluate this new information and decide whether to implement it; however, adjusting existing MPAs is challenging, particularly legislatively. Even when scientific case studies have identified areas where changes to current MPAs should be applied, our review did not find examples where scientific recommendations were used by practitioners.

The result of post-hoc evaluations of connectivity by scientists may also lead to the generation of new conservation objectives (e.g. protect ontogenetic migration of commercially important species in a target area over time). In this case, the steps of the framework should be followed again from the beginning.

2.8.2 Adaptive management: benefits of continuous feedback

Our framework identifies the steps and actors involved in the communication of information that is needed in the consideration of integrating connectivity in the design and management of MPAs and MPAn. The current gap between science and practice, in terms of connectivity, mirrors a similar challenge in the 1990s when managers were unaware of the tools for biodiversity conservation (e.g. reserve selection algorithms, gap analysis) available in the scientific literature (Prendergast et al. 1999). As available tools become more accessible to practitioners, it is presumed that connectivity will be incorporated into planning processes and post-hoc evaluations more frequently.

The Aichi biodiversity targets require immediate action from many countries and candidate areas for MPAs need to be identified and designated under the current level of information on all ecological criteria including connectivity. This underscores the importance of quantifying connectivity in newly designated networks after 2020. The proposed framework facilitates the feedback between managers and scientists to improve the application of connectivity data at local scales.

2.8.3 Future challenges

Integrating our understanding of connectivity over various spatial scales for a wide range of species with different ecological characteristics is a major challenge for conservation science (Magris et al. 2018), and will only be further complicated in a changing ocean that is threatening the functionality of current MPAs (Magris et al. 2014, Lagabrielle et al. 2014, Bruno et al. 2018). Networks of MPAs, when well-designed and with high levels of protection, can reduce biodiversity loss and safeguard important ecological processes to promote recovery (Roberts et al. 2018). In tropical and low-latitude areas, sea-surface temperature and oxygen concentration will exceed natural variability in 42% of 309 existing marine reserves, reducing the benefits of these MPAs to mitigate threats to marine biodiversity (Bruno et al. 2018). Species ranges, ecosystem functioning, reproduction, and spawning windows will likely change due to warming temperatures and increased concentrations of CO_2, and larvae, juveniles and adults will experience different and new environments (Chen et al. 2011, Pankhurst and Munday 2011, Nagelkerken and Connell 2015). These changes may affect connectivity patterns and will require adaptive management, and more explicit recommendations based on empirical studies by scientists, and actions by managers. As scientific information on connectivity develops, it should be made easily available to managers to ensure it can be applied rapidly and effectively.

Ensuring effective and well-connected MPAn will continue after 2020, as the current target of 10% will likely not meet the goals of MPAs intended by the CBD (Gaines et al. 2010, O'Leary et al. 2016) with a new target of > 30% having been proposed (IUCN 2014). Considering both representation and connectivity is likely the best conservation strategy for protecting the persistence of biodiversity (Magris et al. 2018).

Our review demonstrates that the current use of connectivity in MPA design is minimal and geographically biased. However, connectivity has been increasingly considered in MPA planning and should continue to do so with the development of useful tools. We suggest a framework that will promote the implementation of connectivity into the design of MPAs and help bridge the gap between scientific understanding and application by practitioners.

CHAPTER 3

COMPARING APPROACHES FOR ESTIMATING ECOLOGICAL CONNECTIVITY AT A LOCAL SCALE IN A MARINE SYSTEM[2]

3.1 Abstract

Connections among habitat patches through propagule dispersal are critical for designing effective networks of marine protected areas. To meet targets, managers need a diverse toolkit for translating patterns of connectivity to actionable metrics through specific size, spacing, and siting recommendations. Measuring ecological connectivity in the marine realm is particularly challenging because of water movement and the lack of distinct physical boundaries. Additionally, tracking most propagules is not logistically feasible. Here, we compare three approaches of increasing complexity for predicting potential ecological connectivity (measured as passive dispersal by ocean currents) of kelps and two resident invertebrates, the dominant macrograzer (*Strongylocentrotus droebachiensis*) and a destructive invasive epiphyte (*Membranipora membranacea*) among habitat patches in the NW Atlantic coast of Canada. The three approaches differ in the complexity of estimating ocean currents: current speed depth-averaged over time (1D); current velocity decomposed into along-shore and cross-shore components depth-averaged over time (2D); and spatially modelled current velocity derived from a 3D hydrodynamic model (3D). We found that the 1D approach was adequate for species with a short competent propagule duration (CPD), but that dispersal for the 2D and 3D approaches were most similar for mid-long CPD dispersers at the scale of management units, likely because they both account for the directionality of currents, whereas the 1D approach does not. This research helps bridge the gap between connectivity research and

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[2] Balbar, A. C., A. Metaxas, and Y. Wu. (in press.). Comparing approaches for estimating ecological connectivity at a local scale in a marine system. Marine Ecological Progress Series.

My coauthor Dr. Anna Metaxas supervised the development of the study design and analyses, and edited the manuscript. My coauthor Dr. Yongsheng Wu assisted with data analysis and edited the manuscript.

ocean management by demonstrating that the 2D approach requires lower data, time, and resources providing adequate outputs at the scale of management units.

3.2 Introduction

Marine protected areas (MPAs) are implemented globally to meet high-level objectives, such as maintaining persistence and promoting resilience of populations, species and communities (Chambers et al. 2019, Beger et al. 2022). Population connectivity, defined as the linkage of distinct populations mediated by the dispersal of propagules, juveniles, and adults (Pineda et al. 2007, Kool et al. 2013), is one ecological criterion used to site MPAs and can support these objectives, even in the face of climate change (Dakos et al. 2015, Carr et al. 2017, Chambers et al. 2019, Wilson et al. 2020). Identifying patterns of connectivity allows for the identification of source and sink populations across a wider region or metapopulation (Cowen and Sponaugle 2009, Kool et al. 2013). Despite the stated importance of connectivity, only 11% of MPAs considered connectivity as an ecological criterion in their design and 9.7 % of terrestrial protected areas are structurally connected (Balbar and Metaxas 2019, Ward et al. 2020), with geographic biases that mirror those identified in the scientific studies (Bryan-Brown et al. 2017). The post-2020 Convention on Biological Diversity framework proposes 30% of national land and waters to be designated as "well-connected systems" of MPAs by 2030 (CBD 2022). Managers will be challenged to include connectivity into the design of networks of MPAs because of a paucity of baseline data, models, and capacity.

In the marine environment, dispersal (the movement of organisms through their environment from a source to a destination site) of sessile, benthic invertebrates is realized by the earliest life history stages or propagules and is often employed as a proxy for connectivity (similarly to trees on land). The spatial and temporal scales over which propagules disperse depend on several physical (e.g. currents, proximity to coastline, bathymetry) and biological factors (e.g. timing of spawning, fecundity, pelagic duration, mortality, and behaviour) (Largier 2003, Levin 2006, Metaxas and Saunders 2009b, Daigle et al. 2014, D'Aloia et al. 2017). In particular, planktonic duration (PD) is a biological factor which correlates directly with dispersal distance (Shanks 2009).

Competent propagule duration (CPD) refers to the developmental period when a propagule has reached a developmental stage capable of recruiting to habitat and becoming sessile and its timing largely influences metapopulation persistence (Cecino and Treml 2021). In the marine realm, it is not feasible to track propagules because they are small, often occur in low concentrations, and the timing of release cannot be predicted accurately.

Operationalizing measurements of dispersal and connectivity in the design of MPAs requires a suite a tools (Lagabrielle et al. 2014). "Rules of thumb" are less resource intensive, more easily interpreted, and therefore easier to apply to decision making processes than more complex measures (Hilty et al. 2020). In the marine realm, the simplest rule of thumb estimates dispersal distance using a linear relationship between average ocean current speed and PD. This and other data-limited approaches have been proposed to inform size and spacing guidelines for networks of MPAs such as adult home range (Friesen et al. 2019), dispersal ability binned by species in different depth classes (intertidal, nearshore, offshore) and PD (Blackford et al. 2021), or dispersal based on important habitats for species (e.g. migration, nursery, mating) and average currents (Smith and Metaxas 2018). Biophysical modelling provides a more intense data-informed approach to estimate patterns of connectivity, coupling ocean circulation models with particle tracking, and is therefore considered the state-of-the-art approach for studying propagule dispersal (Treml et al. 2008, Schill et al. 2015, Briton et al. 2018, Lequeux et al. 2018, Cristiani et al. 2021). A Lagrangian approach can integrate several factors that influence dispersal, such as fecundity, small-scale variations in currents from wind, tides and topographic complexity, propagule mortality, and precise spawning time, but it is computationally expensive and requires specialized expertise. Consensus in outputs among multiple approaches for estimating connectivity increases the reliability and confidence in the predicted patterns of dispersal; however, outputs from multiple approaches are seldom compared [but see (Christie et al. 2010b, Jahnke et al. 2017)].

The Eastern Shore Islands (ESI) proposed MPA site along the Atlantic coast of Nova Scotia provides an excellent case study for using knowledge on connectivity to inform decision making. In the shallow subtidal zone, kelp beds dominated by two prostrate kelp species, *Laminaria digitata* and *Saccharina latissima*, form a prominent biogenic, complex three-dimensional habitat, providing protection and nursery grounds for fish and benthic invertebrates (Steneck et al. 2002, Graham 2004, Smale et al. 2013). Kelps reduce flow (Eckman et al. 1989) and increase food quality (Krumhansl and Scheibling 2011), supporting a large diversity of marine life, including economically important species (Smale et al. 2013). The green sea urchin, *Strongylocentrotus droebachiensis* is a key species in the dynamics of kelp bed ecosystems. Historically, dense fronts of *S. droebachiensis* grazed kelps, promoting two alternative stable states: kelp beds and urchin barrens (Scheibling et al. 1999, Filbee-Dexter and Scheibling 2017). Disease outbreaks of the pathogenic amoeba *Paramoeba invadens* significantly reduced sea urchin populations from the 1980's to early 2000's resulting in the return of the kelp bed stable state (Scheibling 1986, Feehan and Scheibling 2014, Buchwald et al. 2018). However, since the 1950s, the biomass of kelp beds has concurrently decreased by at least 85% at three long term study sites along the Atlantic coast of Nova Scotia, as a result, in large part, of the introduction of the invasive bryozoan species *Membranipora membranacea* (Watanabe et al. 2010, Filbee-Dexter et al. 2016). In the southwestern shore of Nova Scotia, regime shifts from luxuriant kelp beds to a new, turf-dominated benthos are increasing the vulnerability of coastal kelp ecosystems to other stressors (Kelly et al. 2011, Filbee-Dexter et al. 2016). It is imperative to prioritize planning of MPAs to protect high quality patches of kelp and the biological communities they support.

In this study, we estimate dispersal and infer ecological connectivity using three approaches of increasing complexity, and thus of increasing requirements for computational and human resources, for three species of ecological significance (laminarian kelps, *S. droebachiensis*, and *M. membranacea*) at a proposed MPA site in Nova Scotia, the ESI. The three approaches differ in terms of the specificity of ecological inputs as well as the number of spatial dimensions used to estimate ocean currents: current speed depth-averaged over time (in x; 1D); current velocity decomposed into along-shore and cross-shore components and depth-averaged over time (in x and y; 2D); and spatially modelled current velocity (in x, y, and z; 3D). For each species, we compare dispersal metrics (area, maximum dispersal distance, Jaccard index) among approaches, and of connectivity from the ESI to other potential future coastal MPAs in Nova Scotia.

We predict that the approaches will produce different estimates of dispersal area, but that the 2D and 3D approaches will be more similar to one another than with the 1D approach because they account for directionality of currents in the calculation of dispersal potential. We also predict that species with a mid-long CPD (*S. droebachiensis*, and *M. membranacea*) will have a substantially greater dispersal area, maximum dispersal distance, and number of connections to other potential future MPAs than the species with short CPD (laminarian kelps). Lastly, we evaluate the benefits and costs of applying each approach and provide guidance and tools for managers to determine which approach is best applied depending on the input data and resources available.

3.3 Methods

3.3.1 Estimating kelp distribution

We compiled data on the presence and absence of kelp habitat along the Eastern Shore of Nova Scotia, from the shoreline to a depth of 40 m between 2017 and 2020 (Figure B.1; $n = 492$). The lack of a surface canopy prevents the use of remote sensing (e.g., aerial surveys, Landsat) and requires in situ surveys. The data were from surveys with a drop-camera system done by Fisheries and Oceans Canada (DFO) in 2017 and 2019, as well as surveys done by snorkelling or with SCUBA in 2018 and 2020 (Appendix B.1). Data on the abundance of kelp habitat was collected as either presence/absence or percent cover. For modelling purposes, all data points were converted to presence (1) or absence (0) of kelp habitat. We optimized a classification random forest model to predict the distribution of suitable habitat for kelps using three ecological predictors: depth, presence of hard substrate and an index of relative wave exposure, and presence or absence of kelp habitat as the response variable (Appendix B.1).

3.3.2 Approaches for estimating dispersal

We considered CPD, fecundity, timing, and location of spawning as ecological inputs to generate taxon-specific estimates of dispersal (Table 3.1). We estimated the area over which propagules disperse, in km^2, from kelp patch centroids or survey-based start locations (Table B.2) using three approaches of increasing complexity and computational requirements. The approaches differed in ecological and oceanographic inputs.

Table 3.1: Life-history characteristics of the three species used in this study. CPD = competent planktonic propagule duration.

Species	**CPD (days)**	**Spawning period**	**Settlement period**	**Resources**
Laminarian kelps	0 - 2	October – December	October – December	(Chapman 1984)
Membranipora membranacea	14 - 28	July – September	Mid-July – September	(Saunders and Metaxas 2007, 2010)
Stronglyocentrotus droebachiensis	28 - 60	February – March	March - May	(Strathmann 1978, Himmelman 1978, Pearce and Scheibling 1991, Meidel and Scheibling 1998)

The first approach, 1D for one-dimensional, applies the simplest and most frequently used metric by managers for estimating dispersal distance. In the 1D approach, dispersal distance is estimated by multiplying depth-averaged, time-mean current speed by propagule duration (Shanks 2009). In this paper, we consider CPD, a period during which the developmental stage of a propagule is physiologically competent to readily settle onto the seafloor. In this 1D approach, two circular polygons are calculated: a larger one with a radius equal to the current speed multiplied by total propagule period; and a smaller one with a radius equal to the pre-competency period. To obtain the dispersal area during competency, we subtracted the pre-competency polygon from the one calculated for the total propagule period. For each taxon, we mapped these spatial polygons onto the coast of Nova Scotia centered at the release locations. We produced maps of in-water dispersal area only by subtracting the area of the polygon that intersected with land.

The second approach, 2D for two-dimensional, employs current velocity rather than speed. We obtained current velocity data from two acoustic doppler current profilers deployed in the ESI from 2018 to 2019 from DFO over periods that covered the spawning windows of the species of interest (Table 3.1); data from Ship Harbour were used for laminarian kelps, and data from Liscomb for *M. membranacea* and *S.*

droebachiensis (Table B.3). We produced a polygon that represents dispersal area for the three target species using the same distance relationship as the 1D approach combined with ellipse geometry using the following steps (Figure 3.1):

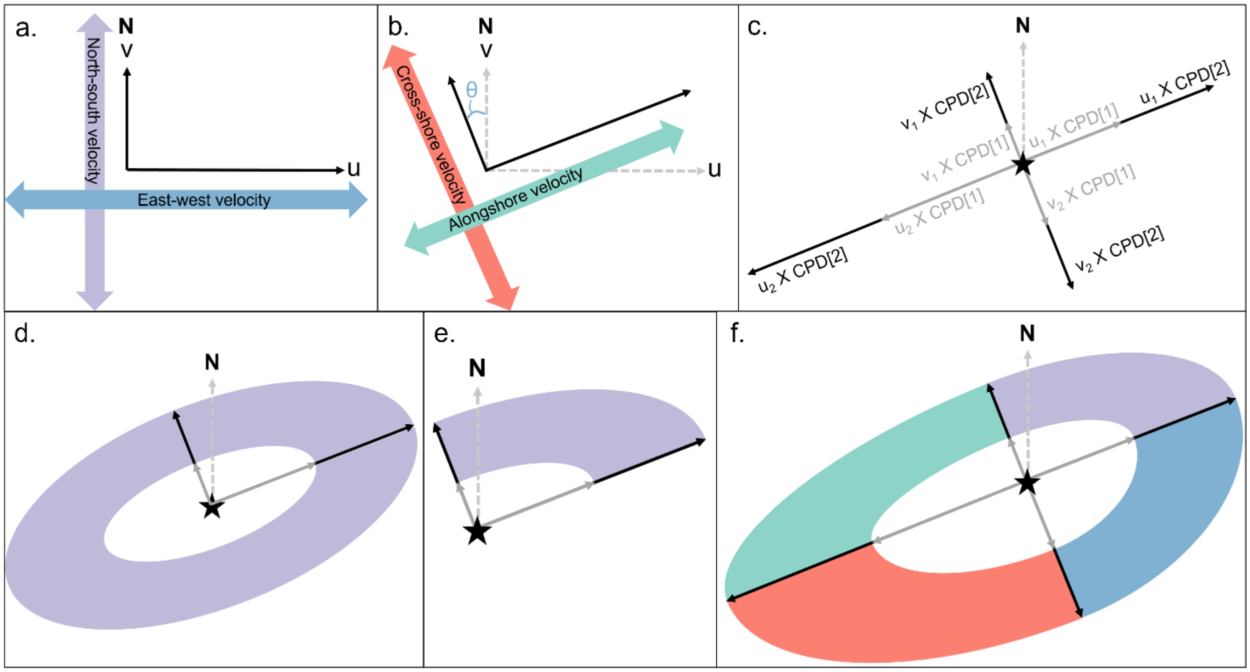


Figure 3.1: Graphical explanation of 2D approach. a. Horizontal components of velocity (depth-averaged), b. Components of velocity rotated about angle θ representing alongshore and cross-shore components of velocity. c. Magnitude of dispersal distance in four directions, where u_1 = positive rotated u (east), u_2 = negative rotated u (west), v_1 = positive rotated v (north), v_2 = negative rotated v (south), and CPD = competent propagule duration. Arrows represent example length scales. Star denotes the example release location/ ellipse centroid. d. Ellipse with radii equal to dispersal distances in north (v_1 x CPD) and east (u_1 x CPD) directions. Dispersal area during the period when larvae are not competent to settle is shown as the white interior of the ellipse and was not included in the estimation of dispersal area. e. Ellipse cropped to northeast quadrant. f. Concatenation of ellipses for all four quadrants forming full dispersal area.

1. *Using a rotation matrix, the u and v components of velocity were rotated relative to the dominant topographic feature* (Figure 3.1ab). In our case study, this corresponded to the angle of the mainland of Nova Scotia between -63° and -62° longitude. In the rotated time-series of velocity, the rotated *u*-axis represents the alongshore current direction, and the rotated *v*-axis represents the cross-shore current direction.

2. *Using the rotated components of velocity, dispersal was calculated.* A current velocity time series allowed us to decompose the magnitude of velocity in four directions, 90° apart. For each component of velocity, we multiplied current speed averaged over depth and between the period from spawning to settlement, by the pre-competency period and the total propagule period, representing the beginning and end of the CPD, respectively. We subtracted the pre-competency polygon from the former, as in the 1D approach, to illustrate the dispersal area for the competent period (Table 3.1; Figure 3.1c).

3. F*or each of the four quadrants, an ellipse was produced with radii equal to the dispersal distances calculated in step 2.* For example, the ellipse in the N-E quadrant was calculated using the rotated north and east radii (Figure 3.1d). This approach considers that the magnitude of the positive and negative (rotated east vs. west and north vs. south) components of velocity may not be equal. Each ellipse was then cropped to retain the quadrant corresponding to the radii used to produce it. For example, only the upper right quadrant was retained for the ellipse produced with positive alongshore and cross-shore velocities (Figure 3.1e).

4. *The four retained quadrants were concatenated to produce a continuous, oblong ellipse* (Figure 3.1f).

All steps were repeated for each potential release location and then geometrically unionized.

The 1D and 2D approaches assume spatial uniformity in ocean currents. In the 3D approach, representing components of velocity in x, y, and z, we tracked passive propagules through space and time using a Lagrangian particle tracking module. The module was driven by hourly 3-D velocity fields were derived from a hydrodynamic model based on the Finite-Volume Community Ocean Model (FVCOM). The model domain covers the Scotian Shelf and the Gulf of Maine with a horizontal resolution varying from approximately 100 m in the ESI area to several kilometers in the open ocean. A generalized sigma coordinate was used in the vertical direction. The model is driven by air forcing from the surface and by open boundary conditions along the lateral boundaries. The model outputs were evaluated against observed water elevations, currents, temperature, and salinity. More detailed description and information about the model setup and validation can be found in (Feng et al. 2022). Release locations were the same as in the 1D and 2D approaches. For each species at each location and for each release, the number of particle trajectories was equal to the fecundity (calculated based on empirical data; Appendix B.2) over 1 m^2 of seabed. Estimated total fecundities for laminarian kelps, *M. membranacea*, and *S. droebachiensis* were 100,000, 50,000, and 2,500 spores or ova m^{-2} seabed, respectively, which we assumed equalled the total number of propagules produced by each species over the season (Appendix B.2). To produce unique trajectories for each particle, we employed vertical random walk in the particle tracking simulations. To represent the spawning pattern over the season, we released propagules every five days, for five releases in total during each of two periods, in turn separated by one month, for a total of ten simulations per species (Table B.4). Propagule locations were extracted every 12, 84, and 96 hours for kelps, *M. membranacea*, and *S. droebachiensis,* respectively. Output locations for the period of CPD were summed across the 10 runs and mapped onto a raster grid (210 m by 210 m), then log-transformed and plotted as a 2D density histogram of points per cell. Lastly, we only considered dispersal in the open coastal ocean, therefore excluding the Bras d'Or lakes, which have limited physical exchange with the open ocean (Tremblay 2002).

There are a few limitations in our approach. Firstly, because we only included a single year of modelled currents the model outputs could be underestimating potential dispersal in the direction opposite to the dominant current (as in Aiken et al. 2007). Secondly, since we are focussed on horizontal displacement, vertical diffusion was not accounted for in the 1D and 2D approaches as currents are depth averaged. For the 3D approach, we applied vertical random walk, not vertical diffusion. Thirdly, because of computing limitations, we modelled the number of propagules proportional to the density of fecund individuals of each species over a full spawning season for 1 m^2 seabed; for kelps, we were constrained to one order of magnitude less than the calculated spore production rate. We expect the magnitudes of absolute propagule dispersal, and therefore connectivity, to be much greater than our modelling predictions. Fourthly, dispersal area for the 3D approach is dependent on the size of grid cell selected to convert particle tracks to an area-based value. For instance, as Δx, representing grid cell size, approaches 0, so does our dispersal area. However, the comparisons of relative outcomes among approaches are valid if the dispersal area predicted from the 3D approach is the greatest (as was the case – see Results). Lastly, we did not consider propagule behaviour or mortality to better align estimates from the 3D approach with those from the 1D and 2D approaches which cannot include those parameters.

3.3.3 Metrics of dispersal/connectivity and comparison of approaches

For each species, we compared dispersal for the three approaches using three metrics: dispersal area (km^2), maximum in-water dispersal distance (km), and connectedness to ecologically relevant spatial units. Dispersal area was calculated as the in-water area (km^2) travelled through by propagules during the CPD. For the 3D approach, this corresponded to the area of the 2D density plot with a cell resolution of 210 m. Maximum dispersal distance was calculated as in-water least cost path (km) either to the furthest point in the polygon, for the 1D and 2D approaches, or as maximum displacement by any released particle for the 3D approach. Connections between management units were calculated as a binary intersection of polygons for the 1D and 2D approaches (0 = no connection, 1 = connection), or mean proportion of total particle tracks (± standard deviation), averaged over CPD and across all runs (10 runs per species), for the 3D approach. For our case study, spatial units were coastal areas in the draft Marine Conservation Network Design for the Scotian Shelf - Bay of Fundy Bioregion, provided by DFO (Figure 3.2). The proposed areas within the draft network design represent potential future MPAs identified through a systematic conservation planning process. The federal Department of Fisheries and Oceans - Canada is currently consulting on the draft network design so the locations of these areas may be subject to change before they are ultimately proposed for designation as MPAs or other types of spatial conservation measures.

To quantify the overlap in dispersal area, we calculated the Jaccard index for each pair of approaches for each species. The Jaccard index is calculated as the geometric intersection divided by the geometric union, producing a number between 0 and 1, where 0 indicates no overlap and 1 indicates complete overlap (Real and Vargas 1996). All calculations were completed in R with packages *tidyverse* (1.3.2), *sf* (1.0-9), *gdistance*

(1.3-6), and *raster* (3.6-14) (van Etten 2012, 2017, Pebesma 2018, Wickham et al. 2019, R Core Team 2020).

To facilitate the adoption of our the 2D approach to on-the-ground conservation efforts, we developed an R package, called "*rcove*", which can be downloaded from GitHub at https://github.com/abalbar/rcove. The rcove function takes ocean current data and species life history information as input and outputs a shapefile describing the dispersal area that can be visualized in R or any other GIS software.

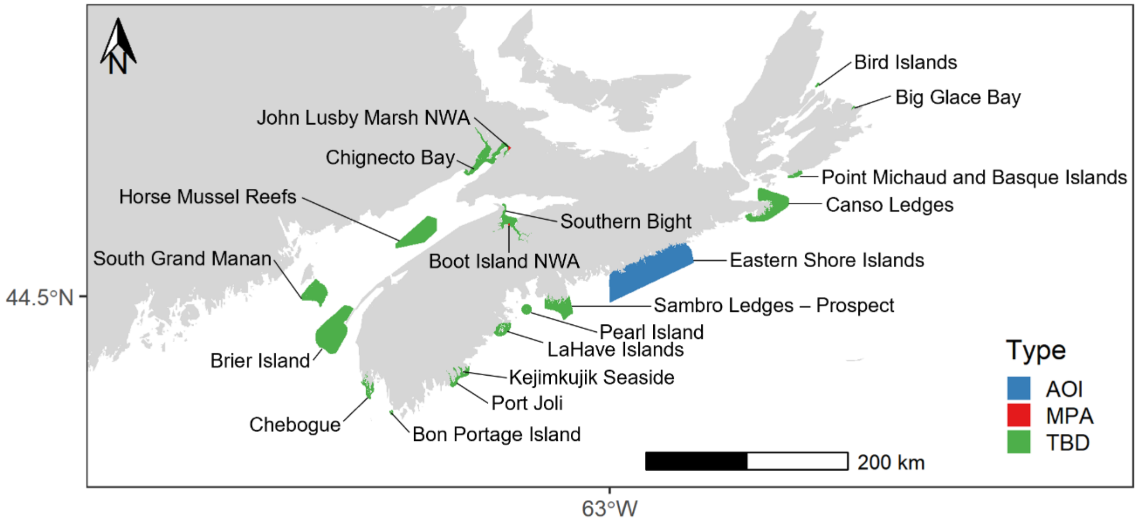


Figure 3.2: Existing (MPA), proposed (area of interest, AOI) and other potential future (TBD) coastal Marine Protected Areas along the Atlantic Coast of Nova Scotia and Bay of Fundy, corresponding to entries listed as rows in Table 3.4. NWA = National Wildlife Area, currently designated MPAs.

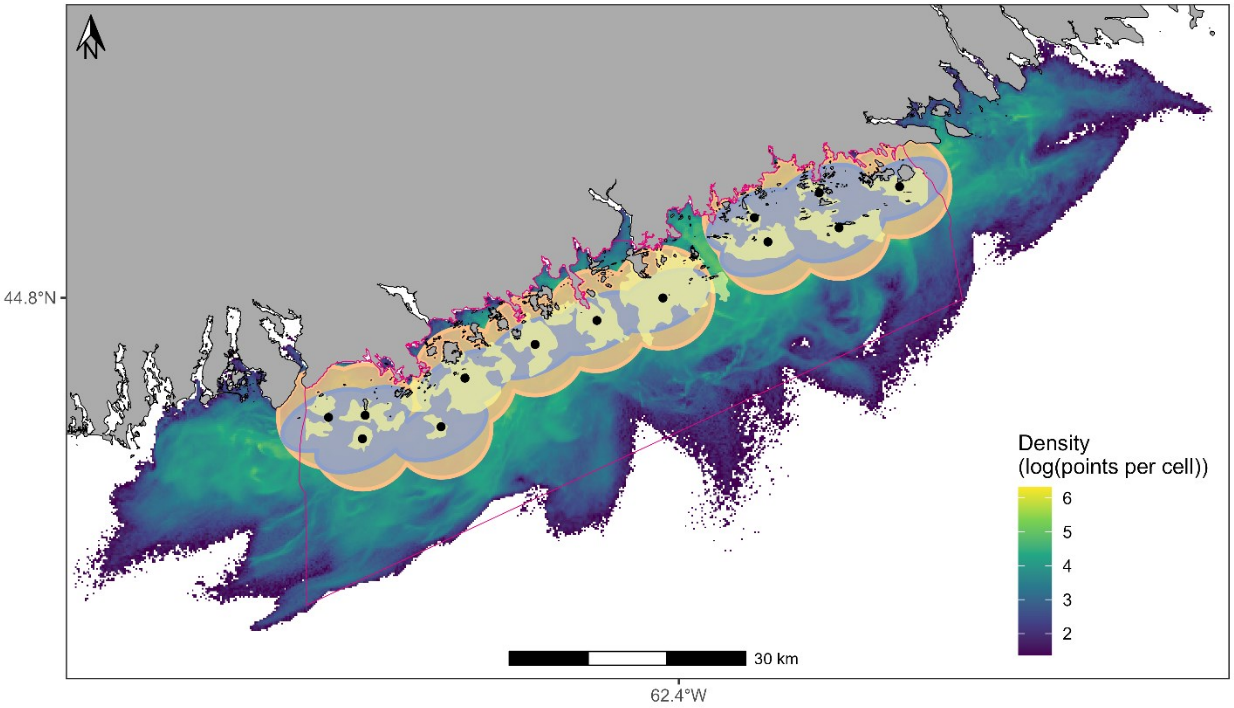
3.4. Results

3.4.1 Patterns of dispersal

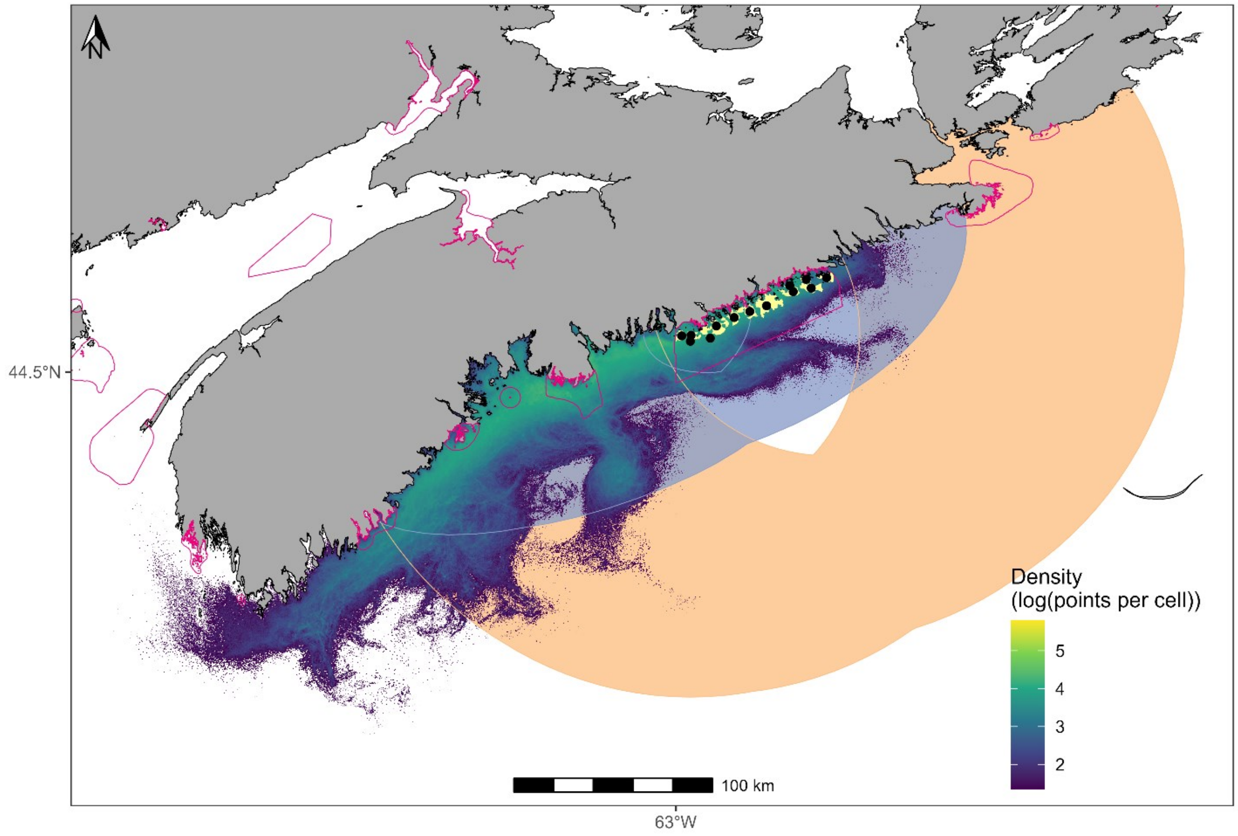
Dispersal patterns differed between species with medium-long CPD and the laminarian kelps with short CPD. For kelps, propagules released from within the boundaries of the Eastern Shore Islands (ESI), and tracked in 3D, dispersed throughout the entire ESI and outside its boundaries (Figure 3.3a). The dispersal area for the 3D approach was greater than that for the 1D and 2D approaches, which were limited to areas immediately surrounding each kelp patch (Figure 3.3a). Propagules of the bryozoan

(*M. membranacea*), when tracked in 3D, dispersed along the entire Atlantic coast of Nova Scotia, with most propagules dispersing south-west of their initial release locations (Figure 3.3b). The 1D and 2D approaches predicted dispersal along a greater distance to the northeast and shorter distance to the southwest than the 3D approach, spanning 450 and 340 km of coastline, respectively. Similarly for the sea urchin (*S. droebachiensis*), propagules released from within the ESI boundaries, dispersed along the entire Atlantic Coast of Nova Scotia and into the Bay of Fundy, although most propagules were retained within the southwestern shore (Figure 3.3c). Using the 2D approach, sea urchins dispersed along ~ 700 km of coastline, with greater dispersal southwest than northeast of the initial release locations (Figure 3.3c). The dispersal area using the 1D approach was much greater than that of both the 3D and 2D approaches and extended along the entire Atlantic coast of Nova Scotia to Prince Edward Island.

a. laminarian kelps



b. Membranipora membranacea



c. *Strongylocentrotus droebachiensis*

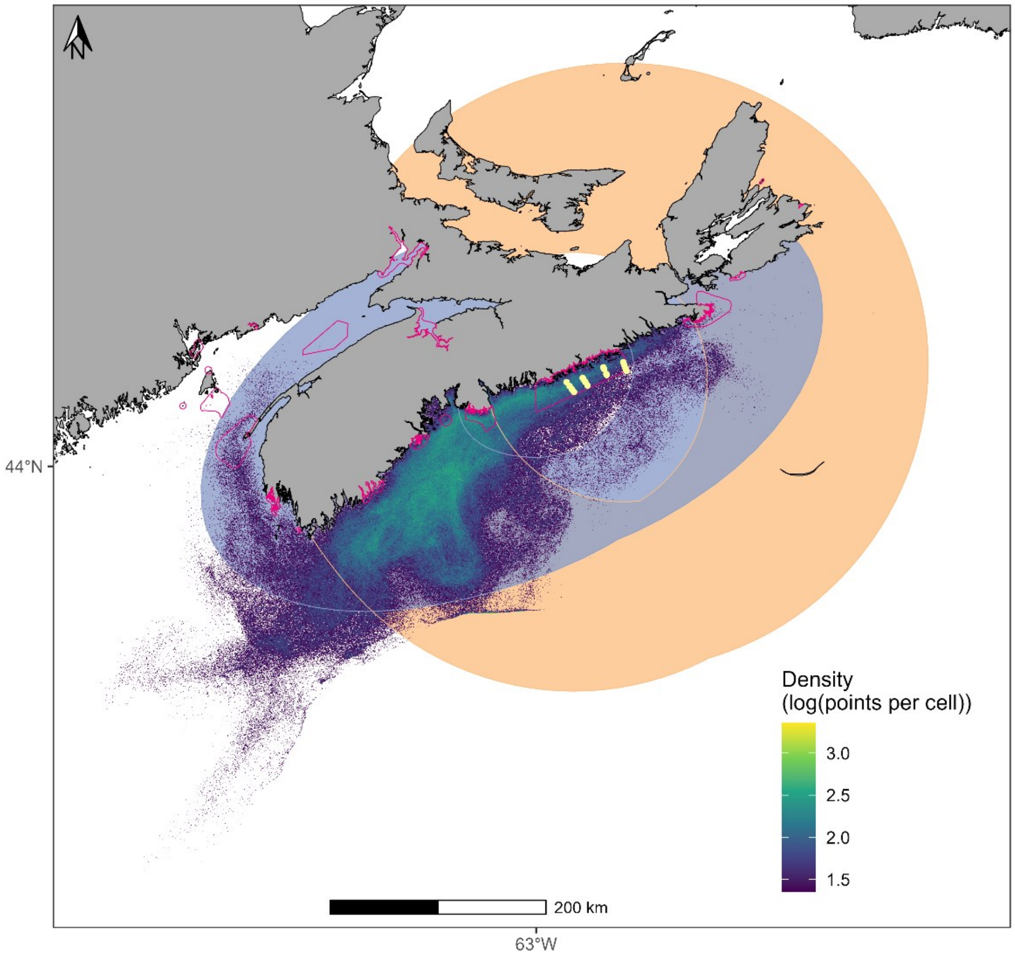


Figure 3.3: Dispersal area of propagules of a) laminarian kelps, b) *Membranipora membranacea*, and c) *Strongylocentrotus droebachiensis* predicted using three approaches of increasing complexity. Kelp patches (a and b) or release locations (c) are shown in yellow, and kelp patch centroids (a and b) are shown in black. The orange and purple polygons represent dispersal area during the CPD predicted using 1D and 2D approaches, respectively. The 2D density histogram (purple-yellow) represents the distribution of propagules from a coupled Lagrangian particle tracking and circulation model (3D approach), plotted as density per area of each grid cell (210-m resolution). The pink outlines indicate the boundaries of the potential future coastal marine protected areas.

3.4.2 Comparison of approaches for estimating dispersal

Dispersal area (km^2) varied greatly among the three approaches. For laminarian kelps, dispersal area of the 3D approach was 3 and 5 times larger than that based on the

1D and 2D approaches, respectively, and the Jaccard index was greatest between the 1D and 2D approaches (Tables 3.2, 3.3). For the bryozoan and sea urchin, dispersal area was largest for the 1D approach (Table 3.2). Dispersal area differed by only 5 % between the 2D and 3D approaches for the bryozoan but was nearly twice as large for the 2D than 3D approach for the sea urchin. The Jaccard index was greatest between the 2D and 3D approaches for both the bryozoan and sea urchin (Table 3.3). Maximum in-water distance was similar for the 1D and 2D approaches for all three species, varying by < 3 %. Maximum in-water distance was largest for the 3D approach for kelps and the bryozoan, whereas it was smallest for the sea urchin (Table 3.2).

Table 3.2: Species dispersal metrics for the three modelling approaches applied'. For maximum in-water distance for the 3D approach, the mean ± standard deviation over 10 runs is shown. See Methods for a full description of each approach.

	Area (km^2)			**Maximum in-water distance (km)**		
Species	**1D**	**2D**	**3D**	**1D**	**2D**	**3D**
Laminarian kelps	1071	655	3297	8	8	45 ± 14
Membranipora membranacea	64281	18757	19820	250	242	307 ± 49
Stronglyocentrotus droebachiensis	171745	87920	45969	797	792	641 ± 42

Table 3.3: Jaccard index of study species based on pair-wise comparison of modelling approaches applied.

Species	**1D & 2D**	**1D & 3D**	**2D & 3D**
Laminarian kelps	0.61	0.32	0.20
Membranipora membranacea	0.20	0.16	0.43
Stronglyocentrotus droebachiensis	0.25	0.13	0.30

The number of connections from the ESI to other coastal MPAs was consistent across approaches for the species with short CPD (kelps), but variable for those with medium-long CPD (bryozoan and sea urchin; Table 3.4). For laminarian kelps, all three approaches predicted retention of propagules within the ESI and no dispersal to adjacent MPAs. Retention of propagules within the ESI decreased with increasing CPD (Table

3.4). Some connections to MPAs northeast of the ESI were predicted by the 1D and 2D approaches, but not by the 3D approach. Conversely, a greater proportion of trajectories and therefore more connections with MPAs to the southwest were predicted by the 2D and 3D approaches than the 1D approach. The most notable differences among approaches were for the sea urchin, where the number of connections varied from 10 to 17. Like the bryozoan, most connections were southwest of the ESI, along the main direction of the Nova Scotia Current, particularly for the 2D and 3D approaches. Connections were more consistent between the 3D and 2D approaches than with the 1D approach (Table 3.4).

Dispersal patterns over time revealed differences in the number of propagules within each MPA throughout the CPD (Figure B.5). In general, there was a consistent supply of propagules to MPAs closer to the source MPA (the ESI) at all time points, with most propagules dispersing to MPAs southwest of their release location. The number of propagules within MPAs generally decreased as distance from the source MPA (the ESI) increased, with fewer than 100 propagules per model run ending up in the farthest reached MPAs.

Table 3.4: Connectivity matrix from the Eastern Shore Islands into other existing and potential future coastal marine protected areas. Columns represent each species and approach, and values represent the connection strength. For the 1D and 2D approaches, a binary value (1 or 0) indicates whether the dispersal area and MPA polygons intersect (0 = no connection, 1 = connection in **bold**). For the 3D approach, **bold** cells indicate a connection and the value in the cell represents the mean proportion of particle tracks (± standard deviation) that passed through the MPA, averaged over the competent propagule duration (CPD) and across all runs (10 runs per species). See table 1 for CPD values for each species. MPA = Marine protected area, NWA = National wildlife area.

	Laminarian kelps			***Membranipora membranacea***			***Strongylocentrotus droebachiensis***		
Proposed MPAs	**1D**	**2D**	**3D**	**1D**	**2D**	**3D**	**1D**	**2D**	**3D**
John Lusby Marsh NWA	0	0	0	0	0	0	0	**1**	0
Chignecto Bay	0	0	0	0	0	0	0	**1**	0
Boot Island NWA	0	0	0	0	0	0	0	**1**	0
Southern Bight	0	0	0	0	0	0	0	**1**	0
Horse Mussel Reefs	0	0	0	0	0	0	0	**1**	**<0.001**
South Grand Manan	0	0	0	0	0	0	0	**1**	**<0.001**
Brier Island	0	0	0	0	0	**<0.001**	0	**1**	**0.002 ± 0.006**
Chebogue	0	0	0	0	0	0	0	**1**	**<0.001**
Bon Portage Island	0	0	0	0	0	**<0.001**	0	**1**	**<0.001**
Port Joli	0	0	0	**1**	**1**	0	**1**	**1**	0
Kejimkujik Seaside	0	0	0	**1**	**1**	0	**1**	**1**	0
LaHave Islands	0	0	0	**1**	**1**	**0.017 ± 0.012**	**1**	**1**	**0.002 ± 0.003**
Pearl Island	0	0	0	**1**	**1**	**0.020 ± 0.012**	**1**	**1**	**0.002 ± 0.002**
Sambro Ledges - Prospect	0	0	0	**1**	**1**	**0.072 ± 0.046**	**1**	**1**	**0.015 ± 0.013**
Eastern Shore Islands	**1**	**1**	**0.910 ± 0.068**	**1**	**1**	**0.172 ± 0.125**	0	**1**	**0.054 ± 0.060**
Canso Ledges	0	0	0	**1**	**1**	0	**1**	**1**	0
Point Michaud and Basque Islands	0	0	0	**1**	0	0	**1**	**1**	**<0.001**
Big Glace Bay	0	0	0	0	0	0	**1**	0	0
Bird Islands	0	0	0	0	0	0	**1**	0	0

3.5. Discussion

We compared three approaches for predicting in-water dispersal with increasingly complex input data on ocean currents, ranging from average current speed to modelled currents on spatial scales of 100s of m, for three dominant shallow subtidal species along the Atlantic Coast of Nova Scotia. Dispersal differed between species with mid-long CPD (*Membranipora membranacea* and *Strongylocentrotus droebachiensis*) and those with short CPD (laminarian kelps). For mid-long CPDs, a qualitative comparison of dispersal area combined with the Jaccard index suggested that the outcomes of the 2D and 3D approaches were more similar to one another than those from the 1D approach. In contrast, for a short CPD, dispersal outputs were more similar between the 1D and 2D approach and less so with the 3D approach. We conclude that the 1D approach is adequate for species with a short CPD, but the 2D and 3D approaches provide significant advantages for conservation for species with a mid-long CPD as they include directional flow, and therefore a more detailed integration of oceanographic processes.

3.5.1 Comparison of dispersal estimates among approaches

Kelps were the only taxon for which dispersal area and maximum in-water distance predicted using the 3D approach were greater than those predicted for the 1D and 2D approaches. This is likely because the linear approximation of particle displacement assumed by the 1D and 2D approaches oversimplifies the dynamics that affect particle dispersal, namely changing velocity fields with x, y, and z, and horizontal diffusion. However, as CPD increases, dispersal trajectories in 3D tend to scale sub-linearly compared to the 1D and 2D approaches. The Eastern Shore Islands region is composed of 282 nearshore islands, which introduce eddies, drag, and small-scale variation in currents supporting retention of propagules (Jeffery et al. 2020, Feng et al. 2022). However, millions of propagules were tracked with the 3D approach and therefore subjected to many flow fields, potentially explaining the broader dispersal area observed. Our measurements for maximum in-water distance (km to 10's of km) were similar to that estimated based on genetic structure of *Laminaria digitata* in the English Channel, using microsatellites (Billot et al. 2003, Couceiro et al. 2013), and spore dispersal for the giant kelp *Macrocystis pyrifera* at the San Clemente artificial reef, California (Reed et al. 2004) and the Carpinteria sand flat, California (Gaylord et al. 2006). Because we do not account for the sexual reproduction phase of gametophytes in our simulations, our dispersal estimates should be interpreted as maximum dispersal potential. In *M. pyrifera*, tissue containing spores, called sori, is found at the base of the plant whereas, for the two dominant kelp species in Nova Scotia, *Saccharina latissima* and *L. digitata*, sori form at the distal end of the thallus and spores are released further from the substratum possibly promoting wider spore dispersal (Billot et al. 2003). Additionally, canopy kelps can generate drag to flows at a magnitude equal to and opposing the horizontal pressure gradient force, resulting in a decrease in tidal currents by 40 – 80 % in the interior of the kelp bed (Wu et al. 2017). Therefore, it is possible that propagules from canopy kelps disperse shorter distances than propagules from prostrate kelps. For a short distance disperser such as kelps, habitat size and quality are typically the target metrics for protection, translating to the design principle of MPA size. To ensure a MPA is large enough to encapsulate the dispersal ability of a species with a short CPD, the 1D approach provides an adequate proxy.

For species with mid-long CPDs, the direction of dispersal was largely influenced by the dominant alongshore current direction when propagules were tracked in 3D; this pattern was captured to a lesser extent with the 2D approach, and not at all with the 1D approach. Dispersal extent in the cross-shore direction was much less than the alongshore direction for the 3D and 2D approaches, but not for the 1D approach for which dispersal potential is assumed to be equal in all directions. Propagules of *S. droebachiensis* were released from depths ≥ 45 m and therefore, those tracked in 3D dispersed across a wider cross-shore range. The broad dispersal area for *S. droebachiensis* measured in this study agrees with the genetic homogeneity of populations across the Northwest Atlantic (Addison and Hart 2004, 2005). Similarly, coastal currents in other ocean basins largely influence the dominant dispersal direction and limit cross-shore transport. For example, propagules with a duration of 10 - 90 days, predominantly travelled southward following the East Australian Current, or were advected offshore, but only south of separation of the East Australian Current (Roughan et al. 2011, 2022). Propagules of Yellow Tang tracked off the island of Hawaii dispersed northward of their release locations following the dominant cyclonic eddy in the region (Christie et al. 2010b).

3.5.2 Relative benefits of approaches

The benefits associated with the outputs of each of the three approaches for estimating dispersal are proportional to the cost of their calculation, in terms of time and resources. For instance, the input data and computation power needed to produce predictions for the 1D approach have the lowest cost but also a low benefit as the least data-informed, only accounting for CPD, spawning locations, and average current speed. Goetze et al. (2021) applied a similar distance-based metric (50-km radius) to assess the number of connections to each marine reserve in Australia, a distance suggested by Almany et al. (2009), as a between-reserve distance for maintaining demographic connectivity of corals and fish populations in this region. Alternatively, the cost to develop and run a fine-scale oceanographic model that can be used to estimate dispersal area (the 3D approach) is in the order of 100s of 1000s of dollars (Table B.6). Those models combine modeled (and validated) data on ocean currents resolved at fine spatial scales (<1 km, depending on the local oceanography), knowledge of ontological and life-history details, in addition to the life history information applied for the 1D approach. There are, however, proportional benefits to this investment as outputs from the 3D approach capture individual propagule locations throughout their CPD, which can be used to produce a density map or connectivity matrix. Using a graph theoretic approach, connectivity metrics that quantitatively inform whether a population is a source, stepping-stone, or central population can be extracted from a connectivity matrix. Several studies employ this methodology to discern spatial dependencies in various regions and answer both scientific and management-based questions (Treml et al. 2008, Thomas et al. 2014, Álvarez-Romero et al. 2018, Ospina-Alvarez et al. 2020). Even though their geographic focus is rapidly expanding, many of these studies are still focussed on certain regions where biophysical model infrastructure exists. For example, in Canada, such oceanographic models at resolutions that are appropriate for nearshore systems (e.g. FVCOM models) currently exist for Nova Scotia and the Gulf of Maine (Feng et al. 2022), the Discovery Islands (Foreman et al. 2012), Queen Charlotte Strait (Lin and Bianucci 2023), and Placentia Bay (Ma et al. 2012). Lastly, the 2D approach can be calculated with an intermediate-level cost 10s of 1000s dollars (Table B.7) and benefit, compared to the 1D and 3D approaches. Time series of ocean currents are coupled with life history information on CPD, spawning locations, and a general spawning window, to produce a polygon describing dispersal area. This output is more data informed than that of the 1D approach because components of velocity in cross-shore and alongshore directions are applied to predict dispersal in four directions, 90° apart, independently.

3.5.3 Management implications

In our case study, we applied the four recommendations proposed by (Balbar and Metaxas 2019) for incorporating connectivity into the design of MPAs. First, we identified three candidate species, with a range of life history characteristics, for which to consider dispersal patterns and estimate connectivity in the case study. We prioritized our efforts on keystone and foundation species, which is an effective strategy for making efficient use of resources for measuring dynamic processes such as dispersal (Jahnke et al. 2017, Alegría-Ortega et al. 2021). Second, we identified the role of the proposed ESI MPA in supporting connectivity, which varied depending on the dispersal ability of the species. We found that the ESI: (1) will serve as a source area, primarily for MPAs downstream along the dominant current direction, for mid-long CPD dispersers and (2) will be self sustaining for short CPD dispersers. Identifying the role each MPA plays in supporting connectivity has also recently been adapted as a rule of thumb for operationalizing connectivity into MPA network design (Cannizzo et al. 2021). Third, we evaluated patterns of dispersal on the spatial scale of the potential future MPAs on the Atlantic coast of Nova Scotia. At spatial scales of management (> 10s km), patterns of connectivity were most similar between the two more complex approaches, supporting application of the simplest of the two to the design or post-hoc analysis of networks of MPAs. We applied the approaches to predict the number of connections from one source MPA to other potential future MPAs in an existing configuration. This post-hoc assessment can be conducted prior to or after designation, depending on the research question. Alternatively, the approaches can be applied to the design process to help determine the size and spacing of MPAs, as was the case with the simplest approach for the design of the network of MPAs along the coast of California (Carr et al. 2010, Moffitt et al. 2011). Fourth, we improved our regional knowledge of connectivity patterns. There have been recent advancements, in Canada (Kenchington et al. 2019, Friesen et al. 2019, Cristiani et al. 2021), and internationally (Assis et al. 2021) in improving our understanding of regional patterns of connectivity to better inform management decisions.

Deciding which tool or approach to use to estimate patterns of dispersal and connectivity can be viewed as an optimization problem, where the goal is to maximize predictive ability, defined here as the ability to detect patterns at a defined spatial and temporal scale, given a set of limited resources. For example, the Atlantic coast of Nova Scotia is a region with a complex coastline, a series of coastal islands, prominent tides, and varied bathymetry, all of which influence current velocity over small spatial (10's – 100's m) and temporal scales (minutes – hours). Under these circumstances, the simplest approach does not capture the complexity of the system, making the other two approaches more appropriate, except for species with a short CPD, such as kelps. The approach of intermediate complexity can be used to identify patterns at the scale of management units with fewer resources than the most complex approach. Research questions that aim to identify patterns of dispersal and connectivity on evolutionary timescales should apply genetic methods, such as isolation-by-distance and gene flow, instead of the three approaches in this study. The 2D approach was developed for species for which dispersal is driven by ocean currents (e.g. planktonic spores and generally passive larvae), and may not be suitable for highly migratory species and those for which complex behaviours play a dominant role in dispersal patterns (e.g. larval fish). Additionally, the 2D approach is best suited for coastal regions with a dominant unidirectional offshore current and may not be suitable in the open ocean (e.g. ocean gyres) or where large-scale currents vary over distances smaller than the average dispersal capability of the species of interest. For conservation practices, the simpler approaches we used for estimating dispersal area can be applied to other coastal MPAs with unidirectional current regimes to identify their role in supporting connectivity for species or functional groups with different life history characteristics.

While research that addresses fundamental questions often prioritizes predictive ability, applied research for management is generally limited by resources, such as human capacity, limited time horizons and limited availability of data, often resulting in the application of "rules of thumb" to inform size and spacing of MPAs in a network in place of more data informed approaches (e.g. Carr et al. 2010). In our case study, the intermediate approach provides a compromise in terms of the cost of inputs and benefit of outputs and can be applied to regions where coastally resolved ocean models have not been developed, but time series data on ocean currents are available. The lower relative cost of the intermediate approach can facilitate faster decision making, particularly in light of global warming. This is important because delaying management action can result in greater habitat loss prior to PA designation (Camaclang et al. 2022). However, understanding the relative importance of each site in a network can inform the best strategy for sequentially designating a series of MPAs to best achieve metapopulation persistence (Kininmonth et al. 2019).

3.5.4 Conclusions

While a wide range of tools exist for measuring and modelling patterns of connectivity, we compared the outputs of three approaches with 1, 2, and 3 dimensions of ocean current data. The intermediate (2D) approach for estimating dispersal strikes a balance between feasibility and specificity of ocean current input data. When comparing approaches on the scale of spatial management units, patterns between the intermediate (2D) and most complex (3D) approaches were more similar than the simple (1D) approach; this outcome supports application of the 2D approach to the design or post-hoc analysis of networks of MPAs for species with a mid-long CPD. Paired with a map of suitable habitat for kelps, which served as the release points for studying the dispersal of Laminarian kelps and *M. membranacea*, we made use of existing point data (presence/absence of a species or Eulerian ocean current measurements) and a newly-developed, regional FVCOM (Feng et al. 2022) to describe patterns of dispersal in a coastal region where connectivity of the selected species had yet to be described. As countries aim to protect 30 % of their national waters by 2030, a comprehensive toolkit and understanding of the costs and benefits of each approach will help researchers and managers optimize their efforts when designing connected networks of MPAs.

CHAPTER 4

EFFECT OF REGIONAL HABITAT FRAGMENTATION OF KELP BEDS ON CONNECTIVITY AND HABITAT STRUCTURE

4.1 Abstract

Kelp beds are an important ecosystem engineer that provide services such as carbon sequestration, a three-dimensional habitat, and enhanced primary and secondary productivity along 25% of our world's coastlines. However, kelps are in decline, exacerbated by anthropogenic changes such as warming temperatures, invasive species, and epiphytism, all causing elevated levels of disturbance leading to habitat loss and fragmentation. Fragmentation impacts, including increased isolation and decreased patch size, may also have negative impacts on connectivity between habitat patches if isolation surpasses dispersal capability. This is of particular concern for kelps, whose propagule stage is relatively short (2 days). To test the impacts of habitat fragmentation on habitat structure and connectivity, I ran two in-silico habitat loss experiments where I randomly removed habitat in 10 % increments up to 90%. For my analysis, kelp habitat was clustered into patches according to their connectivity strength. I found that the negative impacts of habitat fragmentation (increased number of patches, decrease in patch size), were no greater than the impacts of habitat loss alone, except when habitat loss passed a critical threshold (70 – 80% loss). Additionally, clusters were primarily supported by self-replenishment, as opposed to receiving recruits from neighboring populations. The independence of kelp patches may provide a slight advantage if habitat continues to decline, since the demise of one patch will not necessitate further decline to surrounding areas.

4.2 Introduction

Kelps, order Laminariales, are macroalgae that dominate 25 % of the world's coastlines, providing various ecosystem services and economic value (Vásquez et al. 2014, Krumhansl et al. 2016). As ecosystem engineers, kelps form three dimensional biogenic habitats that support a diverse assemblage of commercially important species, including lobsters and other invertebrates (Layton et al. 2019). The structure of healthy kelp beds is reinforced by physical changes that kelps enact on the environment, including shading of the understory, reducing flow, and preventing sedimentation (Eckman et al. 1989, Wernberg et al. 2005, Wu et al. 2017). Lush and dense aggregations of kelp also supply spores to support recruitment, providing positive feedback to maintain populations. Environmentally, kelps require cool, temperate waters (less than 20ºC) to grow optimally, photosynthesize, and survive (Simonson et al. 2015), as well as ample light for sporophyte recruitment (Tatsumi and Wright 2016). Geologically, kelps require hard, rocky substrate to attach their holdfasts (Steneck et al. 2002, Burek et al. 2018). Therefore, kelps tend to form patchy, mosaic distributions following suitable substrate and environmental conditions (Steneck et al. 2002).

Globally, kelp forests are experiencing cumulative effects from anthropogenic changes, including warming temperatures, increased frequency of disturbance, spread of invasive species, and epiphytism, among others (Filbee-Dexter and Scheibling 2012, O'Brien and Scheibling 2016, Wernberg et al. 2016, Denley et al. 2019a, Pratt et al. 2022). Global changes over the past few decades have shown persistent regime shifts to a turf-dominated benthos that do not offer the same benefits as kelp forests, such as carbon storage and increased secondary productivity (Krumhansl et al. 2016, Filbee-Dexter and Wernberg 2018). The Northwest Atlantic Ocean is classified as an ocean warming hotspot, causing considerable concern for the present and future distributions of kelp along the coast from Maine to Northern Labrador (Merzouk and Johnson 2011). In Nova Scotia, four main factors are driving the transition from kelp to turf algae: warming, storms, epiphytism, and species invasion (Filbee-Dexter and Wernberg 2018). The cumulative effect of these stressors is the cause of significant loss of kelp canopy, with up to 89% loss in cover along some regions of the coast (Filbee-Dexter et al. 2016, Filbee-

Dexter and Wernberg 2018). Regime shifts to turf reefs are also adverse because of hysteresis, meaning the tipping point to shift back to a kelp-dominated state requires much more favourable conditions than the tipping point that caused the state shift in the opposite direction (Wilman 2021).

Structurally, loss of habitat is the initial consequence of cumulative impacts on an ecosystem. Changes in habitat configuration and structure from habitat fragmentation are independent of total habitat loss, and at the landscape scale, can cause positive, neutral, or negative ecological responses (Andrén 1994, Fahrig 2003, 2017, Yeager et al. 2020). For example, in a review of responses of habitat fragmentation, Fahrig (2017) found that, out of 381, 76 % were positive, with some attributed to increases in functional connectivity, greater habitat diversity, and positive edge effects. Alternatively, the fragmentation threshold hypothesis suggests that impacts of fragmentation per se only cause significant negative impacts at high levels of habitat loss (70 – 80%) (Yeager et al. 2020).

Habitat fragmentation features associated with habitat loss include changes to patch size and isolation, and the number of patches (Andrén 1994, Fahrig 2003). Each of these habitat fragmentation features have an expected theoretical relationship with total amount of habitat (see Figure 3 of Fahrig, 2003). For instance, number of patches and total edge (perimeter) are expected to have a negative quadratic relationship with habitat amount. Mean patch size is expected to decrease linearly as habitat amount decreases, and size of the largest patch is expected to follow a logistic relationship. Most research on habitat fragmentation and connectivity or ecological corridors exists in the terrestrial realm on forests (Keitt et al. 1997, Damschen et al. 2019), wind-dispersed forbs (Soons et al. 2005), caribou (O'Brien et al. 2006, Prima et al. 2019), red squirrels (Mortelliti et al. 2011) and others. The effect of habitat fragmentation in the ocean is relevant for habitat forming species, such as kelp, but has not received the same amount of research attention as land-based fragmentation.

Kelps have a biphasic life cycle, alternating between a sessile sporophyte stage and dispersing spore/gametophyte stage (Reed 1990). Compared to invertebrates and fish, kelp spores have a relatively short propagule duration, but can still be advected 10s of m to several km by ocean currents (Shanks 2009). Some studies have empirically measured sporophyte recruitment using settlement tiles (Reed et al. 1988, Gaylord et al. 2006), while other have predicted spore dispersal patterns with modelled ocean currents or inferred dispersal capabilities with in-situ current measurements (Gaylord et al. 2002, Giraldo Ospina et al. 2023, Balbar et al. *in press*). However, most studies have focussed on canopy forming kelps such as *Macrocystis pyrifera*. Linking our theoretical understanding of habitat loss with patterns of dispersal and connectivity for habitat-forming species is important, especially because more than one third of kelp forests are in decline (Krumhansl et al. 2016). As kelp patches become smaller and further apart, they will exchange fewer propagules as the distance between patches surpasses the dispersal distance of spores. If patches are isolated, most incoming spores will be supplied from the patch from which they originated, and therefore cannot be rescued by recruits from neighboring patches and may be subject to self-fertilization and inbreeding depression (Henle et al. 2004, Raimondi et al. 2004). Therefore, estimating connectivity between habitat patches for different levels of habitat fragmentation can provide insight as to when recruitment limitation may arise.

In this chapter, I investigated the impacts of kelp habitat fragmentation, considering potential dispersal pathways between habitat clusters. I ran two in-silico habitat removal experiments using regionally subdivided clusters of kelp habitat along the Atlantic coast of Nova Scotia. In the first, I retained the original habitat clusters for all habitat loss treatments (called "consistent clusters"), and in the second, I re-clustered the remaining habitat after each habitat loss increment (called "variable clusters"). I measured outputs related to habitat structure for both experiments, graph theory metrics of connectivity for the consistent clusters experiment, and clustering characteristics for the variable clusters experiment. I expect that structural changes in habitat structure will follow relationships outlined by Fahrig (2003) and that the number of habitat clusters will increase and become more isolated as more habitat is lost. Therefore, I expect the relative input of spores from neighboring clusters to decrease as habitat is lost, but that the largest clusters will remain the most important at the landscape scale. This study is novel because I take a multi-faceted approach by exploring both structural and functional aspects relating to the fragmentation of kelp habitat.

4.3 Methods

4.3.1 Study region and taxa

My study region encompasses 400 km of coastline along the Atlantic coast of Nova Scotia from Yarmouth to Canso Ledges, from the low tide mark to 40 m depth. The shallow subtidal region consists of a habitat mosaic, from bedrock to soft sediment, hosting a variety of biogenic habitat types, including kelp and seagrass beds. I focussed on kelp beds along the coast, primarily composed of two species: *Laminaria digitata* and *Saccharina latissima*.

4.3.2 Quantifying population connectivity

To quantify population connectivity of kelps along the Atlantic coast of Nova Scotia, I ran 23 dispersal simulations of kelp spores originating from all suitable kelp habitat. I used the Finite Volume Community Ocean Model (FVCOM) offline Lagrangian particle tracking module through the Digital Research Alliance of Canada high-computing clusters Graham and Cedar. The data requirements of this model are (1) release locations for each spore-simulating particle, originating from a map of suitable kelp bed habitat, (2) data describing ocean currents, and (3) information on species life histories pertaining to dispersal characteristics (e.g. spawning time, planktonic larval duration) (Figure 4.1). I describe the way I addressed each data requirement in detail below.

4.3.2.1 Modelling kelp habitat

Survey data on kelp presence were compiled from historic and recent surveys (Filbee-Dexter 2016, Filbee-Dexter et al. 2016, Vandermeulen et al. 2017, 2018, Vandermeulen 2018) and a random forest model was trained with geomorphic predictors of depth, slope, fine-scale bathymetric position index, relative wave exposure, and presence of hard substrate. The model output, which maps probability of occurrence, was converted to presence/absence using a threshold of 0.55 from the area under the precision-recall curve. The result was 5252 suitable kelp habitat grid cells, each representing an area of approximately 0.4 km^2, which serve as spore release locations for the particle tracking simulations. Additional details on the methodology for the species distribution model can be found in Appendix C.1.

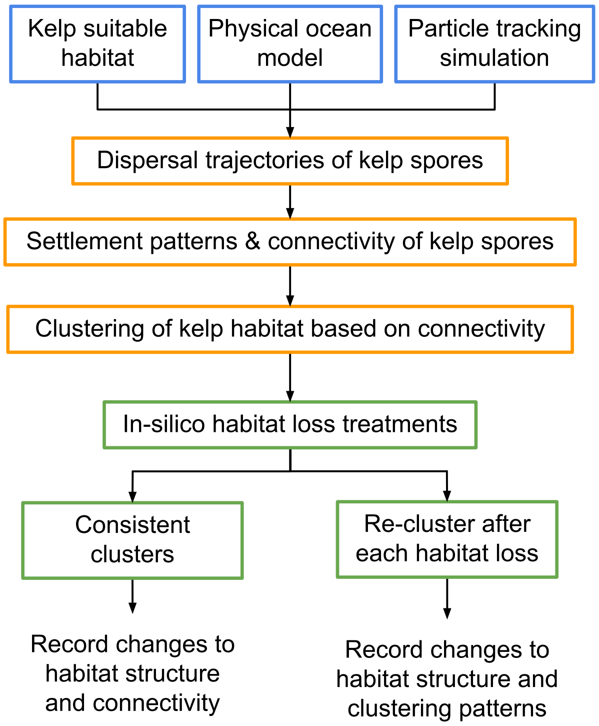


Figure 4.1: Flow of data processing and modelling used to test the impact of kelp habitat loss on connectivity and habitat structure. Blue cells indicate data inputs, orange cells indicate intermediate data processing, and green cells indicate habitat loss experiments. See Methods (section 4.3) for more detail on each data processing step.

4.3.2.2 Oceanographic model

I modelled dispersal of particles using ocean current data derived from a regional Finite Volume Community Ocean Model based on an unstructured mesh. The model domain covers the Scotian Shelf and the Gulf of Maine with a horizontal resolution varying from approximately 100 m in the nearshore to several kilometers in the open ocean. A generalized terrain-following sigma coordinate system with 45 layers was used in the vertical direction. The model is driven by atmospheric forcing from the surface and by open boundary conditions along the lateral boundaries. The time frequency of model outputs were hourly and were evaluated against observed water elevations, currents, temperature, and salinity. More detailed description and information about the model setup and validation can be found in (Feng et al. 2022, Balbar et al. *in press*). Hindcast data were available for 2018 and 2019.

4.3.2.3 Biological parameters for particle tracking

I tracked kelp spores with an offline Lagrangian particle tracking module on the Graham and Cedar clusters associated with the Digital Research Alliance of Canada. As inputs, I provided hindcast ocean current data modelled with FVCOM, biological specifications, and a link to the particle tracking software. The biological input parameters included in the Lagrangian particle tracking module were planktonic propagule duration and spawning period. Since the number of spores released in-situ is several orders of magnitude larger than our computational capacity, I instead optimized the number of tracked particles following the seasonal reproductive cycle of kelps (Chapman 1984). From each kelp cell, I released 1000 particles, spaced approximately 20 m apart, from each kelp cell for their entire propagule duration (48 hours) with simulations every 5 days for two months starting on October 1 over two years (2018 and 2019). The location of each particle was recorded every 0.5 hours. Five of these simulations could not be completed due to technical errors, providing a total of 23 simulations for further analysis.

I processed dispersal trajectories from the outputs of particle tracking simulations to determine settlement locations for further connectivity analysis. I selected particle settlement locations using probabilities associated with a half-normal distribution (μ = 0.5, σ = 16) because kelp spores are more likely to settle shortly after they are released from the adult sporophyte. To calculate the probability of a particle settling at each time point, I took the area under the half-normal distribution using intervals representing the 96 time points (every 0.5 hours) for which each particle location was recorded in the particle tracking module. 99.7 % of the particle trajectories fall within the total propagule duration for kelp spores (48 hours), and therefore 0.3% of particles were omitted at this step. I then selected the settlement time for each particle based on the probabilities calculated from the half-normal distribution. For the 23 dispersal events, settlements times were randomized so each particle released from the exact same location settled at a different time. To quantify the connection strength between each pair of the original 5252 habitat cells, I populated a connectivity matrix for each of the 23 simulations, which were then summed to produce one connectivity matrix.

4.3.3 In silico habitat fragmentation experiments

To investigate the effects of loss of kelp habitat on population connectivity, I simulated fragmentation of kelp bed habitat in silico using R (version 4.2.0) (R Core Team 2020). Firstly, I clustered the 5252 habitat cells into habitat patches using modularity optimization. Modularity is a greedy algorithm that derives community structure from networks (Newman 2006). Specifically, modularity creates optimal divisions of nodes into clusters such that there are many edges within clusters and few edges between clusters (Clauset et al. 2004). The degree of differentiation of clusters from one another is classified with a modularity score ranging from 0 to 1. For a modularity score equal to 0, the division of nodes into clusters is no different than if a network was created randomly. Alternatively, a modularity score greater than 0.3 is a good indicator of significant community structure, meaning clusters can be clearly differentiated from one another. These calculations were varied out using the *cluster_louvain* function in the *igraph* package (version 1.3.4) (Csardi and Nepusz 2006).

To test the effect of habitat fragmentation on recruitment limitation, I ran two in-silico habitat loss experiments. In both experiments, I simulated habitat loss by randomly removing 210 m by 210 m habitat cells in 10 % increments from 10 to 90 percent. Each simulation was replicated 100 times using random seeds. In the first experiment, the original clusters derived using modularity were maintained when calculating the metrics for each level of habitat loss. I recorded the area and perimeter of each cluster for each fraction of habitat loss and replicate. I also calculated graph theory metrics to assess connectivity features of the network for each habitat loss increment, including in-strength, self-replenishment, and PageRank using the *igraph* package (Csardi and Nepusz 2006). In-strength refers to the number of spores arriving at a cluster that originate from a different cluster. This metric quantifies the degree to which a cluster is supported by neighboring clusters, and is therefore an indication of rescue potential (Kininmonth et al. 2011, Roberts et al. 2020). Conversely, self-recruitment refers to the relative contribution of recruits from the cluster from which they originated (Botsford et al. 2009), and is an indicator of the isolation level of a cluster. Finally, PageRank offers a network-scale assessment of the importance of each node based on the strength of connections across the network (Page 1998, Kininmonth et al. 2011) and is used to identify source clusters and connectivity hotspots. In a second experiment, I re-clustered the remaining habitat after each habitat loss increment. For this experiment, I recorded area, perimeter, the number of clusters, and modularity score for each habitat loss increment and replicate to investigate how fragmentation impacts clustering. Associated maps were plotted using the *tmap* package (version 3.3-3) (Tennekes 2018) and other figures were made using *ggplot2* (version 3.0.1) (Wickham 2016).

4.4. Results

4.4.1 Clustering of kelp habitat

The initial modularity optimization resulted in 25 clusters (Figure 4.2). Of the 5252 habitat cells, 223 cells received no particles (spores) through self-replenishment or inflow and were thus not assigned to one of the 25 clusters. I removed these habitat cells for the remaining analyses. The area of each cluster was variable, ranging from 1.6 km^2 to 229 km^2, with most being less than 100 km^2. The largest clusters were along the Eastern Shore of Nova Scotia (clusters 4, 6, and 8) as well as surrounding Lobster Bay (clusters 19, 23, and 25). The modularity score associated with the clustering algorithm was 0.88, supporting strong community structure.

When habitat cells were re-clustered after each habitat loss treatment, the number of clusters and modularity score increased significantly, based on 95 % confidence intervals, for all treatments with > 10 % habitat loss (Figure 4.3 a,b). Both modularity and number of clusters increased exponentially as more habitat was incrementally lost. High fractions of habitat loss (> 70 %) had a much greater impact on the isolation between clusters and on total number of clusters than lower fractions of habitat loss (Table 4.1, Figure 4.2 a,b).

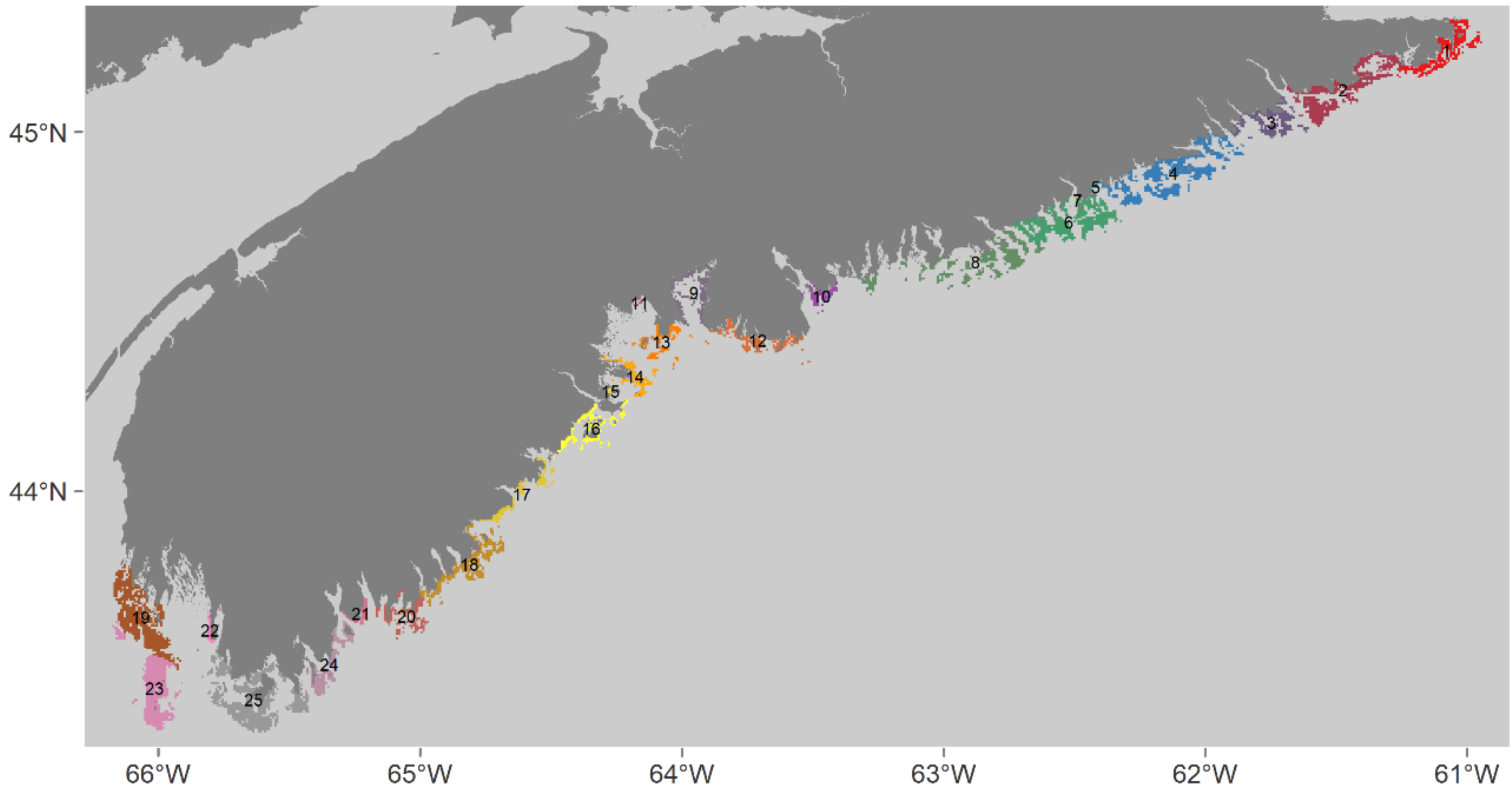


Figure 4.2: Suitable kelp habitat clustered using modularity optimization. Clusters are identified by different colours and were delineated using the summed flow matrix indicating connectivity between each of the 5252 habitat cells.

Table 4.1: Summary of changes to habitat structure for *in silico* kelp habitat loss experiments with a) consistent clustering (remaining habitat cells are not re-clustered after each habitat loss increment) and b) variable clustering (remaining habitat cells are re-clustered after each habitat loss increment). Reported values are the mean ± standard error across 100 random seeds. A subset of habitat loss treatments at equal intervals that illustrate the relationships between variables are shown. Panel b) also includes a summary of the response variables for modularity optimization clustering for the new cluster configuration.

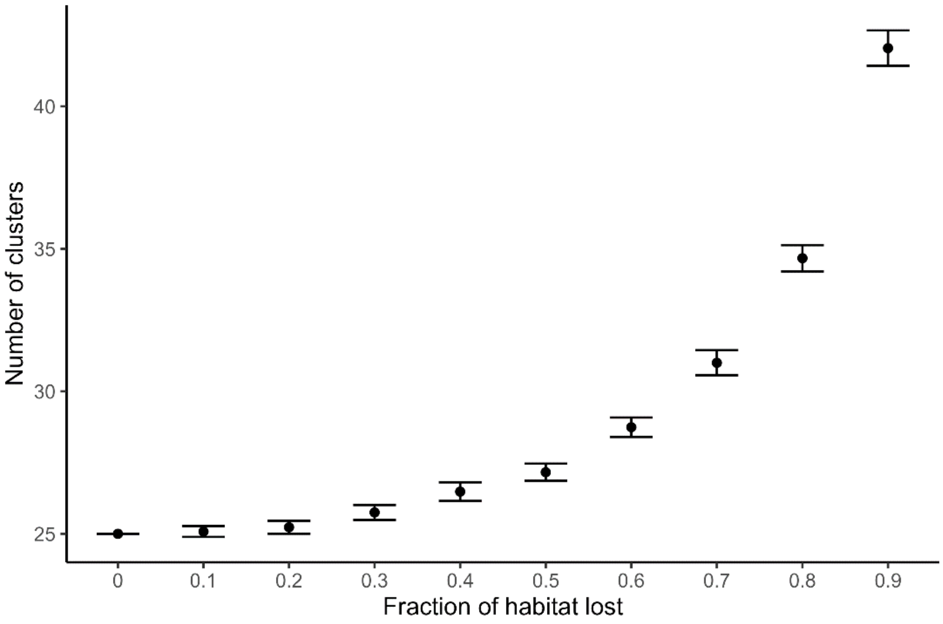
a) Consistent clusters

Habitat response variable	**Kelp habitat loss treatment** 0	0.3	0.6	0.9	**Relationship with habitat loss treatment**
Area (km^2)	79.9 ± 6.9	58.3 ± 5.1	37.1 ± 2.6	16.0 ± 1.3	linear
Perimeter (km)	168.2 ± 11.9	189.4 ± 14.7	163.1 ± 13.3	88.4 ± 7.2	negative quadratic
Largest cluster (km^2)	229.4	167.7 ± 0.4	106.0 ± 0.4	44.4 ± 0.3	linear

b) Variable clusters

Habitat response variable	**Kelp habitat loss treatment** 0	0.3	0.6	0.9	**Relationship with habitat loss treatment**
Area (km^2)	79.9 ± 6.9	57.1 ± 5.1	33.5 ± 3.1	11.0 ± 1.2	linear
Perimeter (km)	168.2 ± 11.9	185.7 ± 14.8	147.1 ± 13.1	61.0 ± 6.6	negative quadratic
Largest cluster (km^2)	229.4 ± 0	173.4 ± 1.7	106.7 ± 1.3	48.4 ± 1.1	linear
Number of clusters	25 ± 0	25.8 ± 0.1	28.7 ± 0.2	42.0 ± 0.3	exponential
Modularity score	0.87 ± 0	0.88 ± 0	0.89 ± 0	0.92 ± 0	exponential

a)



b)

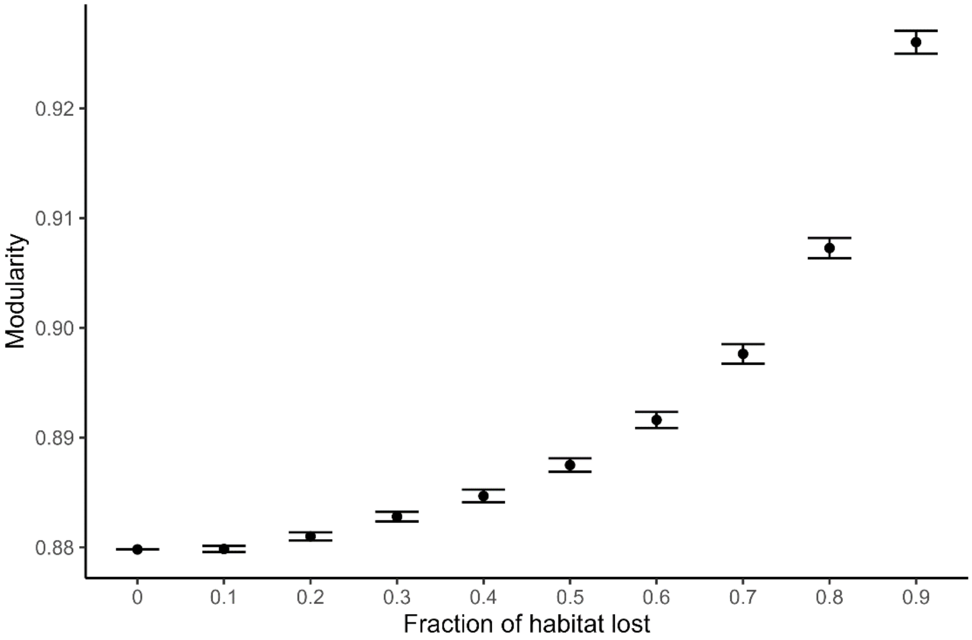


Figure 4.3: Clustering metrics from *in silico* habitat loss treatments for the variable clusters experiment a) Mean number of clusters for each habitat loss treatment and b) modularity score for clustering algorithm at each habitat loss treatment. Error bars represent the 95 % confidence interval across 100 random seeds.

4.4.2 Changes to habitat structure and configuration

With habitat loss increasing randomly in 10 % increments across the entire landscape, habitat clusters became patchy from the edges and within clusters simultaneously (Figure 4.4). Mean area (km^2) and area of the largest cluster (km^2) decreased linearly in both habitat loss experiments (Table 4.1, Figure C.1, C.2). In the “consistent cluster” experiment, mean cluster area was significantly larger, based on 95 % confidence intervals, for habitat loss treatments > 50 % than all lower ones (Figure C.1).

The relationship between habitat loss and average perimeter of clusters (km), resembles a negative quadratic function, whereby perimeter increases until an intermediate level of habitat loss (20 % for variable clusters and 30 % for consistent clusters), then decreases towards zero (Table 4.1, Figure 4.5). Mean perimeter for the “consistent cluster” experiment was significantly greater than the “variable cluster” experiment, based on the 95 % confidence intervals, for habitat loss treatments of ≥ 50 %. Mean perimeter became less than the control (no habitat lost) at 50 % and 60 % of habitat lost for the variable and consistent patch experiments, respectively.

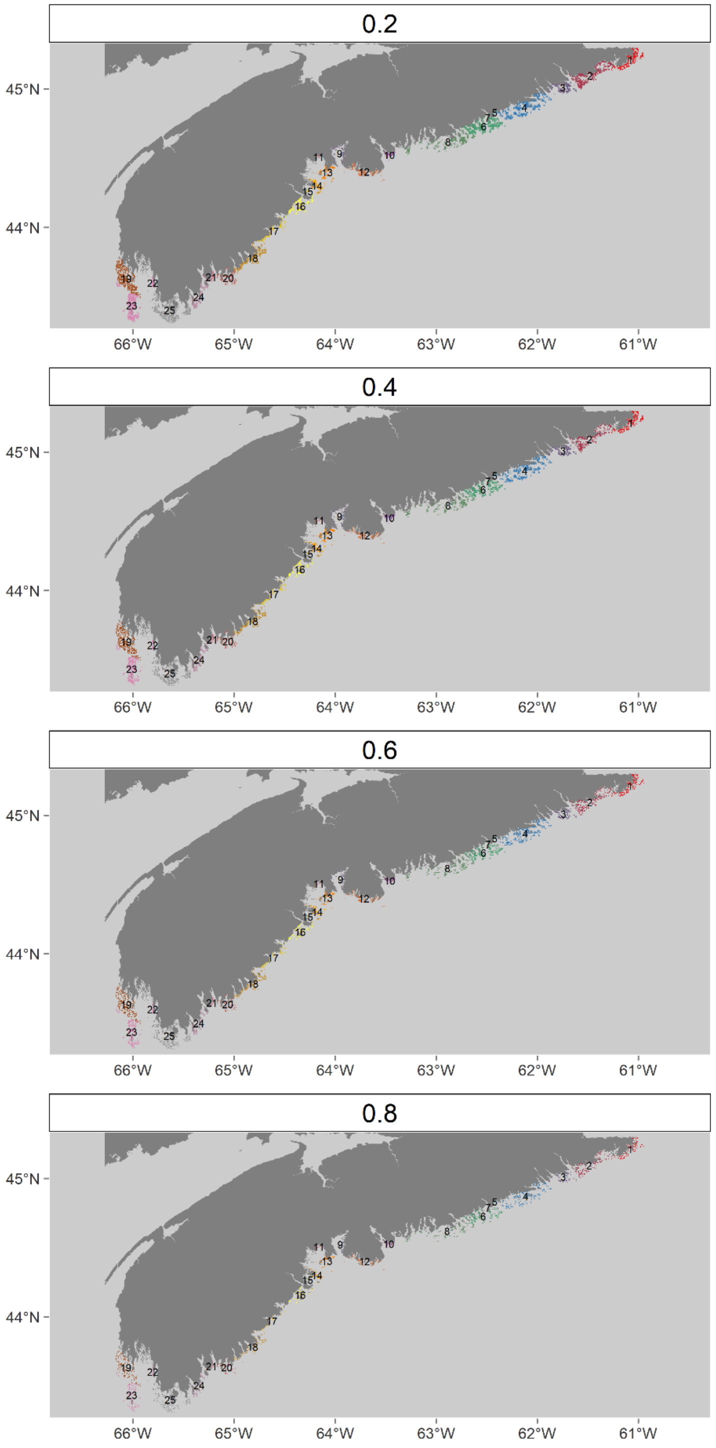


Figure 4.4: Example of the distribution of kelp habitat lost *in silico* for the consistent clusters experiment for one random seed. Each panel represents a different fraction of habitat lost for a subset of treatments.

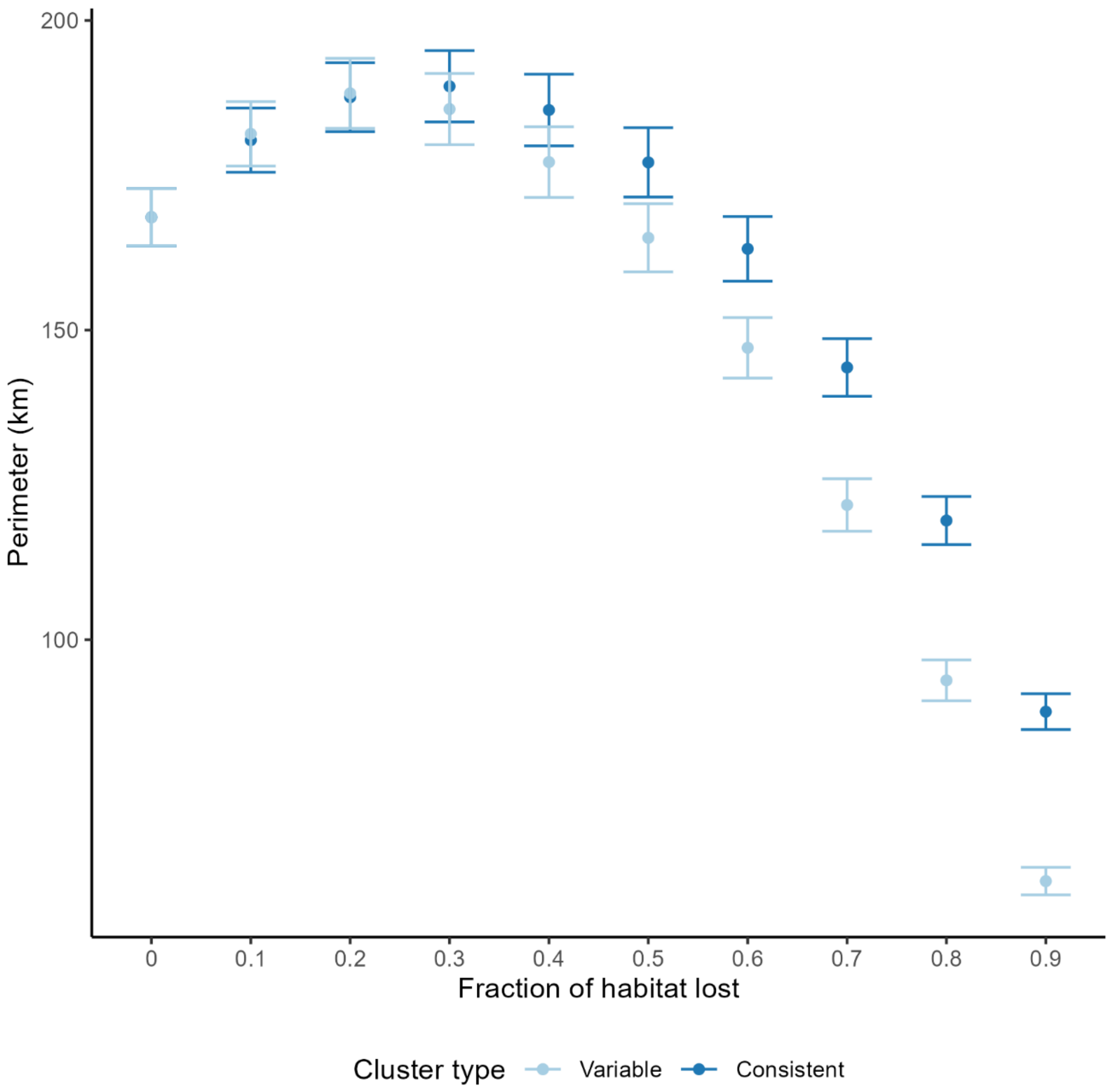


Figure 4.5: Mean perimeter across clusters for each habitat loss treatment shown for each of the two *in silico* habitat loss experiments, where clusters are either re-clustered (variable; light blue) or held constant (consistent; dark blue) after each habitat loss increment. Error bars represent the 95 % confidence intervals for each habitat loss treatment across 100 random seeds.

4.4.3 Changes to connectivity

For all habitat loss treatments, connectivity was greatest within clusters (Figure 4.6, 4.7) and weaker connections with adjacent clusters begin to diminish as more habitat was lost. Although some connections disappeared altogether, most connections remained intact, even at high levels of habitat loss. The relative contribution of self-replenishment compared to inflow was greatly unbalanced for all habitat loss treatments, with orders of magnitude greater self-replenishment, i.e. contribution from within patches (Figure 4.7). Inflow, a proxy for rescue potential, was very low for all clusters and treatments, accounting for only 3 % of incoming spores on average. The number of spores arriving at each cluster was also highly variable, but generally followed a negative quadratic relationship with fraction of habitat loss. The relative importance of clusters, according to PageRank, was highly variable among clusters, habitat loss treatments, and seeds (Figure 4.8). Few clusters showed consistent PageRank scores (cluster 2, 15, 22, 24). The relative importance of clusters to the overall network fluctuated, with PageRank of some clusters decreasing (clusters 8, 17, 18, 23) or increasing (clusters 2, 11, 14, 16, 19, 24) as habitat was lost. The remaining clusters showed no clear patterns with respect to Page Rank as habitat was lost.

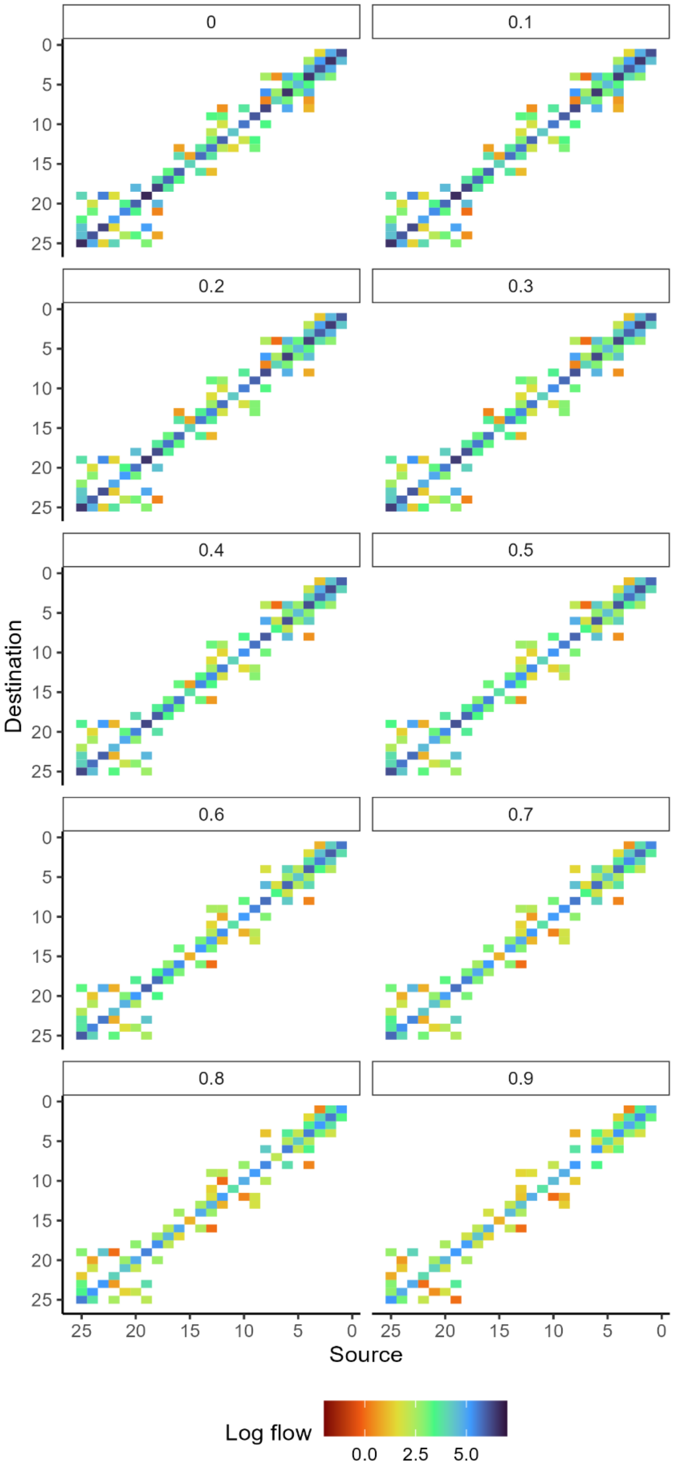


Figure 4.6: Example of connectivity matrices fragmented *in silico* for the consistent clusters experiment for one random seed. Each cell is coloured according to the sum flow over 23 dispersal simulations and grouped into 25 clusters (as mapped in Figure 4.2). Each panel represents a treatment, where the value above each panel indicates the fraction of habitat lost.

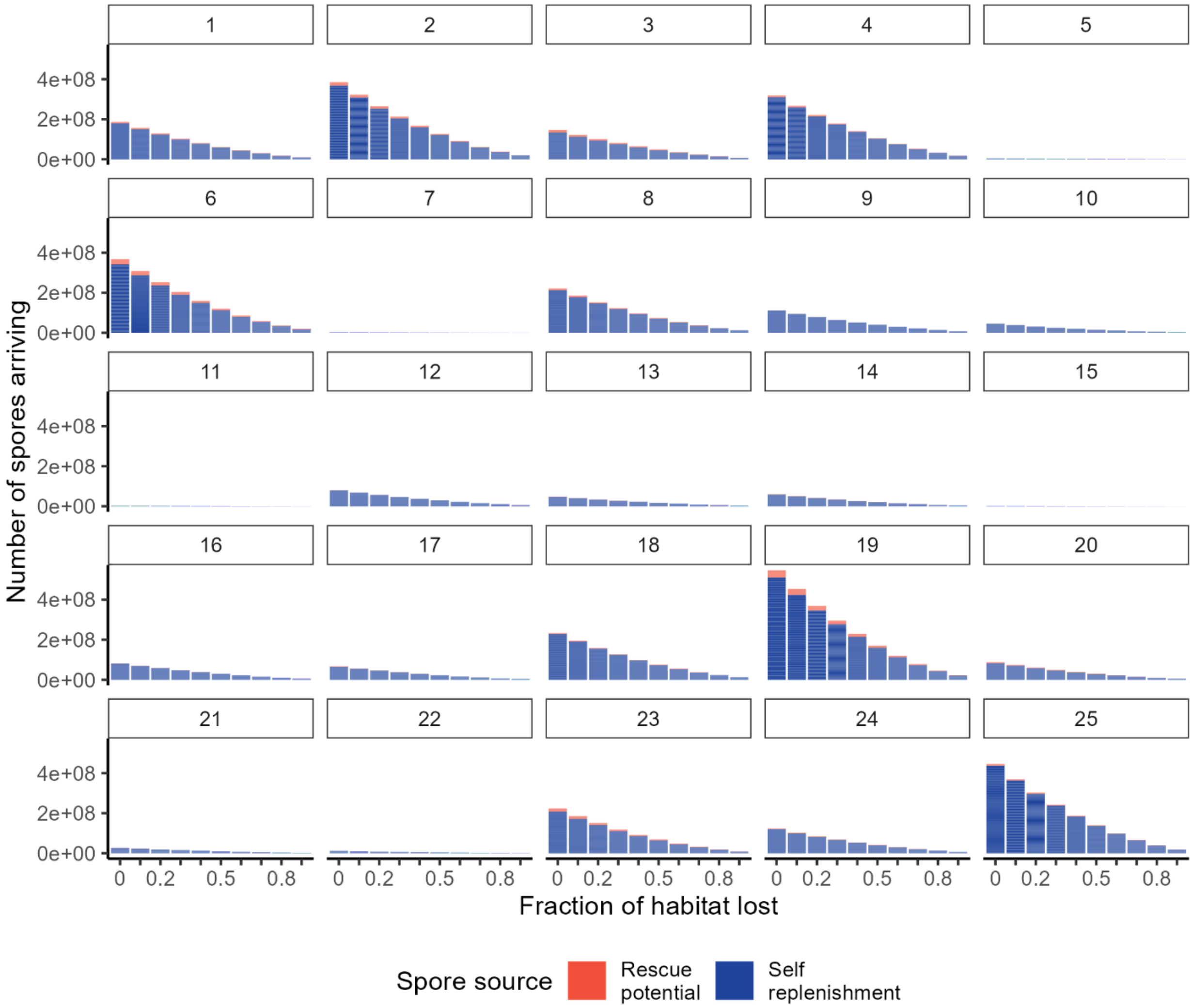


Figure 4.7: Relative contribution of rescue potential (inflow) versus self-replenishment for each cluster and habitat loss treatment for the consistent clusters experiment averaged across 100 random seeds. Each panel refers to a specific cluster, corresponding to labelled clusters in Figure 1.

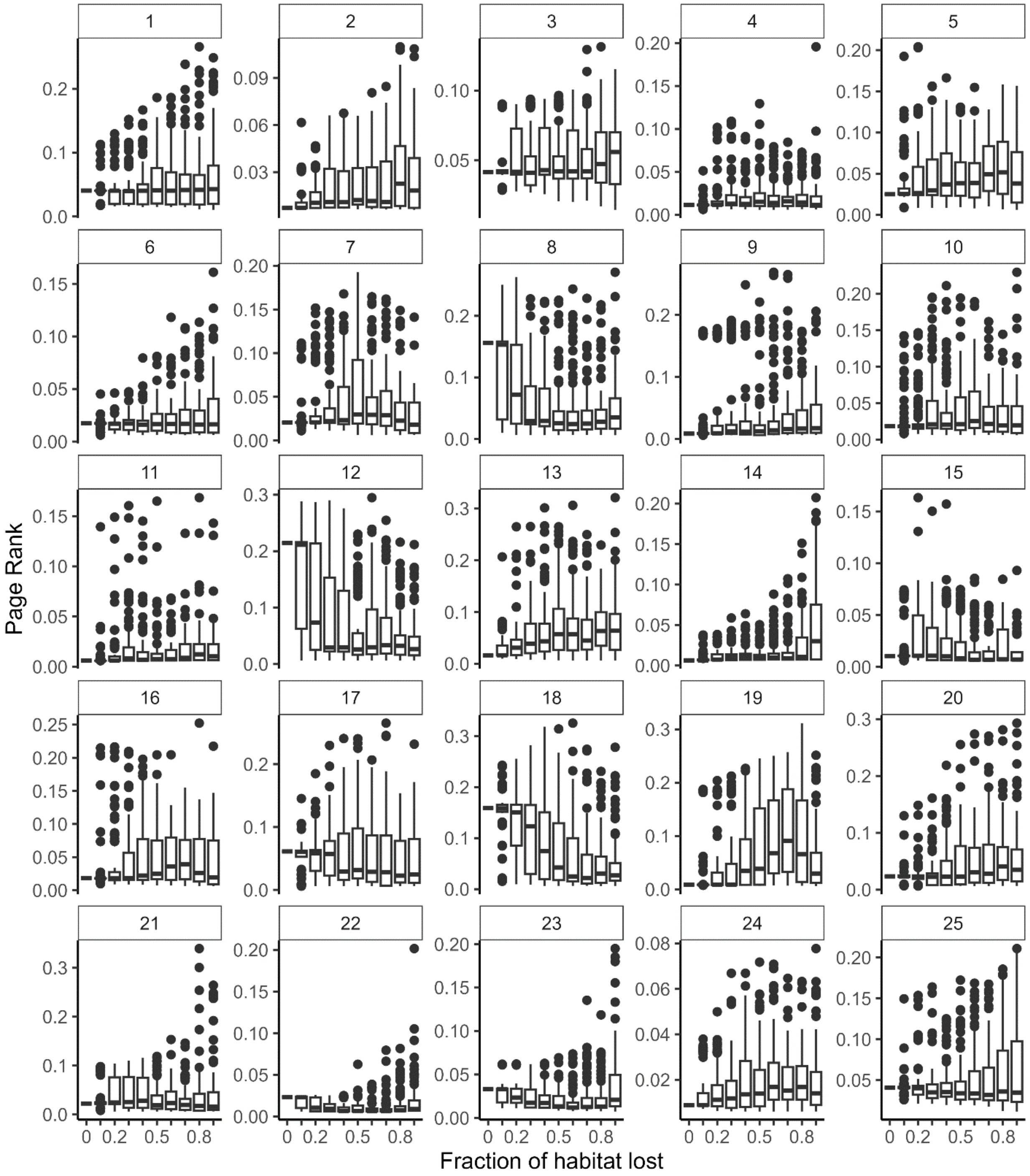


Figure 4.8: Page Rank for each cluster and habitat loss treatment averaged across 100 random seeds. Each panel refers to a specific cluster, corresponding to labelled clusters in Figure 4.2. Y-axis range differs for each panel.

4.5 Discussion

I measured the impact of kelp habitat loss on connectivity and habitat fragmentation measures in-silico including changes in patch structure and configuration, clustering, and graph theory metrics of connectivity. The effects of habitat fragmentation were not exacerbated until high levels of habitat loss (60 – 70 %). For all habitat loss treatments, over 90 % of propagules self-recruited within clusters denoted using a modularity approach. This suggests that degrading kelp bed patches cannot be rescued by adjacent clusters if habitat continues to degrade, and patches become locally extinct along the coast.

The persistence of kelp beds at a regional scale is highly dependent on self-recruitment. Limited flow between kelp clusters at all fractions of habitat loss reinforce that the rescue effect from neighboring populations will be insufficient to restore areas in decline or recolonize clusters gone locally extinct. The definition of patches or clusters is pivotal in this scenario, since patch size and connectivity are directly influenced by these decisions (Cavanaugh et al. 2014). Kelp spores have the potential to travel tens of m to several km, which are sufficient distances to connect neighboring kelp clusters (Gaylord et al. 2002, Reed et al. 2006) and is the spatial scale of dispersal I observed in this study. However, I found that the small contribution of inflow relative to self-recruitment meant that clusters were isolated from one another, with less than 3 % of spores received to each cluster from neighbors. High modularity scores (> 0.85) for all habitat loss treatments further support that clusters are functionally independent from each other, as modularity aims to minimize connections between clusters by definition (Newman 2006). The potential contrasting benefit of this configuration is that local extinction of one cluster will not negatively impact surrounding clusters. At the sub-cluster scale, although smaller than the spatial scale of this study, recruitment of juvenile kelps is only a limiting factor at very small patch sizes (< 1 m^2) (Layton et al. 2020). With this arrangement, protection efforts should likely be focussed on clusters with the largest area, as they have the greatest capacity to support dense populations (Hanski and Ovaskainen 2000).

There may be a critical threshold beyond which there is a disproportionately negative effect of habitat fragmentation on the seascape, coined the fragmentation threshold hypothesis. This hypothesis has received some research attention, but tends to be context dependent and is influenced by other factors such as the time over which habitat deteriorates and habitat configuration (Fahrig 2003, Swift and Hannon 2010). This is because losing habitat can have contrasting impacts on measures of habitat fragmentation, such as the number of clusters, distance between clusters, and average cluster area (Fahrig 2003). The notion of a critical threshold is intuitive ecologically and analogous to the tipping point or regime shift from a favourable (e.g. kelp dominated) to a less favourable (e.g. turf dominated) stable state. Beyond 70 % habitat loss, I observed an accelerated decrease in cluster perimeter and increase in the number of clusters as well as cluster isolation, indicated by modularity score. If, in-situ, these loses coincided with exposed bedrock instead colonized by turf-forming algal species, then this stable state would almost certainly be positively reinforced by sedimentation, lack of uncolonized substrate and decreased spore supply (Filbee-Dexter and Wernberg 2018). At high levels of habitat loss, edge effects also play a role on the abundance and diversity of associated species (Reeves et al. 2022) because animals will be less likely to traverse between patchy and sparse habitat patches (Swift and Hannon 2010). Finally, due to hysteresis, it will be preferable to maintain a kelp-dominated state than to rely on restoration strategies after a regime shift to a turf-dominated state.

Some measures of fragmentation followed expected theoretical relationships, while others did not. For example, mean patch size and total edge followed linear and negative quadratic relationships, respectively, which were also identified by Fahrig (2003). My results for the number of clusters showed an exponential increase and area of largest patch a linear decrease, which both differed from those from Fahrig (2003). This is likely because habitat cells removed at each habitat loss increment were selected randomly. This pattern likely deviates from what is to be expected in-situ; larger patches should be resilient to habitat loss, while smaller patches with a greater edge to area ratio are more likely to continue fragmenting and becoming locally extinct (Layton et al. 2020). Reeves et al. (2022) identified that patches with a perimeter to area ratio greater than 0.7 would undergo a phase shift to urchin barrens or turf for *Ecklonia radiata* in Southern Australia.

Future loss of kelp is likely inevitable due to cumulative impacts negatively affecting aspects of survival, both physiologically and physically (Filbee-Dexter and Wernberg 2018). However, quantifying the fraction and extent of habitat loss as well as the impacts this will have on the surrounding ecosystem remains unknown in our regional system. Some studies have addressed elements of this feedback, providing some insight. For example, Norderhaug et al. (2020) experimentally trawled a *Laminaria hyperborea* kelp bed to test the acute impact on kelp cover and ecosystem function in Norway using a BACI design. Trawling removed 26 % of kelp cover and caused negative impacts across four trophic levels. Over a longer timescale of two years, Shelamoff et al. (2020) measured sub-canopy epifauna associated with natural and artificially transplanted patches of *E. radiata* of patch sizes ranging from 0.12 to 7.68 m^2 and densities from 0-16 kelps m^{-2}. The authors found that epifaunal diversity decreased with decreasing kelp patch size and density, but that a turf-dominated benthos still supported high secondary productivity. More in-situ measurements of fine-scale changes in kelp cover in Nova Scotia will aid in our understanding of local changes to kelp beds, as considerably more research on habitat loss has taken place in Norway (van Son et al. 2020, Norderhaug et al. 2020), Australia (Reeves et al. 2022, Giraldo Ospina et al. 2023, Veenhof et al. 2023), and California (Bell et al. 2020). Although, there is some evidence to support that kelp beds in the Eastern Shore Islands of Nova Scotia are not currently recruitment limited, following the measurements of recruitment to naturally seeded hard substrate at two sites (Charness and Metaxas, unpublished data).

In conclusion, I demonstrated that self-recruitment was the dominant contributor to cluster replenishment, and that inflow from other, surrounding clusters provided only a slight proportion of propagules (3 %), suggesting minimal opportunities for rescue potential. Additionally, I provided some evidence to support the fragmentation threshold hypothesis. However, further research on species associated with kelps is needed to determine if these negative impacts extend to the ecosystem level. In this study, I identified the tipping point for kelp to be between 70-80 % habitat loss, beyond which the negative impacts of fragmentation are accelerated. Fragmentation alone therefore may not exacerbate the negative impacts of habitat loss unless the proposed critical threshold is surpassed. This may provide a silver lining for kelp beds already facing cumulative impacts, such as those in Nova Scotia and among other warming hotspots.

CHAPTER 5

BUILDING CONNECTED MPA NETWORKS TO SUPPORT NATIVE HABITAT BUILDERS WHILST HINDERING INVASIVE SPECIES

5.1 Abstract

Efforts to include patterns of connectivity in the design of marine protected areas (MPAs) tend to focus on maximizing protection for areas that are stepping-stones, source populations or self-sustaining populations; however, they often fail to consider the potential that these areas may facilitate "bad" negative vectors of connectivity, such as invasive species or pathogens. In Nova Scotia, the invasive epiphyte *Membranipora membranacea* has been shown to cause widespread defoliation of kelp beds, an important ecosystem engineer in the shallow subtidal. To determine which areas should be prioritized to maximize connectivity for kelp *and* minimize connectivity of *M. membranacea*, I used Marxan and Marxan Connect, two complementary spatial planning tools. First, I generated estimates of dispersal and connectivity for both species with a biophysical modelling approach by integrating species life history information with hindcast ocean current data from a Finite Volume Community Ocean Model. I tested five different conservation planning scenarios that prioritized different connectivity features. I identified potential priority areas to simultaneously support conservation objectives associated with maximizing connectivity for kelp and minimizing connectivity for *M. membranacea*. I also found that specific connectivity objectives resulted in the selection of different priority areas for conservation, supported by clear differentiation in both hierarchical clustering and a principal coordinates analysis. Considering dispersal pathways for invasive species and pathogens is an important consideration for designing MPAs, particularly in an ocean warming hotspot such as Nova Scotia, which is susceptible to invasions from non-native species.

5.2 Introduction

Coastal oceans are under cumulative pressures from invasive species (Denley et al. 2019b, Garbary et al. 2021), increased ocean temperatures (Lotze et al. 2022), increased frequency and intensity of storms, and ocean acidification (Bernier et al. 2018). It is therefore important to focus marine protection on habitat forming species that provide ecosystem services such as driving primary productivity, enhancing secondary productivity, storing carbon and providing a three-dimensional habitat for various marine organisms (Vásquez et al. 2014, Smale et al. 2020, Eger et al. 2023). International targets for marine protection provide the mechanism by which many countries can enact protection in their exclusive economic zones (CBD 2022). In particular, Target 3 of the Kunming Montreal global biodiversity framework, that aims to protect 30 % of national waters by 2030 as "well-connected" systems of protected areas, is relevant for mitigating stressors. Carefully designing networks of marine protected areas (MPAs) to provide combined benefits that exceed those of individual MPAs improves network performance and resilience in the face of climate change (Magris et al. 2018, Harrison et al. 2020, Goetze et al. 2021). One such consideration, that has not received much attention in the literature, is the notion of minimizing "bad" agents of connectivity such as invasive species, pathogens, or pollutants while simultaneously prioritizing "good" connectivity for other species, such as habitat formers or commercially important species.

Considerable effort has been placed on prioritizing protection for connectivity hubs, stepping stones, or self-sustaining populations because of conservation benefits related to resilience, ecosystems services, and spillover effects (Kough et al. 2019, Frys et al. 2020, Abecasis et al. 2023). However, these marine corridors may also serve as pathways for pathogens or invasive species (McClanhan et al. 2002). Kelp forests provide an important biogenic habitat along 25 % of the worlds coastline, but 38 % of these forests have been in decline over the past 50 years (Krumhansl et al. 2016). These declines are associated with regime shifts to a turf-dominated benthos, mediated by kelps vulnerability to changing ocean conditions such as increased temperature and storm frequency (Simonson et al. 2015, Filbee-Dexter and Wernberg 2018, Vergés et al. 2019). In Nova Scotia, kelps are under siege directly and indirectly through the dispersal of invasive species and epizootics, respectively. An invasive epiphyte, the colonial bryozoan, *Membranipora membranacea*, has contributed significantly to the decline of kelp beds by compromising their structural integrity and making them more susceptible to breakage from wave action (Schwaninger 2008, Krumhansl et al. 2011). Because the bryozoan has planktonic larvae, minimizing connectivity for *M. membranacea* through larval dispersal is an important objective when delineating protection for kelp bed habitat.

Ecological connectivity has been applied to marine conservation primarily through the use of rules of thumb or size and spacing guidelines for MPAs (Balbar and Metaxas 2019, Beger et al. 2022). However, only a few examples of connected networks of MPAs exist to-date (Grorud-Colvert et al. 2014) from which we can learn lessons to improve the design of future networks. For example, the network of MPAs in California was designed with connectivity size and spacing guidelines, but even by their 10-year management review, managers still do not fully understand connectivity patterns in the region (California Department of Fish and Wildlife 2022). Post-hoc evaluations of networks of MPAs in the Mediterranean and Western Africa have revealed that sites identified as connectivity hotspots or stepping-stones are not protected in the current network configuration (Andrello et al. 2013, Assis et al. 2021). A drastic increase in computational capacity now permits more complex connectivity analyses, giving rise to the potential to *design* the new wave of MPAs as connected, rather than evaluating connectivity in networks post design or implementation.

Defining, measuring, and applying connectivity to reach high-level conservation objectives for local or regional systems remains a challenge for both scientists and marine practitioners (Beger et al. 2022). Firstly, definitions, and therefore, interpretation of connectivity vary depending on the measurement method and ecological scale. For instance, genetic measurements of connectivity elucidate patterns over several generations, whereas particle tracking with physical ocean models identifies patterns over a single generation (Hedgecock et al. 2007, Johnson et al. 2018). Secondly, patterns of connectivity in the ocean are dependent on regional oceanographic patterns and dominant forcings making it difficult to generalize patterns across taxa and basins, particularly as ocean circulation patterns may change with climate change (Silva et al. 2021). Coastlines still prove particularly challenging systems for quantifying connectivity because of the complex interplay of physical oceanographic processes such as currents and tides and coastal morphology (Werner et al. 2007). Thirdly, translating information on patterns of connectivity to metrics that can be applied to inform conservation decisions is difficult because connections are not easily represented as area-based features, as is the case for representation and replication objectives.

Spatial prioritization software and biophysical modelling are two important tools that facilitate the inclusion of spatial relationships between habitats or populations into the design of networks of MPAs. One such tool, called Marxan, is a decision support tool that was developed to help practitioners achieve a set of spatial biodiversity protection targets, whilst minimizing cost for a collection of spatial planning units (Ball et al. 2009). Linkages between planning units, called spatial dependencies, can be incorporated into the objective function as the weighted boundary between each pair of planning units (Beger et al. 2010). This approach has been applied to a considerable number of marine, freshwater, and land-based conservation projects (Tulloch et al. 2021, Hermoso et al. 2021, Andrello et al. 2022). A newly developed preprocessing tool for Marxan, called Marxan Connect, introduced an area-based method for incorporating knowledge of connectivity patterns based on graph theory metrics derived from connectivity matrices (Daigle et al. 2020). Muenzel et al. (2022) suggest that the spatial dependency method is more suitable for species with poor dispersal or for highly degraded habitat outside of protected areas. Computing connectivity metrics using graph theory from dispersal trajectories is a routine approach for estimating connectivity of planktonic propagules, but a requirement for this analysis is resolved ocean currents in the form of a physical ocean model. An example of a model suitable for coastal systems is a Finite Volume Community Ocean Model (FVCOM) because its unstructured grid can resolve complex topography and sub-mesoscale oceanographic processes, such as tides, resulting in a high spatial resolution horizontally (100s of m) and vertically through a bathymetry following scheme (Chen et al. 2003, Feng et al. 2022). Planktonic propagule duration, competent propagule duration (Goetze et al. 2021, Cecino and Treml 2021), and time of spawning parameters can be implemented into FVCOM to represent the life histories of different species.

In this chapter, I evaluate differences in the configuration of conservation priority sites under the contrasting objectives of maximizing connectivity for poorly dispersing native kelp and minimizing the dispersal of the invasive species that smothers kelp, with the broad goal of protecting kelp bed habitat using the decision support tool Marxan and preprocessing tool, Marxan Connect (Ball et al. 2009, Daigle et al. 2020). I test five different scenarios by employing connectivity-based conservation priorities, as either spatial dependencies or conservation features, to examine if connectivity for a habitat builder and associated threat can be simultaneously prioritized. I hypothesize that the contrasting life history strategies of kelps and *M. membranacea* will produce opposing dispersal patterns that are difficult to encapsulate in one network design. This study can provide complementary science advice to ongoing MPA network planning in the Maritimes region of Canada.

5.3 Methods

5.3.1 Study area

This case study spans the Atlantic coast of Nova Scotia, Canada, that supports kelp beds in various conditions, ranging from healthy to degraded (Figure 5.1ab). Observations of kelp presence, abundance, percent cover, or biomass have been collected along the coast since the 1980s (Moore and Miller 1983, Moore et al. 1986, Filbee-Dexter et al. 2016). However, a continuous map of suitable habitat throughout this domain was incomplete. I created a habitat suitability map in two steps. First, I collated observational data on kelp presence and absence by reviewing the literature. I then predicted the location of suitable habitat for kelp beds at a spatial resolution of 630 m by 630 m with a random forest model with five geomorphic predictors: depth, slope, fine scale bathymetric position index, relative wave exposure, and presence of hard substrate. Analyses were conducted in R (version 4.2.0) using the *randomForest* (version 4.7-1.1) package. I split the data into training (2/3) and validation (1/3) datasets, with model performance evaluated as the area under the precision-recall curve. The output of the model (probability of occurrence) was converted to presence/absence using a threshold of

0.55, decided upon using the area under the precision-recall curve (Saito and Rehmsmeier 2015). Additional details on this methodology can be found in Appendix C.1.

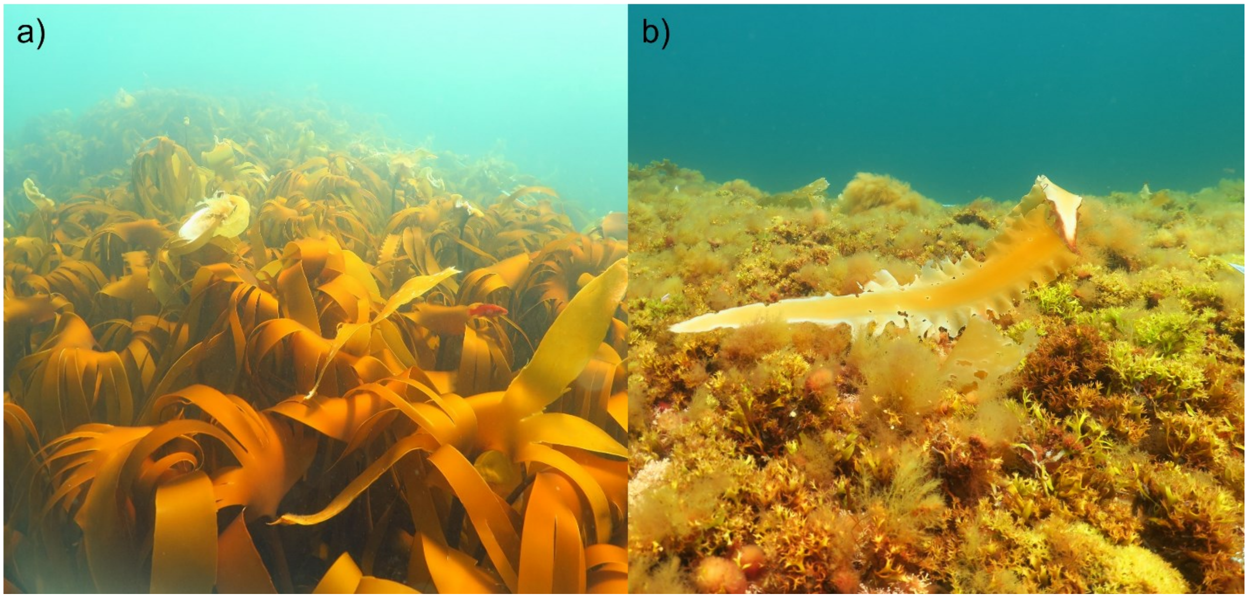


Figure 5.1: (a) Healthy and (b) degraded kelp beds (*Laminaria digitata* [dominant] and *Saccharina latissima*) along the Eastern Shore Islands of Nova Scotia.

To better represent a spatial scale appropriate for management, I grouped kelp suitable habitat from the 630 m by 630 m grid cells to kelp patches using modularity optimization and additional validation observations. Modularity is a greedy algorithm that divides nodes into patches based on weighted edges between each pair of nodes (Newman 2006). The algorithm optimizes patches into groups with many edges within patches and few edges between patches (Clauset et al. 2004). A modularity approach is preferred over patches defined by contiguity, particularly for a semi-continuous habitat like kelp. This is because a contiguity definition tends to agglomerate multiple independent, but adjacent, sub-populations into meta-patches (Cavanaugh et al. 2014). To delineate patches, I calculated a distance matrix between all pairwise suitable habitat cells using least cost path (Cavanaugh et al. 2014); Links between patches were considered intact if cells were within 1.5 km of each other to reflect the spatial scale of patterns I wanted to detect. From the original 5252 suitable habitat cells, I delineated 228 kelp patches using the *cluster_louvain* function in the *igraph* package (version 1.3.4) (Csardi and Nepusz 2006). Since mine is a conservation prioritization study, I was only concerned with larger patches with a relatively significant contribution to kelp populations, and thus removed patches smaller than 5 km^2. I also removed patches with validated modern absence records (2010 or newer) since kelp habitat is ephemeral and suitable habitat does not necessarily convert to the presence of habitat. Thus, I obtained 73 kelp bed patches, ranging in extent from 5 to 75 km^2, which serve as planning units for my conservation prioritization (see 5.3.3 Planning Scenarios).

5.3.2 Generation of connectivity estimates with biophysical models

I calculated dispersal trajectories of kelp spores and bryozoan larvae using a Lagrangian particle tracking module forced by 3-D velocity fields derived from a hydrodynamic model based on the Finite-Volume Community Ocean Model (FVCOM) (Chen et al. 2003). The model domain is constructed from an unstructured triangular mesh, ranging in spatial resolution from approximately 100 m along the coast to several kilometers in the open ocean. In the vertical direction, depth levels are bathymetry-following, also called sigma levels (Griffies et al. 2000), which allow for efficient representation of complex bottom topography and higher spatial resolution in shallow coastal areas. The model is driven by atmospheric forcing from the surface and by open boundary conditions along the lateral boundaries. The model developers evaluated model outputs against observed water elevations, currents, temperature, and salinity. More detailed description and information about the model setup and validation can be found in Feng et al. (2022).

I produced connectivity estimates for kelp spores and larvae of the invasive bryozoan *Membranipora membranacea* by parameterizing life history traits typically used in biophysical dispersal models, such as planktonic duration (Jahnke et al. 2018). For both species, propagules were released from all 73 habitat patches in a grid-like configuration so that each release location was unique. The number of particles released was binned proportionally to the area of each patch. Propagules were tracked as passive particles for 2 and 28 days, and began to settle after 0.5 hours and 14 days, for kelps and *M. membranacea*, respectively (Saunders and Metaxas 2007). Emulating natural reproduction periods, I ran 28 dispersal events for each species, starting on October 1 for kelps and July 1 for *M. membranacea*, and every 5 days after, for a total of 14 releases in both 2018 and 2019 (Saunders and Metaxas 2010) (Table D.1, D.2, D.3).

I determined the settlement location for each particle by assigning a settlement time (between 0.5 hours and 2 days for kelps, and between 14 days and 28 days for *M. membranacea*) based on probabilities associated with a half-normal distribution. I defined the dispersal kernels as a normal distribution ($\mu = 14$, $\sigma = 4.67$ for *M. membranacea* (days); $\mu = 0.5$, $\sigma = 16$ for kelps (hours)), with 99.7 % of particle trajectories falling within the competent propagule duration of each species. I randomized the assignment of settlement times amongst the 28 dispersal events, such that each particle released from the exact same location settled at a different time. Finally, particle end locations were intersected with kelp patches using the *st_intersect* function from the sf package (version 1.0-9) to populate 28 connectivity matrices per species, which were then averaged to produce one connectivity matrix per species.

I applied a graph theoretic approach to provide insight into the complexities of the connectivity matrices (Frys et al. 2020). Specifically, I calculated local retention, self-recruitment, betweenness, PageRank, out-strength, and in-strength from appropriately formatted flow, probability, or migration matrices, depending on the metric (Table 5.1). Each metric was selected because of its potential to inform conservation (Table 5.1). The metrics calculated for each species differed depending on the conservation objective for each planning scenario (see 5.3.3 Planning Scenarios for details). To apply these metrics to conservation planning scenarios, I discretized all metrics to the top quartile, following protocol for Marxan Connect (Daigle et al. 2020). I then applied these discretized metrics as conservation features in the decision support tool Marxan.

5.3.3 Planning scenarios

To assess potential spatial conservation planning strategies and identify priority management areas to meet specific connectivity conservation objectives, I tested different planning scenarios with the decision support tool Marxan with connectivity (Ball et al. 2009, Beger et al. 2010). All supporting analysis was carried out in R (version 4.2.0)

Table 5.1: Graph theory metrics and associated conservation benefits.

Graph theory metric	Description	Matrix type	Potential conservation benefit
Local retention	Proportion of propagules originating from a planning unit that are retained within that planning unit (Botsford et al. 2009).	Probability	Self-replenishment potential
Self-recruitment	Proportion of propagules arriving at a planning unit that originated from that planning unit (Botsford et al. 2009).	Migration	Patch isolation
Betweenness	The number of shortest paths that pass through a focal planning unit (Minor and Urban 2007).	Probability	Stepping stones
PageRank	Importance of a planning unit based on the number and weight of connections with other planning units (Kininmonth et al. 2019).	Probability	Network-wide source/rescue potential
Out-strength	Number of propagules originating from a planning unit and settling in a different planning unit (Urban and Keitt 2001).	Flow	Node-based source potential
In-strength	Number of propagules settling at a planning unit that originated from a different planning unit (Urban and Keitt 2001).	Flow	Node-based rescue potential

(R Core Team 2020), Marxan Connect (Daigle et al. 2020), and the running of Marxan took place in the command window.

The objective function governing Marxan's heuristic prioritization aims to minimize the cost and boundary length of a network of planning units whilst achieving a set of conservation targets (Ball et al. 2009).

$$\sum_{PUs} Cost + BLM \sum_{PUs} Boundary + \sum_{\substack{Con\\Value}} FPF \times Penalty = Score \text{ (Equation 1)}$$

In equation 1, PU refers to planning units, BLM is the boundary length modifier used to tune the weight of boundaries or spatial dependencies between PUs, and FPF is the feature penalty factor used to penalize unmet conservation targets. The sum of these three terms is the score, where the lowest score represents the best solution. I selected a cost metric that was directly related to an opportunity cost associated with designating marine protected areas in the coastal zone. Cost was calculated from inshore lobster landings from 2015-2019 (Serdynska et al. 2022) as the average number of lobster traps per km^2 for a 50-km radius from each patch centroid (Figure 5.2b). Lobster is the Nova Scotia's largest seafood export and has increased in landings by nearly 600 % since the 1980s (DFO 2021). Conservation targets reflected priorities for achieving different connectivity objectives compared to a representativity baseline scenario. I tested one baseline scenario and four connectivity-based scenarios (Table 5.2) that reflected different connectivity attributes for both kelps and *M. membranacea*. The objective of the baseline scenario ($K_{baseline}$) was to protect 30 % of the highest quality kelp habitat. I used a proxy of habitat quality as the amount of habitat in each patch, calculated as the average probability of occurrence from the raw output of the random forest model (Figure 5.2a). I applied 1 000 000 iterations, 100 runs, and a species penalty factor of 10 for each conservation feature for each Marxan scenario.

Table 5.2: Details on Marxan scenarios and objectives.

Scenario	**Conservation Target**	**Operationalization**
$K_{baseline}$	Representation baseline	Protect 30 % of kelp patches
$K_{spatial}$	Prioritize patches with strongest spatial dependencies and self-replenishment of kelps	Protect 30 % of kelp patches + 50 % of the top quartile of local retention of kelp + spatial dependencies between kelp patches
$K_{network}$	Prioritize patches with the greatest network-wide connectivity of kelps	Protect 30 % of kelp patches + 50 % of the top quartile for each of: betweenness, PageRank, and out-strength of kelp
$K_{spillover}$	Balance isolation with spillover for kelps	Protect 30 % of kelp patches + 50 % of the top quartile for each of: self-recruitment and out-strength of kelp
M_{source}	Prioritize patches with lowest source/rescue potential of *M. membranacea*	Protect 30 % of kelp patches + 50 % of the bottom quartile for each of: out-strength and in-strength of *M. membranacea*

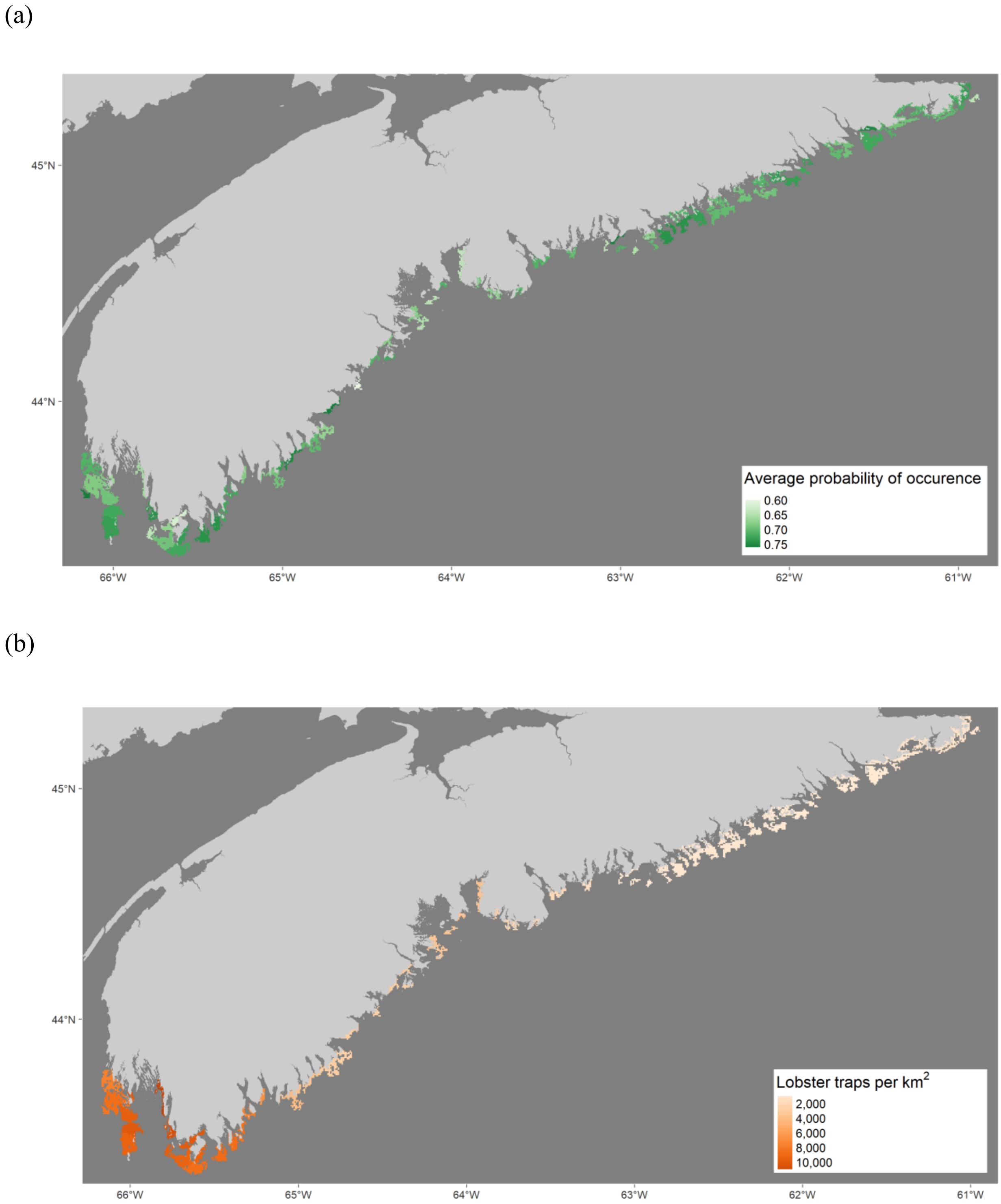


Figure 5.2: (a) Average probability of occurrence (amount in Marxan analysis) and (b) Lobster traps per km^2 (cost metric in Marxan analysis) for irregular planning units, representing suitable habitat for kelp beds, along the Atlantic Coast of Nova Scotia.

Connectivity-based scenarios (2-5) employed functionality from the pre-processing tool Marxan Connect to test different connectivity-based objectives in Marxan as either spatial dependencies or discretized conservation features (Daigle et al. 2020). All connectivity scenarios included the representativity targets from the baseline scenario. Scenario 2 ($K_{spatial}$) applied the spatial dependency method by setting the boundary file as the probability matrix for kelps as well as local retention as conservation features. For the spatial dependencies' method, an additional parameter, called the connectivity strength modifier, is tuned to balance the cost of solutions with overall boundary length (Beger et al. 2010). For the local retention conservation feature, and all other connectivity-based conservation features, I applied a 50 % target to the top quartile of planning units (Table 5.2). In scenario 3 ($K_{network}$), I aimed to prioritize kelp patches with the greatest network-wide (the Atlantic Coast of Nova Scotia) connectivity among kelp patches. I selected three connectivity metrics: betweenness centrality, PageRank, and out-strength to operationalize this objective. In a fourth scenario ($K_{spillover}$), I instead prioritized patches that balanced isolation of kelp patches with spillover. Two connectivity metrics reflected this objective: self-recruitment and out-strength. Lastly, in scenario 5 (M_{source}), I prioritized kelp patches that were least likely to be sources or have high rescue potential for the invasive bryozoan *M. membranacea*. I operationalized this objective with in-strength and out-strength metrics for *M. membranacea*.

5.3.4 Comparison of conservation priorities across scenarios

To compare spatial similarity of all 100 Marxan solutions for each scenario, I calculated a Jaccard similarity matrix with the *vegdist* function in the *vegan* package (version 2.6-4) (Oksanen et al. 2022). The Jaccard similarity method is appropriate because it both excludes joint absences and is constructed explicitly for binary output data, following the solution output structure from Marxan (Harris et al. 2014). Jaccard similarity ranges between 0 and 1, where 1 represents 100 % spatial overlap. I then applied hierarchical clustering using the *hclust* function in the *stats* package to compare solutions within and between scenarios (Harris et al. 2014, R Core Team 2020). I visualized these results as a dendrogram of Jaccard distance (1-similarity) using the

ColorDengrogram function from the *sparcl* package (Witten and Tibshirani 2018) and a principal coordinates (PCoA) plot using the *wcmdscale* function in the *vegan* package (Oksanen et al. 2022) by adapting code from (Teschke et al. 2022).

Selection frequency is also a strong indicator of planning unit importance and can highlight spatial overlap between solutions (Stewart and Possingham 2005). I calculated Cohen's kappa, a pairwise statistic that is used to compare interrater variability (McHugh 2012), to compare to the extent to which selection frequency of patches overlaps among scenarios. This statistic ranges between -1 to 1, with 0 indicating the level of agreement expected due to chance, 1 indicating perfect agreement, and -1 indicating no agreement (McHugh 2012). Following established methods (Ruiz-Frau et al. 2015, Teschke et al. 2022), I classified patch selection frequency into five classes (0, <25%, 25-50%, 50-75%, > 75%). Since I are studying an ecological system, I used the original interpretation of the Cohen's kappa statistic (McHugh 2012), where values greater than 0.41 and 0.61 indicate moderate and substantial agreement, respectively. I calculated Cohen's kappa for all five classes using the *irr* package (version 0.84.1) (Gamer et al. 2019).

5.4 Results

5.4.1 Graph theoretic metrics of connectivity

As anticipated, there was little overlap in the spatial distribution across patches of the different graph-theoretic metrics for both kelps and *M. membranacea* (Figure 5.3). For kelp, local retention and self-recruitment were highest for patches in the easternmost region of the domain as well as in proximity to Halifax (Figure 5.3a). By contrast, patches with the highest Page Rank were distributed throughout the domain (Figure 5.3 b). Betweenness centrality and out-strength peaked in the central domain from Sheet Harbour to LaHave and along the southwest shore from Port Joli to Lobster Bay, respectively (Figure 5.3c,d). For *M. membranacea*, out-strength was lowest in the areas around Lobster Bay and around Halifax and in-strength was lowest for patches scattered along the coastline with no concentrated areas (Figure 5.2e,f).

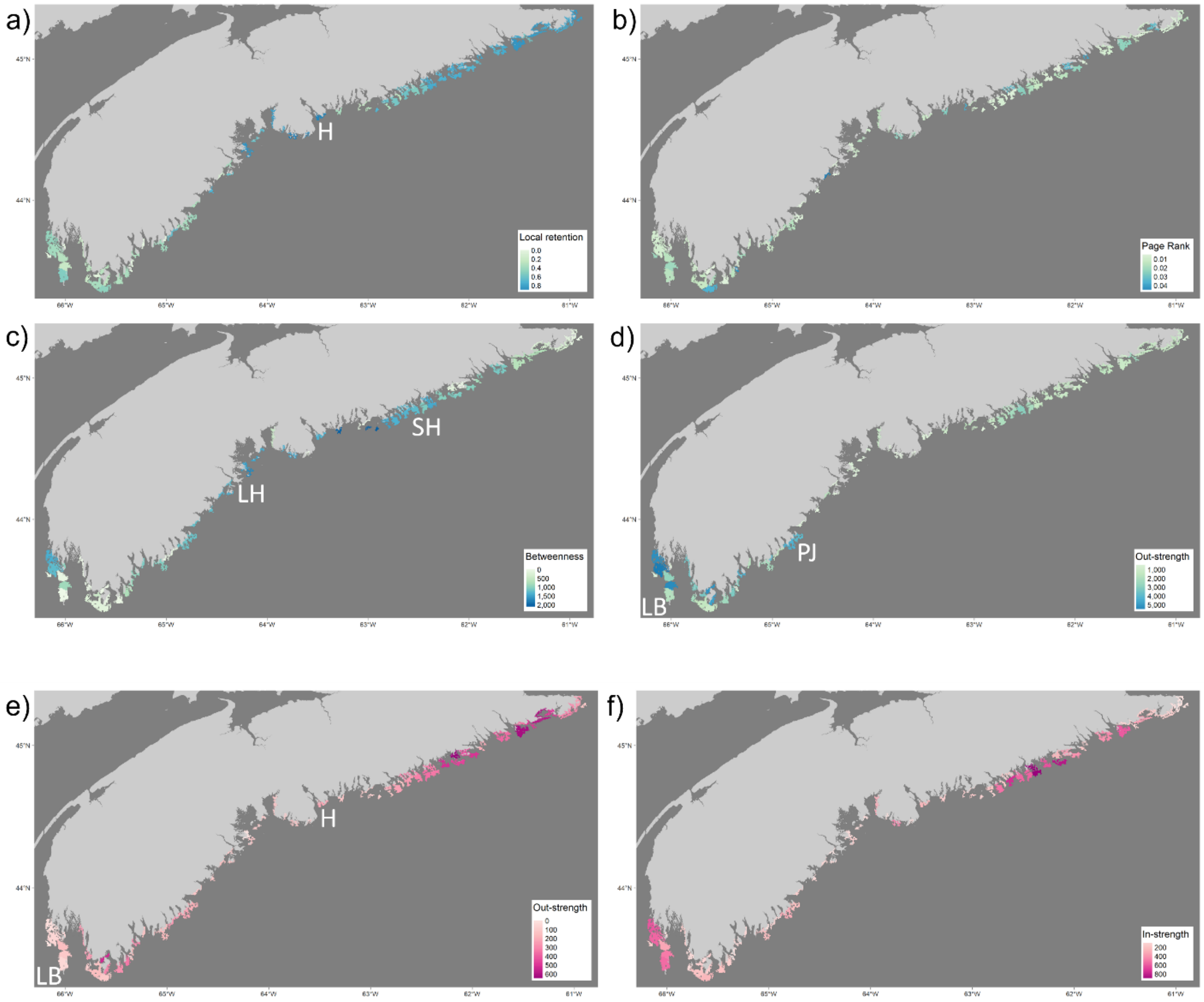


Figure 5.3: Graph theory metrics of connectivity for kelp patches (green) and *Membranipora membranacea* (pink). (a) Local retention, (b) PageRank, (c) Betweenness, (d) Out-strength, (e) Out-strength, (f) In-strength. Not shown: Self-recruitment for kelps (patterns comparable to local retention). White letters correspond to specific regions along the coast (H = Halifax, LH = LaHave, SH = Sheet Harbour, LB = Lobster Bay, and PJ = Port Joli).

5.4.2 Marxan scenario outputs

The distribution of selected patches (selection frequency) varied by scenario. For $K_{baseline}$, most selected patches were along the eastern shore of Nova Scotia, the region with lowest cost (Figure 5.2b, Figure 5.4a). Selection frequency for $K_{spatial}$ was the most variable, with 28 (39%) patches showing a selection frequency between 30 and 60, and only 4 (5 %) patches with a selection frequency above 60 (Figure 5.4b). Selection frequencies for $K_{network}$ and $K_{spillover}$ were more polarized with 31 and 21 patches having a selection frequency of 0 and 19 and 14 patches having a selection frequencies greater than 80, respectively (Figure 5.4c,d). These two scenarios also spanned the entire coast, selecting a greater number of higher cost patches. Lastly, selection frequency for M_{source} was greatest in the central region and eastern domain, with no patches selected along the southwestern shore south of Liverpool (Figure 5.4e).

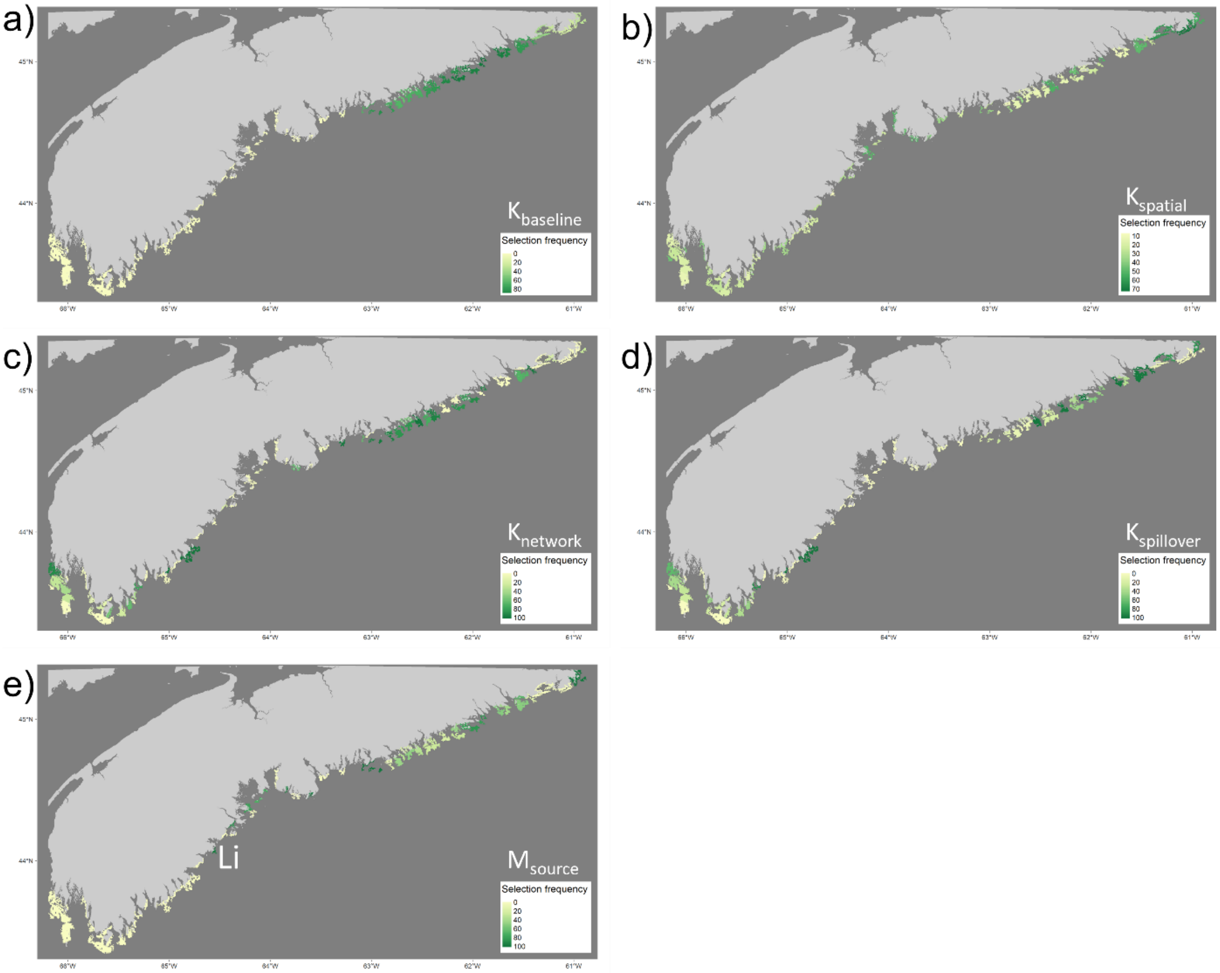


Figure 5.4: Selection frequency of Marxan planning scenarios. See Table 5.2 for a description of the conservation priorities for each scenario. (a) $K_{baseline}$, (b) $K_{spatial}$, (c) $K_{network}$, (d) $K_{spillover}$, (e) M_{source}. White letters correspond to specific regions along the coast (Li = Liverpool).

5.4.3 Spatial similarity between solutions and scenarios

Hierarchical clustering and the PCoA biplot highlight that $K_{spatial}$ is the most dissimilar to all other scenarios (Figure 5.5). $K_{spatial}$ also had the greatest flexibility in terms of solutions, indicated by the greatest range in dissimilarity in the dendrogram and dispersed cluster in the PCoA plot (Figure 5.5). Cohen's Kappa for all pairwise comparisons with $K_{spatial}$ were all below zero, indicating complete disagreement between solution pairs (Table 5.3). Two pairs of scenarios had fair agreement according to Cohen's Kappa; $K_{baseline}$ and M_{source} scenarios with a score of 0.35 and $K_{network}$ and $K_{spillover}$ with a score of 0.3. In the PCoA biplot, all M_{source} scenarios cluster to the far right of dimension one, showing clear differentiation from the other four scenarios (Figure 5.5b).

Four patches were always prioritized when maximizing kelp connectivity (e.g., $K_{network}$) and minimizing *M. membranacea* connectivity (M_{source}), whereas 18 patches were rarely selected; 33 patches selected more often for $K_{network}$ and 18 patches selected more often for M_{source} (Figure 5.6). Patches with a higher selection frequency for kelp connectivity were located in Port Joli, Yarmouth, Eastern Passage, and parts of the Eastern Shore Islands. Patches with a higher selection frequency for minimizing *M. membranacea* connectivity were scattered across the entire spatial domain, but tended to be isolated patches close to the coastline, as opposed to associated with islands.

Table 5.3: Cohen's Kappa for all pairwise scenarios using categorical selection frequencies (0, <25%, 25-50%, 50-75%, > 75%).

Scenarios	**$K_{baseline}$**	**$K_{spatial}$**	**$K_{network}$**	**$K_{spillover}$**	**M_{source}**
$K_{baseline}$	-				
$K_{spatial}$	-0.04	-			
$K_{network}$	0.16	-0.01	-		
$K_{spillover}$	0.18	-0.06	0.3	-	
M_{source}	0.35	-0.02	-0.02	0.14	-

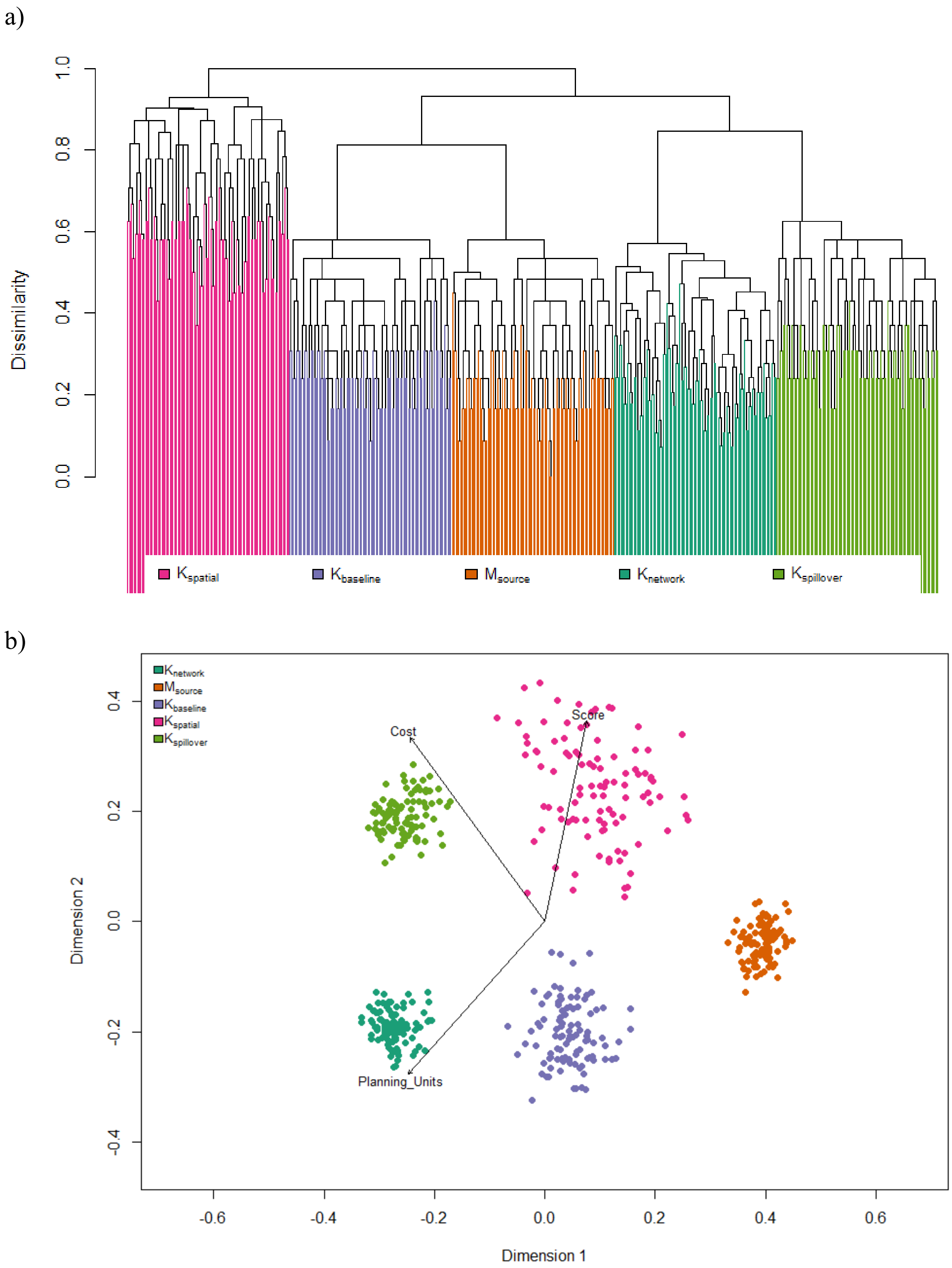


Figure 5.5: Dendrogram displaying spatial similarity between Marxan scenarios paired with a PCoA biplot.

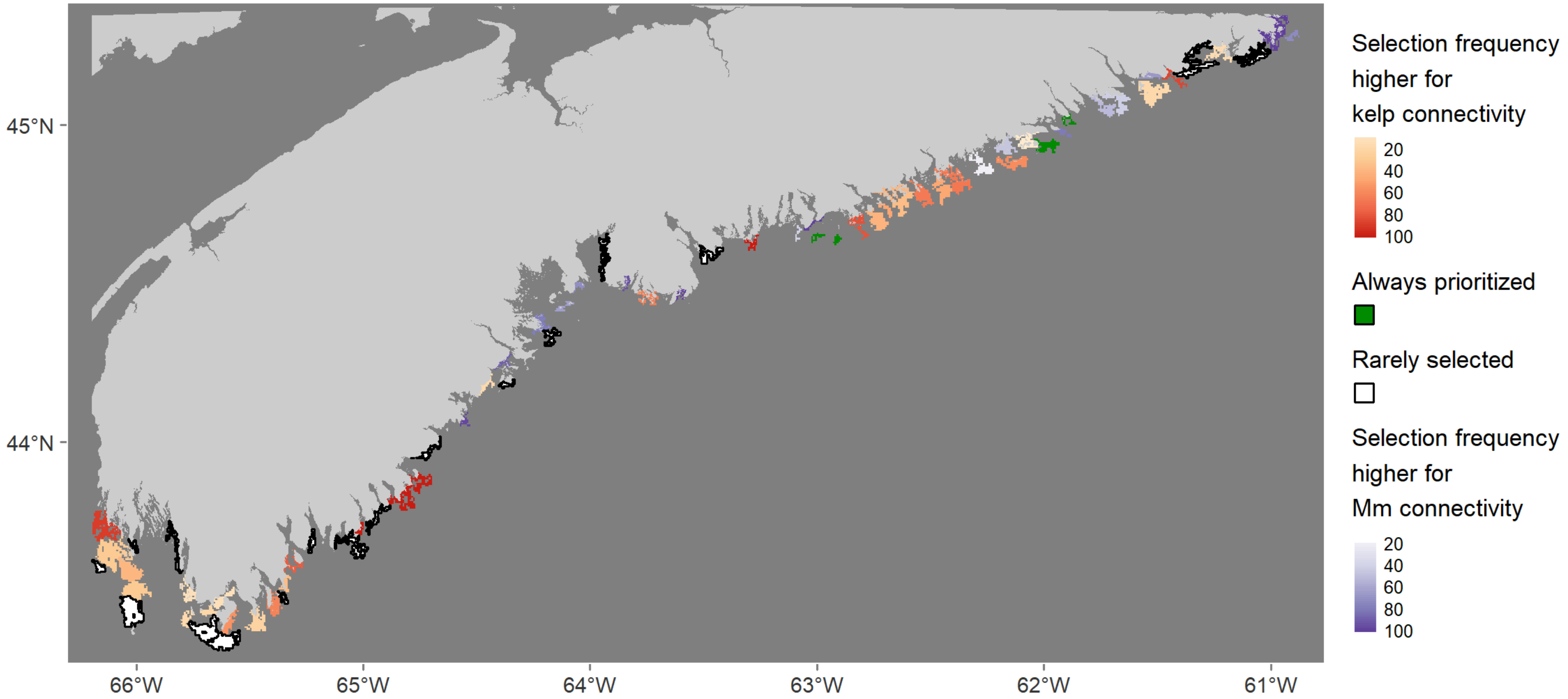


Figure 5.6: Relative difference between scenarios $K_{network}$ and M_{source} (orange patches indicate planning units that were selected more often when kelp connectivity was prioritized). The “Rarely selected” planning units were selected ≤ 5 times in both scenarios. The “Always prioritized” planning units were selected ≥ 80 times in both scenarios.

5.4.4 Significant explanatory variables for differences between scenarios

I selected three vectors from the Marxan solutions outputs (cost, number of planning units, score) that were significantly correlated with the PCoA surface ($p < 0.05$) (Figure 5.4b). Cost ($r^2 = 0.5109$), number of planning units ($r^2 = 0.4111$), and score ($r^2 = 0.4120$) had relatively high correlation coefficients but did not explain all of the differences between scenarios. Marxan scenarios that prioritized kelp connectivity ($K_{spatial}$, $K_{network}$, and $K_{spillover}$) tended to have a higher cost than the $K_{baseline}$ and M_{source} scenarios. The number of planning units was consistent except for $K_{network}$, which tended to select more planning units to meet the conservation objectives (Figure D.1). Finally, score, the sum of the three terms in the objective function of Marxan, was highest for $K_{spatial}$ by orders of magnitude over the other scenarios.

5.4. Discussion

I tested four different connectivity-based Marxan scenarios that implement different conservation objectives, metrics, and species dispersal patterns in Nova Scotia. I found that conservation objectives that aimed to maximize connectivity for kelp resulted in the selection of different priority areas than those that aimed to minimize connectivity for *M. membranacea*. When connectivity for kelps was maximized, large, upstream patches tended to be selected most often, with concentrations near Port Joli and throughout the eastern shore. By contrast, when connectivity for *M. membranacea* was minimized, smaller patches in the eastern and central region were selected most often. These results suggest that there will be trade-offs between maximizing connectivity for kelp and minimizing connectivity for *M. membranacea*. The spatial domain and scale of management units, as well as the specificity of objectives are also important considerations relevant to connectivity for conservation planning efforts.

To maximize the likelihood of preserving kelp habitat, it is important to balance conservation objectives associated with prioritizing habitat patches that are connected for kelps but less connected, or at least not critical dispersal pathways, for invasive species such as *M. membranacea*. With Marxan Connect functionality, customized thresholds can reflect objectives that either maximize or minimize connectivity, as was the case for kelps and the invasive bryozoan, respectively. When comparing Marxan outputs for the scenarios tested, I was able to identify some regions with potential to maximize kelp connectivity, whilst minimizing connectivity for *M. membranacea*. Yarmouth, Canso, Port Joli, and the Eastern Shore Islands were identified as high priority areas for kelp connectivity and low for the M_{source} scenario. However, *M. membranacea* relies on healthy kelp habitat to proliferate, so the interaction between these two species creates a circular argument where protecting healthy kelp cannot avoid also protecting occurrences of the bryozoan. Additionally, the dispersal ability and widespread invasion success of *M. membranacea*, now reaching as far north as Gaspé Peninsula and northern coast of the St. Lawrence (Denley et al. 2019b), suggests that limiting connectivity of this invasive species is an insufficient action by itself to prevent further kelp loss. Both protecting and restoring habitat are typically seen as a mitigation strategies for invasive species with life history characteristics similar to *M. membranacea* (Giakoumi et al. 2019); however, the authors also advise that doing nothing might be a realistic strategy in some instances.

Combinations of different connectivity metrics yielded alternative conservation priorities, further highlighting the importance of carefully selecting metrics that correspond to specific conservation objectives (Beger et al 2022). This flexibility offers the opportunity to be more selective for features of connectivity for certain species. In scenarios $K_{network}$ and $K_{spillover}$, I combined multiple connectivity conservation features that together reflected different conservation objectives. Specifically, I aimed to prioritize network-wide connectivity and balance isolation with spillover for $K_{network}$ and $K_{spillover}$, respectively. Ospina-Alvarez et al. (2020) also combined information from multiple connectivity metrics, including both retention and centrality metrics to discern overall connectivity of a node in the network, and therefore identify the role of different regions in supporting connectivity across the network. Comparable to this study, they found that different nodes/patches supported connectivity in different ways. Moreover, Abecasis et al. (2023) identified stepping-stone and source populations using betweenness centrality and out-strength, respectively. Additionally, the authors showed that these areas were pivotal to the coherence of the overall network using a node deletion analysis. Finally, sites upstream of the dominant current direction were identified as sources to downstream sites (Figure 5.4b,c,d), which is consistent with recommended ideal priority areas along the coast (Frys et al. 2020).

I found that $K_{spatial}$ showed the greatest dissimilarity from the other four scenarios. Similarly, Hanson et al. (2022) also found that tuning the boundary length modifier in Marxan resulted in the most dissimilar prioritization from other approaches for including connectivity in conservation planning. The spatial dispersion of individual solutions of $K_{spatial}$ across the two dimensions shown in the PCoA plot suggests there are multiple possible patch configurations that meet the specified conservation objectives, partially because pairs of sites are selected with the spatial dependencies approach. However, since dispersal for kelps is limited, and future habitat degradation is likely to occur, $K_{spatial}$ may be an advantageous optimal strategy for protection (Muenzel et al. 2022). The three scenarios that consider connectivity through targets set for discretized connectivity metrics (conservation objectives; $K_{network}$, $K_{spillover}$, and M_{source}) had high selection frequencies for a small subset of PUs and low selection frequencies for the remaining PUs, suggesting a consistent, more pointed solution to the outlined objectives; This is not surprising, particularly since some patches were important for multiple connectivity metrics. Because I set higher targets (50 %) for only a subset of the total number of planning units, solutions were likely built around the connectivity conservation objectives in these instances. However, this effect may not be as strong in planning scenarios with a greater overall number of conservation features.

An important consideration when incorporating connectivity with Marxan Connect, and for conservation planning in general, is the spatial scale of management units. Specifically, I assert that the interpretation of graph theory metrics is highly dependent on the spatial scale on which they are calculated. In early sensitivity analyses, I calculated metrics of connectivity at the cell scale (630 m by 630 m grid) but found that this spatial scale was too fine, because there was minimal connectivity between all cells. When I instead grouped connectivity by kelp patch, I was able to identify more consistent and interpretable patterns relevant for management. For instance, kelp patches that wrapped around the SW shore of Nova Scotia towards Yarmouth had higher values of in-strength and out-strength compared to other regions, which tended to have high levels of self-recruitment or local retention. However, when interpreted regionally, there is instead a high level of retention of kelp spores within SW Nova Scotia. Understanding regional and patch level patterns of connectivity are relevant for translating metrics of connectivity to useful recommendations for practitioners. In areas with fine-scale variability in topography and bathymetry, modelling patterns of connectivity with fine-scale ocean models (250 – 500 m around coastal features) is key to not over- or under-estimate connectivity in these regions (Saint-Amand et al. 2023).

Traditional Marxan summary information (e.g., penalty, cost, score) might not be the best metrics to directly compare the spatial dependencies and conservation features methods when irregular planning units are used. In my case study, the boundary sum term in the objective function is non-zero for the spatial dependencies scenario ($K_{spatial}$), but zero for the other four scenarios because no boundary information is supplied. There is no boundary information supplied for these scenarios because I used irregular planning units that do not have systematically quantifiable contiguous edges with other planning units (kelp patches). Therefore, the overall Marxan score is substantially higher for $K_{spatial}$ irrespective of similarities among the other two terms (cost and conservation features). Other independent measures such as lifetime egg production or population viability analysis are likely better metrics to measure persistence if the intention is to directly compare the outputs of these contrasting methods (Muenzel et al. 2022). However, choosing between these two methods can instead be governed by the specificity of your conservation objective and overall network goals.

My study combines modelling output from several methodologies including species distribution modelling, biophysical modelling, and spatial planning, and is therefore subject to some assumptions and limitations. First, in my spatial planning setup, I had a small number of planning units and conservation features to cater to the desired spatial scale for detecting patterns of connectivity. However, a low number of planning units may inflate differences between scenarios. Second, I may have had unintended edge effects at either edge of the mapping extent because those patches may have a lower probability of receiving propagules from nearby patches as other suitable habitat patches were bounded on one side.

Studies that model dispersal and connections across a landscape or seascape tend to focus on maximizing source populations, stepping-stones, corridors, or connectivity hubs. In this paper, I aimed to broaden that perspective to test the alternative: minimizing connectivity of an invasive species, whilst still trying to understand and prioritize protection for the biogenic habitat threatened by the invasive species (in this case *M. membranacea*). While MPAs cannot prevent effects of climate change such as increasing temperatures, they may be able to facilitate protection and recovery if "bad" connectivity is disrupted and favourable connections are reinforced. The trade-off between enacting protection swiftly versus delaying management action to further understand complex dispersal patterns still remains (Camaclang et al. 2022). I hope that this study will prompt future research questions around minimizing "bad" connectivity of pollutants, invasive species, pathogens, or other harmful agents of dispersal.

CHAPTER 6

DISCUSSION

It is widely recognized that connectivity is an important ecological criterion to consider in the design of MPAs and MPAn. However, prior to this research, a systematic review quantifying the extent to which connectivity had been applied to MPAs to-date had not been conducted. Additionally, recommendations and advice for how to bridge the supposed gap preventing connectivity patterns from being applied to decision making for management was limited and only applicable in specific contexts, primarily coral reef ecosystems. Using a combination of scuba diving, machine learning, biophysical modelling, and spatial planning tools, I have illustrated that there is a diverse toolkit available for delineating and applying patterns of connectivity to the design and evaluation of MPAs. Specifically, I have demonstrated the suitability of different methods for use in coastal systems, as exemplified with a comprehensive case study along the Atlantic coast of Nova Scotia, where oceanographic features, such as tides and coastal islands, are dominant drivers of dispersal and retention.

I investigated the current application of marine population connectivity in regions with advanced systematic conservation planning. Of the 746 MPAs I reviewed, 11 % considered connectivity in their design (**Chapter 2**), suggesting there is a disconnect between scientific research and management application. As a result of this disconnect, I proposed a series of recommendations and a framework to facilitate the inclusion of knowledge on connectivity patterns into the design of MPAs. These recommendations included (1) considering whether to prioritize connectivity, (2) identifying the role a MPA plays in supporting connectivity across a network, (3) identifying the appropriate temporal and spatial scale, and (4) improving regional patterns of connectivity (**Chapter 2**). The remainder of the thesis focussed on the application of these recommendations and associated framework.

I identified species to prioritize my efforts for improving regional knowledge on connectivity patterns along the Atlantic coast of Nova Scotia, focussing on kelps (**Chapters 3, 4, 5**), the invasive species *Membranipora membranacea* (**Chapters 3, 5**) and the dominant mesograzer of kelps *Strongylocentrotus droebachiensis* (**Chapter 3**). When I tested three different approaches for estimating connectivity with increasing complexity of ocean current data, I found that the approach of intermediate complexity produced results similar to those from the more complex outputs from biophysical modelling (**Chapter 3**). The approach I developed requires a lower cost and investment of resources than biophysical modelling, but still accounts for current directionality, a key factor for predicting patterns of dispersal in coastal ecosystems (**Chapter 3**). I translated connectivity outputs to useful metrics for practitioners by identifying the Eastern Shore Islands as a source to downstream potential MPAs (**Chapter 3**) and Yarmouth, Canso, Port Joli, and the Eastern Shore Islands as priority areas to promote connectivity of kelps and minimize connectivity of *M. membranacea* (**Chapter 5**). This research will aid in supporting sites for designation as MPAs along the Atlantic Coast of Nova Scotia. Broadly, this research can also provide guidance on how to prioritize connectivity in other regions where MPA networks are being designed.

I studied threats to kelps by modelling potential habitat loss (**Chapter 4**) and identifying priority areas for conservation that limit connectivity of *M. membranacea* whilst maximizing connectivity for kelps (**Chapter 5**). By fragmenting kelp bed habitat along the Atlantic coast of Nova Scotia in an in silico experiment, I showed that kelps primary rely on self-recruitment to replenish their populations (**Chapter 4**). Additionally, I showed that, to the potential benefit of kelp beds, habitat fragmentation effects did not compound habitat loss until over 70 % of the habitat was removed (**Chapter 4**). When I tested various connectivity objectives to protect either source populations, stepping-stones, or connectivity hotspots for maximizing connectivity for kelp whilst minimizing connectivity for *M. membranacea*, different priority areas emerged, with some overlap between objectives (**Chapter 5**). Upstream sites were most important for connectivity of kelps compared to smaller, downstream sites for minimizing connectivity of *M. membranacea* (**Chapter 5**). However, trade-offs still persist because invasive species often benefit most from healthy populations for invasion and settlement. Overall, this research is beneficial because it supports conservation efforts for kelps, which are an important ecosystem engineer and primary producer locally in Nova Scotia and internationally across 25% of the world's coastline.

The study of marine ecological connectivity continues to emerge as scientists refine their toolkit for making estimates of connectivity patterns. At this pivotal time, when 30% of our world's oceans are being set aside for conservation purposes, it is crucial that we make informed decisions regarding the placement, size, and spacing of MPAs to ensure their efficacy with our present knowledge and tools. For example, applying the intermediate approach introduced in chapter 3 to other coastal regions can be a low-cost option for identifying whether planned networks of MPAs will be or are connected. On a broader scale, many regions would benefit from reassessing potential connectivity patterns with proposed changes to oceanographic currents under future climate scenarios, taking into account changes to species ranges and dominant physical factors mediating dispersal patterns. Moreover, identifying and accounting for the dispersal of species or vectors that negatively impact the natural state of our ecosystems is a new development in connectivity research that should receive further investigation. Lastly, selecting a focus region whereby multiple measurement methods for estimating connectivity can be compared to one another can help further guide scientists and researchers in selecting the tools appropriate for their research questions.

This thesis highlights the interdisciplinary nature of working at the science-policy interface. Whether providing science advice, demystifying the concept of connectivity, or developing new tools for scientists and practitioners, an understanding of biological oceanography provides context for informed decision making. In this thesis, I propose that it is necessary to always consider connectivity in the design of MPAs. However, prioritizing connectivity depends on the research or management objective, as well as logistical and resource constraints. I provide evidence that simpler, most commonly used metrics of connectivity oversimplify dispersal patterns of mid-long distance dispersers and are therefore not suitable in a coastal setting. For habitat forming species such as kelp with poor dispersal ability, large, relatively pristine habitats are the best targets areas for conservation. My hope is that this thesis contributes to our growing understanding of the dynamic ecological process that is marine ecological connectivity and can have a positive impact on conservation efforts worldwide.

APPENDIX A

CHAPTER 3

Table A.1: Metadata for scientific literature database (MPA = marine protected area, MPAn = marine protected area network)

Column Header	**Description**
Title	Title of scientific article
Authors	Authors of scientific article
Published Year	Published year of scientific article
MPA Implications Stated	Indicates articles that did not provide specific MPA recommendations
Country	Country of study
Category of MPA	Category of MPA studied
MPA	Name of MPA studied (if stated)
MPAn	Name of MPAn studied (if stated and applicable)
Theme	Guideline study or application study
Phyla	Phyla studied (if multiple, separated by commas)
Design or Post-hoc	Design or post-hoc evaluation
Design element	Design elements (e.g. size, spacing; if applicable)
Classification of connectivity	Landscape, demographic or genetic connectivity
Measurement method	Genetics, modelling, tagging or other
Recommendation	Summary of recommendation based on measurement of connectivity patterns (application studies only)
Guideline	Summary of recommendation based on theoretical discussion (guideline studies only)

Table A.2: Metadata for management literature database (MPA = marine protected area)

Column Header	**Description**
Country	Country name
Latitude	Latitude of MPA in decimal degrees
Longitude	Longitude of MPA in decimal degrees
Managing authority	Managing authority of the MPA
Authority level	Level of authority that manages the MPA (local, regional, national, international)
National legislation	For countries with both international and national guidelines, state the national legislation in addition to the international legislation
International legislation	Legislation the MPA was designated under
IUCN category	Level of protection using the IUCN guidelines (if applicable)
Name	Name of MPA
Category of MPA	Category of MPA
Management plan	Indicate whether the MPA has a management plan (1 for TRUE and 0 or FALSE)
Year of designation	Year the MPA was designated under the listed legislation
Marine km sq	Marine area of the MPA in square kilometers
Ecological criteria	List of ecological criteria considered in the MPA design. 14 criteria were considered: representative features, areas of high productivity, areas of high biodiversity, biogenic habitats, nursery areas, foraging areas, spawning areas, migratory areas, species at risk, fisheries, complex or unique geomorphology, unique or rare oceanography, culturally important species, and connectivity
Classification of connectivity	Landscape, demographic or genetic connectivity

Table A.3: List of analyzed scientific papers

#	**Title**	**Citation**	**Theme**
1	Predicting reef fish connectivity from biogeographic patterns and larval dispersal modelling to inform the development of marine reserve networks	(Abesamis et al. 2016)	applied
2	Reef-fish larval dispersal patterns validate no-take marine reserve network connectivity that links human communities	(Abesamis et al. 2017)	applied
3	Applying ecological criteria to marine reserve design: A case study from the California Channel Islands	(Airamé et al. 2003)	guideline
4	Biodiversity conservation: an example of a multidisciplinary approach to marine dispersal	(Aliani et al. 2015)	applied
5	Local replenishment of coral reef fish populations in a marine reserve	(Almany et al. 2007)	applied
6	Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs	(Almany et al. 2009)	guideline
7	Larval fish dispersal in a coral-reef seascape	(Almany et al. 2017)	applied
8	Quantifying the Spatial Ecology of Wide-Ranging Marine Species in the Gulf of California: Implications for Marine Conservation Planning	(Anadón et al. 2011)	applied
9	Habitat-specific larval dispersal and marine connectivity: implications for spatial conservation planning	(Anadón et al. 2013)	applied
10	Low Connectivity between Mediterranean Marine Protected Areas: A Biophysical Modeling Approach for the Dusky Grouper Epinephelus marginatus	(Andrello et al. 2013)	applied
11	Global mismatch between fishing dependency and larval supply from marine reserves	(Andrello et al. 2017)	applied
12	A synthesis of genetic connectivity in deep-sea fauna and implications for marine reserve design	(Baco et al. 2016)	guideline
13	Sharp genetic breaks among populations of Haptosquilla pulchella (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences	(Barber et al. 2002)	applied

#	Title	Citation	Theme
14	Resilience to Disturbance Despite Limited Dispersal and Self-Recruitment in Tropical Barrel Sponges: Implications for Conservation and Management	(Bell et al. 2014)	applied
15	High connectivity between sea lough populations of a planktonic larval disperser with the adjacent open coast	(Bell 2012)	applied
16	Effective Dispersal of Caribbean Reef Fish is Smaller than Current Spacing Among Marine Protected Areas	(Beltrán et al. 2017)	applied
17	Optimal selection of marine protected areas based on connectivity and habitat quality	(Berglund et al. 2012)	applied
18	Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network	(Berumen et al. 2012)	applied
19	Surrogates for reef fish connectivity when designing marine protected area networks	(Bode et al. 2012)	applied
20	Planning Marine Reserve Networks for Both Feature Representation and Demographic Persistence Using Connectivity Patterns	(Bode et al. 2016)	guideline
21	The role of marine reserves in the replenishment of a locally impacted population of anemonefish on the Great Barrier Reef	(Bonin et al. 2016)	applied
22	Patterns of Deep-Sea Genetic Connectivity in the New Zealand Region: Implications for Management of Benthic Ecosystems	(Bors et al. 2012)	applied
23	Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs	(Botsford et al. 2009)	guideline
24	Marine Protected Area Networks in California, USA	(Botsford et al. 2014)	guideline
25	Population Structure, Genetic Diversity, Effective Population Size, Demographic History and Regional Connectivity Patterns of the Endangered Dusky Grouper, Epinephelus marginatus (Teleostei: Serranidae), within Malta's Fisheries Management Zone	(Buchholz-Sørensen and Vella 2016)	applied

#	Title	Citation	Theme
26	Limited realized dispersal and introgressive hybridization influence genetic structure and conservation strategies for brown rockfish, Sebastes auriculatus	(Buonaccorsi et al. 2005)	applied
27	Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design	(Burgess et al. 2014)	guideline
28	Siting marine protected areas based on habitat quality and extent provides the greatest benefit to spatially structured metapopulations	(Cabral et al. 2016)	guideline
29	Spatial genetic structure in the saddled sea bream (Oblada melanura [Linnaeus, 1758]) suggests multi-scaled patterns of connectivity between protected and unprotected areas in the Western Mediterranean Sea	(Calò et al. 2016)	applied
30	The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment	(Carr et al. 2017)	guideline
31	Patterns of connectivity among populations of a coral reef fish	(Chittaro and Hogan 2013)	applied
32	Spatially resolved fish population analysis for designing MPAs: influence on inside and neighbouring habitats	(Christensen et al. 2009)	applied
33	Self-recruitment and sweepstakes reproduction amid extensive gene flow in a coral-reef fish	(Christie et al. 2010a)	applied
34	Larval Connectivity in an Effective Network of Marine Protected Areas	(Christie et al. 2010b)	applied
35	Connectivity within and among a Network of Temperate Marine Reserves	(Coleman et al. 2011)	applied
36	Anticipating changes to future connectivity within a network of marine protected areas	(Coleman et al. 2017)	applied
37	Connectivity of the Habitat-Forming Kelp, Ecklonia radiata within and among Estuaries and Open Coast	(Coleman 2013)	applied
38	Population Connectivity Shifts at High Frequency within an Open-Coast Marine Protected Area Network	(Cook et al. 2014)	applied

#	Title	Citation	Theme
39	Depth distribution of larvae critically affects their dispersal and the efficiency of marine protected areas	(Corell et al. 2012)	applied
40	Surviving at the edge of a fragmented range: patterns of genetic diversity in isolated populations of the endangered giant Mediterranean limpet (Patella ferruginea)	(Cossu et al. 2017)	applied
41	Management and conservation of the kelp species Laminaria digitata: using genetic tools to explore the potential exporting role of the MPA "Parc naturel marin d'Iroise"	(Couceiro et al. 2013)	applied
42	A model-based assessment of reef larvae dispersal in the Western Indian Ocean reveals regional connectivity patterns - Potential implications for conservation policies	(Crochelet et al. 2016)	applied
43	Population genetic structure between Yap and Palau for the coral Acropora hyacinthus	(Cros et al. 2016)	applied
44	Connecting Palau's marine protected areas: a population genetic approach to conservation	(Cros et al. 2017)	applied
45	Population connectivity in the temperate damselfish Parma microlepis: Analyses of genetic structure across multiple spatial scales	(Curley and Gillings 2009)	applied
46	An adaptable toolkit to assess commercial fishery costs and benefits related to marine protected area network design	(Daigle et al. 2015)	applied
47	A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas	(D’Aloia et al. 2017)	applied
48	Systematic conservation planning in the eastern English Channel: comparing the Marxan and Zonation decision-support tools	(Delavenne et al. 2012)	guideline
49	Assessing Dispersal Patterns of Fish Propagules from an Effective Mediterranean Marine Protected Area	(Di Franco et al. 2012a)	applied
50	Dispersal Patterns of Coastal Fish: Implications for Designing Networks of Marine Protected Areas	(Di Franco et al. 2012b)	applied
51	Dispersal of larval and juvenile seabream: Implications for Mediterranean marine protected areas	(Di Franco et al. 2015)	applied

#	Title	Citation	Theme
52	A potential larval recruitment pathway originating from a Florida marine protected area	(Domeier 2004)	applied
53	Comparative Phylogeography in Fijian Coral Reef Fishes: A Multi-Taxa Approach towards Marine Reserve Design	(Drew and Barber 2012)	applied
54	Genetic structure and consequences of stock exploitation of Chrysoblephus puniceus, a commercially important sparid in the South West Indian Ocean	(Duncan et al. 2015)	applied
55	Implications of Macroalgal Isolation by Distance for Networks of Marine Protected Areas	(Durrant et al. 2014)	applied
56	Population Connectivity Measures of Fishery-Targeted Coral Reef Species to Inform Marine Reserve Network Design in Fiji	(Eastwood et al. 2016)	applied
57	Incorporating ontogenetic dispersal, ecological processes and conservation zoning into reserve design	(Edwards et al. 2010)	applied
58	Prioritising seascape connectivity in conservation using network analysis	(Engelhard et al. 2017)	applied
59	Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: implications for management	(Espinoza et al. 2015)	applied
60	Strong genetic but not spatial subdivision of two reef fish species targeted by fishers on the Great Barrier Reef	(Evans et al. 2010)	applied
61	Discordant patterns of genetic connectivity between two sympatric species, Mullus barbatus (Linnaeus, 1758) and Mullus surmuletus (Linnaeus, 1758), in south-western Mediterranean Sea	(Félix-Hackradt et al. 2013)	applied
62	The science of European marine reserves: Status, efficacy, and future needs	(Fenberg et al. 2012)	guideline
63	Ocean circulation drives heterogeneous recruitments and connectivity among coral populations on the North West Shelf of Australia	(Feng et al. 2016)	applied
64	A GIS-Based Tool for Representing Larval Dispersal for Marine Reserve Selection	(Fischer et al. 2011)	applied

#	Title	Citation	Theme
65	Habitat continuity effects on gradients of fish biomass across marine protected area boundaries	(Forcada et al. 2008)	applied
66	Size and spacing rules can balance conservation and fishery management objectives for marine protected areas	(Fovargue et al. 2018)	guideline
67	Genetic population structure of the endemic fourline wrasse (Larabicus quadrilineatus) suggests limited larval dispersal distances in the Red Sea	(Froukh and Kochzius 2007)	applied
68	Avoiding current oversights in marine reserve design	(Gaines et al. 2003)	guideline
69	Bio-physical connectivity patterns of benthic marine species used in the designation of Scottish nature conservation marine protected areas	(Gallego et al. 2017)	applied
70	The role of dispersal and demography in determining the efficacy of marine reserves	(Gerber et al. 2005)	guideline
71	Climate change impacts on connectivity in the ocean: Implications for conservation	(Gerber et al. 2014)	guideline
72	Wandering mussels: using natural tags to identify connectivity patterns among Marine Protected Areas	(Gomes et al. 2016)	applied
73	Genetic considerations on the introduction of farmed fish in marine protected areas: The case of study of white seabream restocking in the Gulf of Castellammare (Southern Tyrrhenian Sea)	(González-Wangüemert et al. 2012)	applied
74	Designing Marine Reserves for Fisheries Management, Biodiversity Conservation, and Climate Change Adaptation	(Green et al. 2014)	guideline
75	Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design	(Green et al. 2015)	guideline
76	Using larval dispersal simulations for marine protected area design: Application to the Gulf of Lions (northwest Mediterranean)	(Guizien et al. 2012)	applied
77	Marine reserves and seascape context shape fish assemblages in seagrass ecosystems1	(Henderson et al. 2017)	applied

#	**Title**	**Citation**	**Theme**
78	Estimating dispersal distance in the deep sea: Challenges and applications to marine reserves	(Hilário et al. 2015)	guideline
79	Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem	(Hitt et al. 2011)	applied
80	Contrasting patterns of population structure and gene flow facilitate exploration of connectivity in two widely distributed temperate octocorals	(Holland et al. 2017)	applied
81	Consistency and inconsistency in multispecies population network dynamics of coral reef ecosystems	(Holstein et al. 2014)	applied
82	Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish	(Huijbers et al. 2013)	applied
83	Conservation, Spillover and Gene Flow within a Network of Northern European Marine Protected Areas	(Huserbråten et al. 2013)	applied
84	Incorporating historical and ecological genetic data for leopard grouper (Mycteroperca rosacea) into marine reserve design in the Gulf of California	(Jackson et al. 2015)	applied
85	Identification of subpopulations from connectivity matrices	(Jacobi et al. 2012)	applied
86	Potential and realized connectivity of the seagrass Posidonia oceanica and their implication for conservation	(Jahnke et al. 2017)	applied
87	The quick and the dead: larval mortality due to turbulent tidal transport	(Jessopp 2007)	applied
88	Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges	(Jones et al. 2009)	guideline
89	How to select networks of marine protected areas for multiple species with different dispersal strategies	(Jonsson et al. 2016)	guideline
90	Alongshore advection and marine reserves: consequences for modeling and management	(Kaplan 2006)	guideline
91	Dispersal connectivity and reserve selection for marine conservation	(Kininmonth et al. 2011)	applied

#	Title	Citation	Theme
92	Four-dimensional connectivity modelling with application to Australia's north and northwest marine environments	(Kool and Nichol 2015)	applied
93	Efficacy of an established marine protected area at sustaining a queen conch Lobatus gigas population during three decades of monitoring	(Kough et al. 2017)	applied
94	Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science	(Kritzer and Sale 2004)	guideline
95	Incorporating larval dispersal into MPA design for both conservation and fisheries	(Krueck et al. 2017)	guideline
96	Connecting MPAs - eight challenges for science and management	(Lagabrielle et al. 2014)	guideline
97	Determining natal sources of capelin in a boreal marine park using otolith microchemistry	(Lazartigues et al. 2016)	applied
98	Temperate marine protected area provides recruitment subsidies to local fisheries	(Le Port et al. 2017)	applied
99	Recent progress in understanding larval dispersal: New directions and digressions	(Levin 2006)	guideline
100	Population connectivity of neon damsel, Pomacentrus coelestis, inferred from otolith microchemistry and mtDNA	(Liu et al. 2011)	applied
101	The Effects of Dispersal Patterns on Marine Reserves: Does the Tail Wag the Dog?	(Lockwood et al. 2002)	guideline
102	The influence of environmental characteristics on fish larvae spatial patterns related to a marine protected area: The Medes islands (NW Mediterranean)	(López-Sanz et al. 2011)	applied
103	Evaluation of rockfish conservation area networks in the United States and Canada relative to the dispersal distance for black rockfish (Sebastes melanops)	(Lotterhos et al. 2014)	applied
104	Testing source-sink theory: the spill-over of mussel recruits beyond marine protected areas	(Ludford et al. 2012)	applied
105	Integrating connectivity and climate change into marine conservation planning	(Magris et al. 2014)	guideline
106	Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs	(Magris et al. 2016)	applied

#	Title	Citation	Theme
107	Effective protection of fish on inshore coral reefs depends on the scale of mangrove-reef connectivity	(Martin et al. 2015)	applied
108	High gene flow in reef fishes and its implications for ad-hoc no-take marine reserves	(Matias et al. 2013)	applied
109	Designing marine protected area networks to address the impacts of climate change	(McLeod et al. 2009)	guideline
110	Spatial, socio-economic, and ecological implications of incorporating minimum size constraints in marine protected area network design	(Metcalfe et al. 2015)	applied
111	Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia	(Meynecke et al. 2008)	applied
112	Protection of Genetic Diversity and Maintenance of Connectivity among Reef Corals within Marine Protected Areas	(Miller and Ayre 2008)	applied
113	Conflicting estimates of connectivity among deep-sea coral populations	(Miller et al. 2010)	applied
114	Population connectivity of Ezo abalone on the northern Pacific coast of Japan in relation to the establishment of harvest refugia	(Miyake et al. 2011)	applied
115	The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks	(Moffitt et al. 2011)	applied
116	From global to local genetic structuring in the red gorgonian Paramuricea clavata: the interplay between oceanographic conditions and limited larval dispersal	(Mokhtar-Jamaï et al. 2011)	applied
117	Improving the interpretability of climate landscape metrics: An ecological risk analysis of Japan's Marine Protected Areas	(Molinos et al. 2017)	applied
118	Limited ecologically relevant genetic connectivity in the south-east African coral populations calls for reef-level management	(Montoya-Maya et al. 2016)	applied
119	Reserve design for uncertain responses of coral reefs to climate change	(Mumby et al. 2011)	applied
120	Connectivity of reef fish between mangroves and coral reefs: Algorithms for the design of marine reserves at seascape scales	(Mumby 2006)	guideline

#	Title	Citation	Theme
121	Climate change and coral reef connectivity	(Munday et al. 2009)	guideline
122	Marine reserves help preserve genetic diversity after impacts derived from climate variability: Lessons from the pink abalone in Baja California	(Munguía-Vega et al. 2015)	applied
123	A modelling study of the role of marine protected areas in metapopulation genetic connectivity in Delaware Bay oysters	(Munroe et al. 2014)	applied
124	Population genetics information for the regional conservation of a tropical seagrass, Enhalus acoroides, around the Guimaras Strait, Philippines	(Nakajima et al. 2017)	applied
125	Synergistic effects of reserves and connectivity on ecological resilience	(Olds et al. 2012b)	applied
126	Primacy of seascape connectivity effects in structuring coral reef fish assemblages	(Olds et al. 2012a)	applied
127	Mangrove-reef connectivity promotes the effectiveness of marine reserves across the western Pacific	(Olds et al. 2013)	applied
128	New wave: high-tech tools to help marine reserve research	(Palumbi et al. 2003)	guideline
129	Population genetics, demographic connectivity, and the design of marine reserves	(Palumbi 2003)	guideline
130	Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling	(Paris et al. 2005)	applied
131	Effects of fishing protection on the genetic structure of fish populations	(Pérez-Ruzafa et al. 2006)	applied
132	Fish with Chips: Tracking Reef Fish Movements to Evaluate Size and Connectivity of Caribbean Marine Protected Areas	(Pittman et al. 2014)	applied
133	Larval dispersal connects fish populations in a network of marine protected areas	(Planes et al. 2009)	applied
134	Spatial overlaps of foraging and resting areas of black-legged kittiwakes breeding in the English Channel with existing marine protected areas	(Ponchon et al. 2017)	applied

#	Title	Citation	Theme
135	Metapopulation dynamics guide marine reserve design: importance of connectivity, demographics, and stock enhancement	(Puckett and Eggleston 2016)	applied
136	Larval dispersal and population connectivity among a network of marine reserves	(Puckett et al. 2014)	applied
137	Understanding the effectiveness of marine protected areas using genetic connectivity patterns and Lagrangian simulations	(Pujolar et al. 2013)	applied
138	Spatial and temporal patterns of larval dispersal in a coral-reef fish metapopulation: evidence of variable reproductive success	(Pusack et al. 2014)	applied
139	Genetic connectivity patterns of Pocillopora verrucosa in southern African Marine Protected Areas	(Ridgway et al. 2008)	applied
140	Ecological criteria for evaluating candidate sites for marine reserves	(Roberts et al. 2003)	guideline
141	Far-field connectivity of the UK's four largest marine protected areas: Four of a kind?	(Robinson et al. 2017)	applied
142	Towards `ecological coherence': Assessing larval dispersal within a network of existing Marine Protected Areas	(Ross et al. 2017)	applied
143	Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves	(Rossi et al. 2014)	applied
144	Fish sound production and acoustic telemetry reveal behaviors and spatial patterns associated with spawning aggregations of two Caribbean groupers	(Rowell et al. 2015)	applied
145	Patterns of Fish Connectivity between a Marine Protected Area and Surrounding Fished Areas	(Sahyoun et al. 2016)	applied
146	A general model for designing networks of marine reserves	(Sala et al. 2002)	guideline
147	When are no-take zones an economically optimal fishery management strategy?	(Sanchirico et al. 2006)	guideline
148	Additivity properties in metapopulation models: Implications for the assessment of marine reserves	(Sanchirico 2005)	guideline

#	Title	Citation	Theme
149	Metapopulation structure informs conservation management in a heavily exploited coastal shark (Mustelus henlei)	(Sandoval-Castillo and Beheregaray 2015)	applied
150	Marine protected area restricts demographic connectivity: Dissimilarity in a marine environment can function as a biological barrier	(Sato et al. 2017)	applied
151	No Reef Is an Island: Integrating Coral Reef Connectivity Data into the Design of Regional-Scale Marine Protected Area Networks	(Schill et al. 2015)	applied
152	Predictive mapping of reproductive fish habitats to aid marine conservation planning	(Schmiing et al. 2017)	applied
153	Genetic connectivity patterns in an endangered species: The dusky grouper (Epinephelus marginatus)	(Schunter et al. 2011)	applied
154	Reserve site selection for data-poor invertebrate fisheries using patch scale and dispersal dynamics: a case study of sea cucumber (Cucumaria frondosa)	(Shackell et al. 2013)	applied
155	Linking bio-oceanography and population genetics to assess larval connectivity	(Soria et al. 2012)	applied
156	Dynamic connectivity patterns from an insular marine protected area in the Gulf of California	(Soria et al. 2014)	applied
157	Thinking and managing outside the box: coalescing connectivity networks to build region-wide resilience in coral reef ecosystems	(Steneck et al. 2009)	guideline
158	Modeling fine-scale coral larval dispersal and interisland connectivity to help designate mutually-supporting coral reef marine protected areas: Insights from Maui Nui, Hawaii	(Storlazzi et al. 2017)	applied
159	Ocean circulation model predicts high genetic structure observed in a long-lived pelagic developer	(Sunday et al. 2014)	applied
160	Ecological coherence of marine protected area networks: A spatial assessment using species distribution models	(Sundblad et al. 2011)	applied

#	Title	Citation	Theme
161	Large-scale connectivity of Grapsus grapsus (Decapoda) in the Southwestern Atlantic oceanic islands: integrating genetic and morphometric data	(Teschima et al. 2016)	applied
162	Connectivity between marine reserves and exploited areas in the philopatric reef fish Chrysoblephus laticeps (Teleostei: Sparidae)	(Teske et al. 2010)	applied
163	Numerical modelling and graph theory tools to study ecological connectivity in the Great Barrier Reef	(Thomas et al. 2014)	applied
164	Genetic evidence from the spiny lobster fishery supports international cooperation among Central American marine protected areas	(Truelove et al. 2015a)	applied
165	Genetic analysis reveals temporal population structure in Caribbean spiny lobster (Panulirus argus) within marine protected areas in Mexico	(Truelove et al. 2015b)	applied
166	Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience	(Underwood et al. 2009)	applied
167	Integrating connectivity science and spatial conservation management of coral reefs in north-west Australia	(Underwood et al. 2013)	guideline
168	Larval supply to a marine reserve and adjacent fished area in the Soufriere Marine Management Area, St Lucia, West Indies	(Valles et al. 2001)	applied
169	Genetic Connectivity among and Self-Replenishment within Island Populations of a Restricted Range Subtropical Reef Fish	(van der Meer et al. 2012)	applied
170	Population connectivity and the effectiveness of marine protected areas to protect vulnerable, exploited and endemic coral reef fishes at an endemic hotspot	(van der Meer et al. 2015)	applied
171	Site-fidelity and movement patterns of bottlenose dolphins (Tursiops truncatus) in central Argentina: essential information for effective conservation	(Vermeulen et al. 2017)	applied

#	Title	Citation	Theme
172	Small-scale genetic connectivity of bicolor damselfish (Stegastes partitus) recruits in Mexican Caribbean reefs	(Villegas-Sánchez et al. 2010)	applied
173	Settlement and recruitment of coral reef fishes in moderately exploited and overexploited Caribbean ecosystems: implications for marine protected areas	(Watson and Munro 2004)	applied
174	Identifying critical regions in small-world marine metapopulations	(Watson et al. 2011)	applied
175	Population genetic structure of the European lobster (Homarus gammarus) in the Irish Sea and implications for the effectiveness of the first British marine protected area	(Watson et al. 2016)	applied
176	Effectiveness of Marine Protected Areas in the Philippines for Biodiversity Conservation	(Weeks et al. 2010)	applied
177	Incorporating seascape connectivity in conservation prioritisation	(Weeks 2017)	applied
178	Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal	(White et al. 2010)	guideline
179	The Value of Larval Connectivity Information in the Static Optimization of Marine Reserve Design	(White et al. 2014a)	applied
180	Assessing the effectiveness of a large marine protected area for reef shark conservation	(White et al. 2017)	applied
181	Marine reserve design theory for species with ontogenetic migration	(White 2015)	applied
182	Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park	(Williamson et al. 2016)	applied
183	Genetic isolation by distance reveals restricted dispersal across a range of life histories: implications for biodiversity conservation planning across highly variable marine environments	(Wright et al. 2015)	applied
184	Network theory and metapopulation persistence: incorporating node self-connections	(Zamborain-Mason et al. 2017)	applied

#	Title	Citation	Theme
185	Evaluating Connectivity between Marine Protected Areas Using CODAR High-Frequency Radar	(Zelenke et al. 2009)	applied
186	Population genetic structure and connectivity of deep-sea stony corals (Order Scleractinia) in the New Zealand region: Implications for the conservation and management of vulnerable marine ecosystems	(Zeng et al. 2017)	applied

Table A.4: List of analyzed MPAs (MPA = marine protected area)

#	Name	Country	Year of designation	Category of MPA
1	Abalone Cove	United States of America	2012	State Marine Conservation Area
2	Abers - Côtes des légendes	France	1995	Site of Community Importance (Habitats Directive)
3	Abrolhos Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
4	Abrolhos Islands	Australia	1999	Fish Habitat Protection Area
5	Agoa	France	2010	Sanctuaire de mammifères marins (Marine Mammals Sanctuary)
6	Ahihi-Kinau	United States of America	1973	Natural Area Reserve
7	Ailsa Craig	United Kingdom	2011	Special Protection Areas
8	Albany Mudflats	United States of America	1986	State Marine Park
9	Alde, Ore and Butley Estuaries	United Kingdom	2005	Special Areas of Conservation
10	Alde-Ore Estuary	United Kingdom	1996	Special Protection Areas
11	Allonby Bay	United Kingdom	2016	Marine Conservation Zone
12	Aln Estuary	United Kingdom	2013	Marine Conservation Zone
13	American Bank	Canada	2011	Area of Interest
14	Anacapa Island	United States of America	2006	Essential Fish Habitat
15	Anacapa Island	United States of America	2003	Federal and State Marine Conservation Area
16	Anacapa Island	United States of America	2003	Federal and State Marine Reserve
17	Anacapa Island	United States of America	2005	Special Closure

#	Name	Country	Year of designation	Category of MPA
18	Anglesey Terns / Morwenoliaid Ynys Môn	United Kingdom	1992	Special Protection Areas
19	Anguniaqvia niqiqyuam	Canada	2016	Marine Protected Area
20	Año Nuevo	United States of America	2007	State Marine Reserve
21	Anse de Goulven, dunes de Keremma	France	2007	Site of Community Importance (Habitats Directive)
22	Anse de Vauville	France	2014	Site of Community Importance (Habitats Directive)
23	Apollo	Australia	2007	Commonwealth Marine Reserve
24	Arafura Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
25	Archipel des Glénan	France	2007	Site of Community Importance (Habitats Directive)
26	Argo-Rowley Terrace Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
27	Arnhem Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
28	Arrow Point to Lion Head Point (Catalina Island)	United States of America	2012	State Marine Conservation Area
29	Ascrib, Isay and Dunvegan	United Kingdom	2005	Special Areas of Conservation
30	Ashmore Reef Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
31	Asilomar	United States of America	2007	State Marine Reserve
32	Bae Caerfyrddin/Carmarthen Bay	United Kingdom	2003	Special Protection Areas
33	Bae Cemlyn/ Cemlyn Bay	United Kingdom	2004	Special Areas of Conservation
34	Baie d'Audierne	France	2016	Site of Community Importance (Habitats Directive)

#	Name	Country	Year of designation	Category of MPA
35	Baie de Canche et couloir des trois estuaires	France	2015	Site of Community Importance (Habitats Directive)
36	Baie de la Ciotat	France	2015	Site of Community Importance (Habitats Directive)
37	Baie de l'Aiguillon	France	1996	Réserve Naturelle Nationale
38	Baie de Lancieux, Baie de l'Arguenon, Archipel de Saint Malo et Dinard	France	2014	Site of Community Importance (Habitats Directive)
39	Baie de Morlaix	France	2016	Site of Community Importance (Habitats Directive)
40	Baie de Saint-Brieuc	France	NA	Réserve naturelle nationale
41	Baie de Saint-Brieuc - Est	France	2014	Site of Community Importance (Habitats Directive)
42	Baie de Seine occidentale	France	2014	Site of Community Importance (Habitats Directive)
43	Baie de Somme	France	1994	Réserve Naturelle Nationale
44	Baie du mont Saint-Michel	France	2016	Site of Community Importance (Habitats Directive)
45	Bair Island	United States of America	1986	State Marine Park
46	Ball Bay - Sand Bay	Australia	1983	Dugong Protection Area B
47	Banc d'Arguin	France	1972	Réserve Naturelle Nationale
48	Banc et récifs de Surtainville	France	2014	Site of Community Importance (Habitats Directive)
49	Bancs des Flandres	France	2016	Site of Community Importance (Habitats Directive)
50	Barker Inlet-St Kilda	Australia	2007	Aquatic Reserve
51	Barrenjoey Head	Australia	2002	Aquatic Reserve
52	Barrow Island	Australia	2006	Marine Management Area

#	Name	Country	Year of designation	Category of MPA
53	Barrow Island	Australia	2006	Marine Park
54	Barwon Bluff	Australia	2002	Marine Sanctuary
55	Basin Head	Canada	2005	Marine Protected Area
56	Bassin d'Arcachon	France	2014	Parc naturel marin
57	Bassin d'Arcachon et Cap Ferret	France	2016	Site of Community Importance (Habitats Directive)
58	Batemans	Australia	2006	Marine Park
59	Batiquitos Lagoon	United States of America	2012	State Marine Conservation Area
60	Beachy Head West	United Kingdom	2013	Marine Conservation Zone
61	Beagle	Australia	2007	Commonwealth Marine Reserve
62	Begg Rock (San Nicolas Island)	United States of America	2003	State Marine Reserve
63	Belfast Lough	United Kingdom	1998	Special Protection Areas
64	Belfast Lough Open Water	United Kingdom	2009	Special Protection Areas
65	Benfleet and Southend Marshes	United Kingdom	1994	Special Protection Areas
66	Berwickshire and North Northumberland Coast	United Kingdom	2005	Special Areas of Conservation
67	Beware Reef	Australia	2002	Marine Sanctuary
68	Bideford to Foreland Point	United Kingdom	2016	Marine Conservation Zone
69	Big Creek	United States of America	2007	State Marine Conservation Area
70	Big Creek	United States of America	2007	State Marine Reserve
71	Big Flat	United States of America	2012	State Marine Conservation Area
72	Big River Estuary	United States of America	2012	State Marine Conservation Area
73	Blackman Rivulet	Australia	2009	Marine Conservation Area
74	Blackwater Estuary (Mid-Essex Coast Phase 4)	United Kingdom	1995	Special Protection Areas

#	Name	Country	Year of designation	Category of MPA
75	Blackwater, Crouch, Roach and Colne Estuaries	United Kingdom	2013	Marine Conservation Zone
76	Blue Cavern (Catalina Island) Offshore	United States of America	2012	State Marine Conservation Area
77	Blue Cavern (Catalina Island) Onshore	United States of America	2012	State Marine Conservation Area
78	Boags	Australia	2007	Commonwealth Marine Reserve
79	Boat Harbour	Australia	2002	Aquatic Reserve
80	Bodega Head	United States of America	2010	State Marine Conservation Area
81	Bodega Head	United States of America	2010	State Marine Reserve
82	Bolsa Bay	United States of America	2012	State Marine Conservation Area
83	Bolsa Chica Basin	United States of America	2012	State Marine Conservation Area
84	Boodie, Double Middle Islands	Australia	2006	Nature Reserve
85	Bouches de Bonifacio	France	1999	Réserve Naturelle de Corse
86	Bouches de Bonifacio, Iles des Moines	France	2015	Site of Community Importance (Habitats Directive)
87	Bowie Seamount	Canada	2008	Marine Protected Area
88	Bowling Green Bay	Australia	2011	Dugong Protection Area B
89	Braemar Pockmarks	United Kingdom	2015	Special Areas of Conservation
90	Bremer Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
91	Breydon Water	United Kingdom	1996	Special Protection Areas
92	Bronte-Coogee	Australia	2002	Aquatic Reserve
93	Brush Island	Australia	1963	Nature Reserve
94	Buchan Ness to Collieston Coast	United Kingdom	1998	Special Protection Areas
95	Bunurong	Australia	2002	Marine National Park

#	Name	Country	Year of designation	Category of MPA
96	Bunurong	Australia	2002	Marine Park
97	Burry Inlet	United Kingdom	1992	Special Protection Areas
98	Bushrangers Bay	Australia	1982	Aquatic Reserve
99	Cabbage Tree Bay	Australia	2002	Aquatic Reserve
100	Cabrillo	United States of America	2012	State Marine Reserve
101	Calanques	France	2012	Parc National
102	Calanques et îles marseillaises - Cap Canaille et massif du Grand Caunet	France	2014	Site of Community Importance (Habitats Directive)
103	Calf of Eday	United Kingdom	1998	Special Protection Areas
104	Cambria	United States of America	2007	State Marine Park/State Marine Conservation Area
105	Campus Point	United States of America	2012	State Marine Conservation Area
106	Canna and Sanday	United Kingdom	1998	Special Protection Areas
107	Cap d'Erquy-Cap Fréhel	France	2007	Site of Community Importance (Habitats Directive)
108	Cap Ferrat	France	2015	Site of Community Importance (Habitats Directive)
109	Cap Martin	France	2016	Site of Community Importance (Habitats Directive)
110	Cap rossu, Scandola, Pointe de la Reveletta, Canyon de Calvi	France	2015	Site of Community Importance (Habitats Directive)
111	Cap Sicie - Six Fours	France	2014	Site of Community Importance (Habitats Directive)
112	Cap Sizun	France	2014	Site of Community Importance (Habitats Directive)
113	Cape Banks	Australia	2002	Aquatic Reserve
114	Cape Byron	Australia	2002	Marine Park

#	Name	Country	Year of designation	Category of MPA
115	Cape Howe	Australia	2002	Marine National Park
116	Cape Wrath	United Kingdom	1996	Special Protection Areas
117	Cardigan Bay/ Bae Ceredigion	United Kingdom	2004	Special Areas of Conservation
118	Carlingford Lough	United Kingdom	2016	Marine Conservation Zone
119	Carlingford Lough	United Kingdom	1998	Special Protection Areas
120	Carmarthen Bay and Estuaries/ Bae Caerfyrddin ac Aberoedd	United Kingdom	2004	Special Areas of Conservation
121	Carmel Bay	United States of America	2007	State Marine Conservation Area
122	Carmel Pinnacles	United States of America	2007	State Marine Reserve
123	Carnarvon Canyon Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
124	Carrington Point (Santa Rosa Island)	United States of America	2003	State Marine Reserve
125	Cartier Island Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
126	Casino Point (Catalina Island)	United States of America	2012	State Marine Conservation Area
127	Casse de la Belle Henriette	France	2011	Réserve Naturelle Nationale
128	Castle Rock	United States of America	2012	Special Closure
129	Casuarina	Australia	1982	Coastal Reserve
130	Cat Harbor (Catalina Island)	United States of America	2012	State Marine Conservation Area
131	Central Channel	Australia	2009	Marine Conservation Area
132	Central Eastern Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve

#	Name	Country	Year of designation	Category of MPA
133	Central Fladen	United Kingdom	2014	Nature Conservation Marine Protected Area
134	Cerbere-Banyuls	France	1990	Réserve Naturelle Nationale
135	Chausey	France	2009	Site of Community Importance (Habitats Directive)
136	Chaussée de Sein	France	2014	Site of Community Importance (Habitats Directive)
137	Chesil and the Fleet	United Kingdom	2015	Special Areas of Conservation
138	Chesil Beach and Stennis Ledges	United Kingdom	2013	Marine Conservation Zone
139	Chesil Beach and the Fleet	United Kingdom	1985	Special Protection Areas
140	Chichester and Langstone Harbours	United Kingdom	1987	Special Protection Areas
141	Churchill Island	Australia	2002	Marine National Park
142	Clairview Bluff - Carmilla Creek	Australia	1983	Dugong Protection Area B
143	Cleveland Bay - Magnetic Island	Australia	1983	Dugong Protection Area A
144	Cloudy Bay Lagoon	Australia	2009	Marine Conservation Area
145	Clyde Sea Sill	United Kingdom	2014	Nature Conservation Marine Protected Area
146	Cobourg Peninsula	Australia	1974	Ramsar Site, Wetland of International Importance
147	Cod Grounds Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
148	Colne Estuary (Mid-Essex Coast Phase 2)	United Kingdom	1994	Special Protection Areas
149	Comerong Island	Australia	1986	Nature Reserve

#	Name	Country	Year of designation	Category of MPA
150	Coobowie	Australia	2007	Aquatic Reserve
151	Cook Island	Australia	1998	Aquatic Reserve
152	Copinsay	United Kingdom	1994	Special Protection Areas
153	Coquet Island	United Kingdom	1985	Special Protection Areas
154	Coquet to St Mary’s	United Kingdom	2016	Marine Conservation Zone
155	Coral Sea Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
156	Cordell Bank	United States of America	1989	National Marine Sanctuary
157	Corner Inlet	Australia	2002	Marine National Park
158	Corniche Varoise	France	2014	Site of Community Importance (Habitats Directive)
159	Corse et de l'Agriate	France	2016	Parc Naturel Marin
160	Corte Madera Marsh	United States of America	1977	State Marine Park
161	Côte basque rocheuse et extension au large	France	2015	Site of Community Importance (Habitats Directive)
162	Côte de Cancale à Paramé	France	2014	Site of Community Importance (Habitats Directive)
163	Côte de Granit rose-Sept-Iles	France	2007	Site of Community Importance (Habitats Directive)
164	Côtes de Crozon	France	2014	Site of Community Importance (Habitats Directive)
165	Cottesloe Reef	Australia	2001	Fish Habitat Protection Area
166	Cours inférieur de l'Aude	France	2016	Site of Community Importance (Habitats Directive)
167	Cromarty Firth	United Kingdom	1999	Special Protection Areas
168	Cromer Shoal Chalk Beds	United Kingdom	2016	Marine Conservation Zone

#	Name	Country	Year of designation	Category of MPA
169	Crouch and Roach Estuaries (Mid-Essex Coast Phase 3)	United Kingdom	1998	Special Protection Areas
170	Crystal Cove	United States of America	2012	State Marine Conservation Area
171	Cumbria Coast	United Kingdom	2013	Marine Conservation Zone
172	Dampier Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
173	Dana Point	United States of America	2012	State Marine Conservation Area
174	Darwin Mounds	United Kingdom	2015	Special Areas of Conservation
175	Deben Estuary	United Kingdom	1996	Special Protection Areas
176	Dee Estuary/ Aber Dyfrdwy	United Kingdom	2009	Special Areas of Conservation
177	Del Mar Landing	United States of America	2010	State Marine Reserve
178	Dengie (Mid-Essex Coast Phase 1)	United Kingdom	1994	Special Protection Areas
179	Discovery Bay	Australia	2002	Marine National Park
180	Don Edwards San Francisco Bay	United States of America	1972	Nation Wildlife Refuge
181	Dornoch Firth and Loch Fleet	United Kingdom	1997	Special Protection Areas
182	Dornoch Firth and Morrich More	United Kingdom	2005	Special Areas of Conservation
183	Double Cone Rock	United States of America	2012	State Marine Conservation Area
184	Double Point/Stormy Stack Rock	United States of America	2010	Special Closure
185	Dover to Deal	United Kingdom	2016	Marine Conservation Zone
186	Dover to Folkestone	United Kingdom	2016	Marine Conservation Zone
187	Drakes Estero	United States of America	2010	State Marine Conservation Area
188	Drigg Coast	United Kingdom	2005	Special Areas of Conservation

#	Name	Country	Year of designation	Category of MPA
189	Dungeness, Romney Marsh and Rye Bay	United Kingdom	2016	Special Protection Areas
190	Duxbury Reef	United States of America	2010	State Marine Conservation Area
191	Eagle Rock	Australia	2002	Marine Sanctuary
192	East Caithness Cliffs	United Kingdom	1996	Special Protection Areas
193	East Caithness Cliffs	United Kingdom	2014	Nature Conservation Marine Protected Area
194	East Gippsland	Australia	2007	Commonwealth Marine Reserve
195	East of Gannet and Montrose Fields	United Kingdom	2014	Nature Conservation Marine Protected Area
196	East of Haig Fras	United Kingdom	2013	Marine Conservation Zone
197	East Sanday Coast	United Kingdom	1997	Special Protection Areas
198	Eastern Recherche Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
199	Eastern Spencer Gulf	Australia	2009	Marine Park
200	Eastport	Canada	2005	Marine Protected Area
201	Edgecumbe Bay - Bowen	Australia	1983	Dugong Protection Area B
202	Edward F. Ricketts	United States of America	2007	State Marine Conservation Area
203	Egg (Devil's Slide) Rock to Devil's Slide	United States of America	2010	Special Closure
204	Eighty Mile Beach	Australia	2013	Marine Park
205	Eighty Mile Beach Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
206	Eileanan agus Sgeiran Lios mór	United Kingdom	2005	Special Areas of Conservation
207	Elkhorn Slough	United States of America	2007	State Marine Conservation Area

#	Name	Country	Year of designation	Category of MPA
208	Elkhorn Slough	United States of America	2007	State Marine Reserve
209	Embiez - cap Sicie	France	2015	Site of Community Importance (Habitats Directive)
210	Encounter	Australia	2005	Marine Park
211	Endeavour Hydrothermal Vents	Canada	2003	Marine Protected Area
212	Essex Estuaries	United Kingdom	2005	Special Areas of Conservation
213	Estero Americano	United States of America	2010	State Marine Recreational Management Area
214	Estero de Limantour	United States of America	2010	State Marine Reserve
215	Estero de San Antonio	United States of America	2010	State Marine Recreational Management Area
216	Estuaire de la Loire Nord	France	2015	Site of Community Importance (Habitats Directive)
217	Estuaire de la Loire Sud - Baie de Bourgneuf	France	2015	Site of Community Importance (Habitats Directive)
218	Estuaire de la Seine	France	1997	Réserve Naturelle Nationale
219	Estuaires et littoral picards (baies de Somme et d'Authie)	France	2010	Site of Community Importance (Habitats Directive)
220	Estuaires picards et mer d'Opale	France	2012	Parc Naturel Marin
221	Exe Estuary	United Kingdom	1992	Special Protection Areas
222	Fagan Marsh	United States of America	1979	State Marine Park
223	Fair Isle	United Kingdom	1994	Special Protection Areas
224	Fal and Helford	United Kingdom	2005	Special Areas of Conservation
225	Falaise du Cap-Romain	France	1984	Réserve naturelle nationale

#	Name	Country	Year of designation	Category of MPA
226	False Klamath Rock	United States of America	2012	Special Closure
227	Famosa Slough	United States of America	2012	State Marine Conservation Area
228	Far West Coast	Australia	2009	Marine Park
229	Faray and Holm of Faray	United Kingdom	2005	Special Areas of Conservation
230	Farnes East	United Kingdom	2016	Marine Conservation Zone
231	Farnsworth Offshore (Catalina Island)	United States of America	2012	State Marine Conservation Area
232	Farnsworth Onshore (Catalina Island)	United States of America	2012	State Marine Conservation Area
233	Faroe-Shetland Sponge Belt	United Kingdom	2014	Nature Conservation Marine Protected Area
234	Fetlar	United Kingdom	1994	Special Protection Areas
235	Fetlar to Haroldswick	United Kingdom	2014	Nature Conservation Marine Protected Area
236	Firth of Forth	United Kingdom	2001	Special Protection Areas
237	Firth of Forth Banks Complex	United Kingdom	2014	Nature Conservation Marine Protected Area
238	Firth of Lorn	United Kingdom	2005	Special Areas of Conservation
239	Firth of Tay and Eden Estuary	United Kingdom	2000	Special Protection Areas
240	Firth of Tay and Eden Estuary	United Kingdom	2005	Special Areas of Conservation
241	Flamborough Head	United Kingdom	2005	Special Areas of Conservation
242	Flannan Isles	United Kingdom	1992	Special Protection Areas
243	Flinders	Australia	2007	Commonwealth Marine Reserve

#	Name	Country	Year of designation	Category of MPA
244	Folkestone Pomerania	United Kingdom	2013	Marine Conservation Zone
245	Footprint (Anacapa Channel)	United States of America	2003	Federal and State Marine Reserve
246	Forth Islands	United Kingdom	1990	Special Protection Areas
247	Foula	United Kingdom	1995	Special Protection Areas
248	Foulness (Mid-Essex Coast Phase 5)	United Kingdom	1996	Special Protection Areas
249	Fowlsheugh	United Kingdom	1992	Special Protection Areas
250	Franklin	Australia	2007	Commonwealth Marine Reserve
251	Franklin Harbor	Australia	2009	Marine Park
252	French Island	Australia	2002	Marine National Park
253	Freycinet	Australia	2007	Commonwealth Marine Reserve
254	Fulmar	United Kingdom	2016	Marine Conservation Zone
255	Fylde	United Kingdom	2013	Marine Conservation Zone
256	Gambier Islands Group	Australia	2009	Marine Park
257	Gascoyne Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
258	Geikie Slide and Hebridean Slope	United Kingdom	2014	Nature Conservation Marine Protected Area
259	Geographe Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
260	Gerstle Cove	United States of America	2010	State Marine Reserve
261	Gibraltar Point	United Kingdom	1993	Special Protection Areas
262	Gifford Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
263	Gilbert Bay	Canada	2005	Marine Protected Area

#	Name	Country	Year of designation	Category of MPA
264	Glannau Aberdaron and Ynys Enlli/ Aberdaron Coast and Bardsey Island	United Kingdom	1992	Special Protection Areas
265	Glannau Môn: Cors heli / Anglesey Coast: Saltmarsh	United Kingdom	2004	Special Areas of Conservation
266	Goleta Slough	United States of America	2012	State Marine Conservation Area
267	Golfe d'Ajaccio	France	2015	Site of Community Importance (Habitats Directive)
268	Golfe du Lion	France	2011	Parc Naturel Marin
269	Golfe du Morbihan, côte ouest de Rhuys	France	2007	Site of Community Importance (Habitats Directive)
270	Governor Island	Australia	1991	Marine Nature Reserve
271	Grand herbier de la côte orientale	France	2015	Site of Community Importance (Habitats Directive)
272	Grassholm	United Kingdom	1986	Special Protection Areas
273	Great Australian Bight Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
274	Great Barrier Reef	Australia	1975	Marine Park
275	Great Sandy	Australia	2006	Marine Park
276	Greater Farallones	United States of America	1981	National Marine Sanctuary
277	Greater Haig Fras	United Kingdom	2016	Marine Conservation Zone
278	Greyhound Rock	United States of America	2007	State Marine Conservation Area
279	Gruinart Flats, Islay	United Kingdom	1988	Special Protection Areas
280	Gulf of Carpentaria Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
281	Gull Island (Santa Cruz Island)	United States of America	2003	State and Federal Marine Reserve

#	**Name**	**Country**	**Year of designation**	**Category of MPA**
282	Gwaii Haanas	Canada	2010	National Park Reserve, National Marine Conservation Area Reserve
283	Haig Fras	United Kingdom	2015	Special Areas of Conservation
284	Hamelin Pool	Australia	1990	Marine Nature Reserve
285	Hamford Water	United Kingdom	1993	Special Protection Areas
286	Hanauma Bay	United States of America	1967	Marine Life Conservation District
287	Handa	United Kingdom	1990	Special Protection Areas
288	Harris Point (San Miguel Island)	United States of America	2003	State and Federal Marine Reserve
289	Hartland Point to Tintagel	United Kingdom	2016	Marine Conservation Zone
290	Hatton-Rockall Basin	United Kingdom	2014	Nature Conservation Marine Protected Area
291	Hawaiian Islands Humpback Whale	United States of America	1992	National Marine Sanctuary
292	Heard Island and McDonald Islands	Australia	2002	Commonwealth Marine Reserve
293	Hecate Straight/ Queen Charlotte Sound Glass Sponge Reefs	Canada	2017	Marine Protected Area
294	Hermaness, Saxa Vord and Valla Field	United Kingdom	1994	Special Protection Areas
295	Hervey Bay - Tin Can Bay	Australia	1983	Dugong Protection Area A
296	Hinchinbrook Island area	Australia	1983	Dugong Protection Area A
297	Hippolyte Rocks	Australia	2009	Marine Conservation Area
298	Holderness Inshore	United Kingdom	2016	Marine Conservation Zone

#	Name	Country	Year of designation	Category of MPA
299	Honolua-Mokuleia Bay	United States of America	1978	Marine Life Conservation District
300	Hoy	United Kingdom	2000	Special Protection Areas
301	Humber Estuary	United Kingdom	2009	Special Areas of Conservation
302	Humber Estuary	United Kingdom	2009	Special Protection Areas
303	Hunter Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
304	Huon	Australia	2007	Commonwealth Marine Reserve
305	Huon Estuary	Australia	2009	Marine Conservation Area
306	Ile de Groix	France	2014	Site of Community Importance (Habitats Directive)
307	Iles Cerbicale	France	1981	Réserve Naturelle Nationale
308	Iles Cerbicale et frange littoral	France	2016	Site of Community Importance (Habitats Directive)
309	Iles et pointe Bruzzi, étangs de Chevanu et d'Arbitru	France	2016	Site of Community Importance (Habitats Directive)
310	Iles Houat-Hoedic	France	2007	Site of Community Importance (Habitats Directive)
311	Ince Bay (Cape Palmerston - Allom Point)	Australia	1983	Dugong Protection Area A
312	Inner Clyde Estuary	United Kingdom	2000	Special Protection Areas
313	Inner Moray Firth	United Kingdom	1999	Special Protection Areas
314	Investigator	Australia	2009	Marine Park
315	Iroise	France	2007	Parc Naturel Marin
316	Isle of May	United Kingdom	2005	Special Areas of Conservation
317	Isles of Scilly Complex	United Kingdom	2005	Special Areas of Conservation

#	Name	Country	Year of designation	Category of MPA
318	Isles of Scilly Sites	United Kingdom	2013	Marine Conservation Zone
319	Jawbone	Australia	2002	Marine Sanctuary
320	Jervis Bay	Australia	1998	Marine Park
321	Jervis Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
322	Joseph Bonaparte Gulf Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
323	Judith Rock (San Miguel Island)	United States of America	2003	State Marine Reserve
324	Jurien Bay	Australia	2003	Marine Park
325	Jurien Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
326	Kaho'olawe	United States of America	1993	Island Reserve
327	Kalaupapa	United States of America	1980	National Historical Park
328	Kalbarri Blue Holes	Australia	2007	Fish Habitat Protection Area
329	Kaloko-Honokohau	United States of America	1978	National Historical Park
330	Kashtayit	United States of America	2012	State Marine Conservation Area
331	Kealakekua Bay	United States of America	1969	Marine Life Conservation District
332	Kenfig/ Cynffig	United Kingdom	2004	Special Areas of Conservation
333	Killough Bay	United Kingdom	2003	Special Protection Areas
334	Kimberley Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
335	Kingmere	United Kingdom	2013	Marine Conservation Zone
336	La Pointe Fauconnière	France	2010	Site of Community Importance (Habitats Directive)
337	Laguna Beach	United States of America	2012	State Marine Conservation Area

#	Name	Country	Year of designation	Category of MPA
338	Laguna Beach	United States of America	2012	State Marine Reserve
339	Lagune du Brusc	France	2014	Site of Community Importance (Habitats Directive)
340	Lalang-garram / Camden Sound	Australia	2012	Marine Park
341	Lalang-garram / Horizontal Falls	Australia	2016	Marine Park
342	Lamlash Bay	United Kingdom	2008	No take zone
343	Lancelin Island Lagoon	Australia	2001	Fish Habitat Protection Area
344	Lapakahi	United States of America	1979	Marine Life Conservation District
345	Larne Lough	United Kingdom	1997	Special Protection Areas
346	Laurentian Channel	Canada	2010	Area of Interest
347	Limestone Coast of South West Wales/ Arfordir Calchfaen de Orllewin Cymru	United Kingdom	2004	Special Areas of Conservation
348	Limmen Bight	Australia	2012	Marine Park
349	Limmen Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
350	Lindisfarne	United Kingdom	1992	Special Protection Areas
351	Littoral Cauchois	France	2016	Site of Community Importance (Habitats Directive)
352	Littoral Ouest du Cotentin de Bréhal à Pirou	France	2015	Site of Community Importance (Habitats Directive)
353	Liverpool Bay / Bae Lerpwl	United Kingdom	2010	Special Protection Areas
354	Llewellyn Bay	Australia	1983	Dugong Protection Area B
355	Loch Carron	United Kingdom	2017	Emergency Nature Conserveration Marine Protected Area

#	Name	Country	Year of designation	Category of MPA
356	Loch Creran	United Kingdom	2014	Nature Conservation Marine Protected Area
357	Loch Creran	United Kingdom	2005	Special Areas of Conservation
358	Loch Laxford	United Kingdom	2005	Special Areas of Conservation
359	Loch Moidart and Loch Shiel Woods	United Kingdom	2005	Special Areas of Conservation
360	Loch nam Madadh	United Kingdom	2005	Special Areas of Conservation
361	Loch of Stenness	United Kingdom	2005	Special Areas of Conservation
362	Loch Roag Lagoons	United Kingdom	2005	Special Areas of Conservation
363	Loch Sunart	United Kingdom	2014	Nature Conservation Marine Protected Area
364	Loch Sunart to the Sound of Jura	United Kingdom	2014	Nature Conservation Marine Protected Area
365	Loch Sween	United Kingdom	2014	Nature Conservation Marine Protected Area
366	Lochs Duich, Long and Alsh	United Kingdom	2014	Nature Conservation Marine Protected Area
367	Lochs Duich, Long and Alsh Reefs	United Kingdom	2005	Special Areas of Conservation
368	Long Point (Catalina Island)	United States of America	2012	State Marine Reserve
369	Long Reef	Australia	1980	Aquatic Reserve
370	Lord Howe Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
371	Lord Howe Island	Australia	1999	Marine Park
372	Lough Foyle	United Kingdom	1999	Special Protection Areas

#	Name	Country	Year of designation	Category of MPA
373	Lover's Cove (Catalina Island)	United States of America	2012	State Marine Conservation Area
374	Lovers Point - Julia Platt	United States of America	2007	State Marine Reserve
375	Lower South East	Australia	2009	Marine Park
376	Lower Yorke Peninsula	Australia	2009	Marine Park
377	Luce Bay and Sands	United Kingdom	2005	Special Areas of Conservation
378	Lucinda to Allingham - Halifax Bay	Australia	1983	Dugong Protection Area B
379	Lundy	United Kingdom	2010	Marine Conservation Zone
380	Lundy	United Kingdom	2005	Special Areas of Conservation
381	MacKerricher	United States of America	2012	State Marine Conservation Area
382	Macquarie Island	Australia	1999	Commonwealth Marine Reserve
383	Manele-Hulopoe	United States of America	1976	Marine Life Conservation District
384	Marais Breton, baie de Bourgneuf, île de Noirmoutier et forêt de Monts	France	2014	Site of Community Importance (Habitats Directive)
385	Marais de Moeze	France	1993	Réserve Naturelle Nationale
386	Marengo Reefs	Australia	2002	Marine Sanctuary
387	Maria Island	Australia	1991	National Park
388	Marin Islands	United States of America	1993	State Marine Park
389	Marmion	Australia	1987	Marine Park
390	Marwick Head	United Kingdom	1994	Special Protection Areas
391	Massif dunaire Gâvres-Quiberon et zones humides associées	France	2014	Site of Community Importance (Habitats Directive)
392	Matlahuayl	United States of America	2012	State Marine Reserve

#	Name	Country	Year of designation	Category of MPA
393	Mattole Canyon	United States of America	2012	State Marine Reserve
394	Medway Estuary	United Kingdom	2013	Marine Conservation Zone
395	Medway Estuary and Marshes	United Kingdom	1993	Special Protection Areas
396	Mermaid Reef Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
397	Merri	Australia	2002	Marine Sanctuary
398	Mersey Estuary	United Kingdom	1995	Special Protection Areas
399	Mersey Narrows and North Wirral Foreshore	United Kingdom	2013	Special Protection Areas
400	Miaboolya Beach	Australia	2003	Fish Habitat Protection Area
401	Midway Atoll	United States of America	1988	National Wildlife Refuge
402	Mingulay and Berneray	United Kingdom	1994	Special Protection Areas
403	Minsmere-Walberswick	United Kingdom	1992	Special Protection Areas
404	Moëze-Oléron	France	1993	Réserve naturelle nationale
405	Mòine Mhór	United Kingdom	2005	Special Areas of Conservation
406	Moku-o-loe Island (Coconut Island)	United States of America	1953	Marine Laboratory Refuge
407	Molokini Shoal	United States of America	1977	Marine Life Conservation District
408	Monach Islands	United Kingdom	2005	Special Areas of Conservation
409	Monach Isles	United Kingdom	2014	Nature Conservation Marine Protected Area
410	Monk Bay	Australia	2009	Marine Conservation Area
411	Montara	United States of America	2010	State Marine Reserve

#	Name	Country	Year of designation	Category of MPA
412	Montebello Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
413	Montebello Islands	Australia	2004	Marine Park
414	Monterey Bay	United States of America	1992	National Marine Sanctuary
415	Montrose Basin	United Kingdom	1995	Special Protection Areas
416	Moray and Nairn Coast	United Kingdom	1997	Special Protection Areas
417	Moray Firth	United Kingdom	2005	Special Areas of Conservation
418	Morecambe Bay	United Kingdom	2005	Special Areas of Conservation
419	Morecambe Bay and Duddon Estuary	United Kingdom	2017	Special Protection Areas
420	Moreton Bay	Australia	1993	Marine Park
421	Moro Cojo Slough	United States of America	2007	State Marine Reserve
422	Morro Bay	United States of America	2007	State Marine Recreational Management Area
423	Morro Bay	United States of America	2007	State Marine Reserve
424	Mounts Bay	United Kingdom	2016	Marine Conservation Zone
425	Mousa	United Kingdom	2005	Special Areas of Conservation
426	Mousa to Boddam	United Kingdom	2014	Nature Conservation Marine Protected Area
427	Muiron Islands	Australia	2004	Marine Management Area
428	Murat Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
429	Murlough	United Kingdom	2005	Special Areas of Conservation
430	Murray	Australia	2007	Commonwealth Marine Reserve
431	Mushroom Reef	Australia	2002	Marine Sanctuary

#	Name	Country	Year of designation	Category of MPA
432	Musquash Estuary	Canada	2006	Marine Protected Area
433	Naples	United States of America	2012	State Marine Conservation Area
434	Narrabeen Head	Australia	2002	Aquatic Reserve
435	Natural Bridges	United States of America	2007	State Marine Reserve
436	Navarro River Estuary	United States of America	2012	State Marine Conservation Area
437	Nelson	Australia	2007	Commonwealth Marine Reserve
438	Neptune Islands Group	Australia	2009	Marine Park
439	Newquay and The Gannel	United Kingdom	2016	Marine Conservation Zone
440	Ngari Capes	Australia	2012	Marine Park
441	Ninepin Point	Australia	1991	Marine Nature Reserve
442	Ninety Mile Beach	Australia	2002	Marine National Park
443	Ningaloo	Australia	1987	Marine Park
444	Ningaloo Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
445	Norfolk Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
446	North (Sydney) Harbour	Australia	1982	Aquatic Reserve
447	North Caithness Cliffs	United Kingdom	1996	Special Protection Areas
448	North Colonsay and Western Cliffs	United Kingdom	1997	Special Protection Areas
449	North East of Farnes Deep	United Kingdom	2016	Marine Conservation Zone
450	North Farallon Islands	United States of America	2010	State Marine Reserve
451	North Farallon Islands	United States of America	2010	Special Closure
452	North Lalang-garram	Australia	2016	Marine Park
453	North Norfolk Coast	United Kingdom	1989	Special Protection Areas
454	North Norfolk Coast	United Kingdom	2005	Special Areas of Conservation

#	Name	Country	Year of designation	Category of MPA
455	North Rona	United Kingdom	2005	Special Areas of Conservation
456	North Rona and Sula Sgeir	United Kingdom	2001	Special Protection Areas
457	North Uist Machair and Islands	United Kingdom	1999	Special Protection Areas
458	North-east Faroe-Shetland Channel	United Kingdom	2014	Nature Conservation Marine Protected Area
459	Northern Cardigan Bay / Gogledd Bae Ceredigion	United Kingdom	2017	Special Protection Areas
460	Northumberland Marine	United Kingdom	2017	Special Protection Areas
461	Northumbria Coast	United Kingdom	2000	Special Protection Areas
462	North-West of Jones Bank	United Kingdom	2016	Marine Conservation Zone
463	North-west Orkney	United Kingdom	2014	Nature Conservation Marine Protected Area
464	Norwegian boundary sediment plain	United Kingdom	2014	Nature Conservation Marine Protected Area
465	Noss	United Kingdom	1996	Special Protection Areas
466	Noss Head	United Kingdom	2014	Nature Conservation Marine Protected Area
467	Nuyts Archipelago	Australia	2009	Marine Park
468	Obain Loch Euphoirt	United Kingdom	2005	Special Areas of Conservation
469	Oceanic Shoals Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
470	Offshore Brighton	United Kingdom	2016	Marine Conservation Zone
471	Offshore Overfalls	United Kingdom	2016	Marine Conservation Zone

#	Name	Country	Year of designation	Category of MPA
472	Offshore Pacific	Canada	2017	Area of Interest
473	Old Kona Airport	United States of America	1992	Marine Life Conservation District
474	Opossum Bay	Australia	2009	Marine Conservation Area
475	Orfordness - Shingle Street	United Kingdom	2005	Special Areas of Conservation
476	Ouessant-Molène	France	2014	Site of Community Importance (Habitats Directive)
477	Outer Ards	United Kingdom	2002	Special Protection Areas
478	Outer Belfast Lough	United Kingdom	2016	Marine Conservation Zone
479	Outer Thames Estuary	United Kingdom	2010	Special Protection Areas
480	Pacific Grove Marine Gardens	United States of America	2007	State Marine Conservation Area
481	Padstow Bay and Surrounds	United Kingdom	2013	Marine Conservation Zone
482	Pagham Harbour	United Kingdom	2013	Marine Conservation Zone
483	Pagham Harbour	United Kingdom	1988	Special Protection Areas
484	Painted Cave (Santa Cruz Island)	United States of America	2003	State Marine Conservation Area
485	Panache de la Gironde et plateau rocheux de Cordouan (Système Pertuis Gironde)	France	2015	Site of Community Importance (Habitats Directive)
486	Papa Stour	United Kingdom	2005	Special Areas of Conservation
487	Papa Westray	United Kingdom	2014	Nature Conservation Marine Protected Area
488	Papahanaumokuakea	United States of America	2006	Marine National Monument
489	Pearl Harbor	United States of America	1972	National Wildlife Refuge

#	Name	Country	Year of designation	Category of MPA
490	Pembrokeshire Marine/ Sir Benfro Forol	United Kingdom	2004	Special Areas of Conservation
491	Pen Llyn a`r Sarnau/ Lleyn Peninsula and the Sarnau	United Kingdom	2004	Special Areas of Conservation
492	Perth Canyon Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
493	Pertuis Charentais	France	2014	Site of Community Importance (Habitats Directive)
494	Peytonia Slough	United States of America	1976	State Marine Park
495	Piedras Blancas	United States of America	2007	State Marine Conservation Area
496	Piedras Blancas	United States of America	2007	State Marine Reserve
497	Pillar Point	United States of America	2010	State Marine Conservation Area
498	Pitt Water	Australia	1995	Nature Reserve
499	Plateau de Pertusato/ Bonifacio et îles Lavezzi	France	2016	Site of Community Importance (Habitats Directive)
500	Plateau du Cap Corse	France	2015	Site of Community Importance (Habitats Directive)
501	Plateau du Four	France	2015	Site of Community Importance (Habitats Directive)
502	Plateau rocheux de l'île d'Yeu	France	2015	Site of Community Importance (Habitats Directive)
503	Plymouth Sound and Estuaries	United Kingdom	2005	Special Areas of Conservation
504	Point Addis	Australia	2002	Marine National Park
505	Point Arena	United States of America	2010	State Marine Reserve
506	Point Arena	United States of America	2010	State Marine Conservation Area

#	Name	Country	Year of designation	Category of MPA
507	Point Buchon	United States of America	2007	State Marine Conservation Area
508	Point Buchon	United States of America	2007	State Marine Reserve
509	Point Cabrillo	United States of America	2012	State Marine Reserve
510	Point Conception	United States of America	2012	State Marine Reserve
511	Point Cooke	Australia	2002	Marine Sanctuary
512	Point Danger	Australia	2002	Marine Sanctuary
513	Point Dume	United States of America	2012	State Marine Conservation Area
514	Point Dume	United States of America	2012	State Marine Reserve
515	Point Hicks	Australia	2002	Marine National Park
516	Point Lobos	United States of America	2007	State Marine Conservation Area
517	Point Lobos	United States of America	2007	State Marine Reserve
518	Point Quobba	Australia	1987	Fish Habitat Protection Area
519	Point Resistance Rock	United States of America	2010	Special Closure
520	Point Reyes	United States of America	2010	State Marine Reserve
521	Point Reyes	United States of America	2010	State Marine Conservation Area
522	Point Reyes Headlands	United States of America	2010	Special Closure
523	Point St. George Reef Offshore	United States of America	2012	State Marine Conservation Area
524	Point Sur	United States of America	2007	State Marine Conservation Area
525	Point Sur	United States of America	2007	State Marine Reserve
526	Point Vicente	United States of America	2012	State Marine Conservation Area

#	Name	Country	Year of designation	Category of MPA
527	Pointe de Senetosa et prolongements	France	2015	Site of Community Importance (Habitats Directive)
528	Poole Harbour	United Kingdom	1999	Special Protection Areas
529	Poole Rocks	United Kingdom	2013	Marine Conservation Zone
530	Port Clinton (Reef Point - Cape Clinton)	Australia	1983	Dugong Protection Area A
531	Port Cygnet	Australia	2009	Marine Conservation Area
532	Port D'Alon - la Nartette	France	1980	Terrains acquis par le Conservatoire du Littoral
533	Port of Gladstone - Rodds Bay	Australia	1983	Dugong Protection Area B
534	Port Phillip Heads	Australia	2002	Marine National Park
535	Port Stephens - Great Lakes	Australia	2005	Marine Park
536	Port-Cros	France	1963	Parc National
537	Portion du littoral sableux de la côte aquitaine	France	2015	Site of Community Importance (Habitats Directive)
538	Portsmouth Harbour	United Kingdom	1995	Special Protection Areas
539	Portuguese Ledge	United States of America	2007	State Marine Conservation Area
540	Pulu Keeling	Australia	1995	National Park
541	Pupukea	United States of America	1983	Marine Life Conservation District
542	Pyramid Point	United States of America	2012	State Marine Conservation Area
543	Race Rocks	Canada	1998	Area of Interest
544	Rade de Brest, estuaire de l'Aulne	France	2014	Site of Community Importance (Habitats Directive)
545	Rade d'Hyères	France	2014	Site of Community Importance (Habitats Directive)

#	Name	Country	Year of designation	Category of MPA
546	Ramsey Bay	United Kingdom	2012	Marine Nature Reserve
547	Rathlin	United Kingdom	2016	Marine Conservation Zone
548	Rathlin Island	United Kingdom	2005	Special Areas of Conservation
549	Rathlin Island	United Kingdom	1999	Special Protection Areas
550	Reading Rock	United States of America	2012	State Marine Conservation Area
551	Reading Rock	United States of America	2012	State Marine Reserve
552	Récifs et landes de la Hague	France	2015	Site of Community Importance (Habitats Directive)
553	Récifs et marais arrière-littoraux du Cap Lévi à la Pointe de Saire	France	2014	Site of Community Importance (Habitats Directive)
554	Récifs Gris-Nez Blanc-Nez	France	2015	Site of Community Importance (Habitats Directive)
555	Redwood Shores	United States of America	1976	State Marine Park
556	Repulse Bay	Australia	1983	Dugong Protection Area B
557	Réserve Naturelle Nationale des Terres Australes Francaises	France	2006	Réserve Naturelle Nationale
558	Ria d'Etel	France	2016	Site of Community Importance (Habitats Directive)
559	Ribble and Alt Estuaries	United Kingdom	1995	Special Protection Areas
560	Richardson Rock (San Miguel Island)	United States of America	2003	State and Federal Marine Reserve
561	Richmond River	Australia	1986	Nature Reserve
562	Ricketts Point	Australia	2002	Marine Sanctuary
563	Ridens et Dunes Hydrauliques du Detroit du Pas-de-Calais	France	2016	Site of Community Importance (Habitats Directive)

#	Name	Country	Year of designation	Category of MPA
564	River Derwent	Australia	2009	Marine Conservation Area
565	Rivière de Penerf, marais de Suscinio	France	2007	Site of Community Importance (Habitats Directive)
566	Roberts Point	Australia	2009	Marine Conservation Area
567	Roches de Penmarch	France	2014	Site of Community Importance (Habitats Directive)
568	Rockport Rocks	United States of America	2012	Special Closure
569	Roebuck Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
570	Rosemary Bank Seamount	United Kingdom	2014	Nature Conservation Marine Protected Area
571	Rousay	United Kingdom	2002	Special Protection Areas
572	Rowley Shoals	Australia	1990	Marine Park
573	Rum	United Kingdom	1982	Special Protection Areas
574	Runnel Stone	United Kingdom	2016	Marine Conservation Zone
575	Runswick Bay	United Kingdom	2016	Marine Conservation Zone
576	Russian Gulch	United States of America	2012	State Marine Conservation Area
577	Russian River	United States of America	2010	State Marine Conservation Area
578	Russian River	United States of America	2010	State Marine Recreational Management Area
579	Saguenay-St. Lawrence	Canada	1998	Marine Park
580	Salt Point	United States of America	2010	State Marine Conservation Area
581	Samoa	United States of America	2012	State Marine Conservation Area
582	San Diego Bay	United States of America	1988	National Wildlife Refuge

#	Name	Country	Year of designation	Category of MPA
583	San Diego-Scripps Coastal	United States of America	2012	State Marine Conservation Area
584	San Dieguito Lagoon	United States of America	2012	State Marine Conservation Area
585	San Elijo Lagoon	United States of America	2012	State Marine Conservation Area
586	San Francisco Bay	United States of America	2003	National Estuarine Research Reserve
587	San Miguel Island	United States of America	2005	Special Closure
588	San Pablo Bay	United States of America	1974	National Wildlife Refuge
589	Sanday	United Kingdom	2005	Special Areas of Conservation
590	Santa Barbara Island	United States of America	2003	State and Federal Marine Reserve
591	Saunders Reef	United States of America	2010	State Marine Conservation Area
592	Scandola	France	1975	Réserve Naturelle de Corse
593	Scanner Pockmark	United Kingdom	2015	Special Areas of Conservation
594	Scorpion (Santa Cruz Island)	United States of America	2003	State and Federal Marine Reserve
595	Sea Lion Cove	United States of America	2010	State Marine Conservation Area
596	Sea Lion Gulch	United States of America	2012	State Marine Reserve
597	Sept Iles	France	1976	Réserve Naturelle Nationale
598	Severn Estuary	United Kingdom	1995	Special Protection Areas
599	Severn Estuary/ Môr Hafren	United Kingdom	2010	Special Areas of Conservation
600	Shark Bay	Australia	1990	Marine Park
601	Shark Bay Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
602	Shediac Valley	Canada	2011	Area of Interest

#	Name	Country	Year of designation	Category of MPA
603	Shiant Isles	United Kingdom	1992	Special Protection Areas
604	Shiprock	Australia	1982	Aquatic Reserve
605	Shoalwater Islands	Australia	1990	Marine Park
606	Simpsons Point	Australia	2009	Marine Conservation Area
607	Sir Joseph Banks Group	Australia	2009	Marine Park
608	Skerries Bank and Surrounds	United Kingdom	2013	Marine Conservation Zone
609	Skomer	United Kingdom	2014	Marine Conservation Zone
610	Skomer, Skokholm and the Seas off Pembrokeshire / Sgomer, Sgogwm a Moroedd Penfro	United Kingdom	1982	Special Protection Areas
611	Skunk Point (Santa Rosa Island)	United States of America	2003	State Marine Reserve
612	Sloping Island	Australia	2009	Marine Conservation Area
613	Small Isles	United Kingdom	2016	Nature Conservation Marine Protected Area
614	Solent and Isle of Wight Lagoons	United Kingdom	2005	Special Areas of Conservation
615	Solent and Southampton Water	United Kingdom	1998	Special Protection Areas
616	Solent Maritime	United Kingdom	2005	Special Areas of Conservation
617	Solitary Islands	Australia	1998	Marine Park
618	Solitary Islands (Commonwealth Waters)	Australia	1993	Marine Reserve
619	Solitary Islands Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
620	Solway Firth	United Kingdom	2005	Special Areas of Conservation
621	Soquel Canyon	United States of America	2007	State Marine Conservation Area

#	Name	Country	Year of designation	Category of MPA
622	Sound of Arisaig (Loch Ailort to Loch Ceann Traigh)	United Kingdom	2005	Special Areas of Conservation
623	South Arm	Australia	2009	Marine Conservation Area
624	South Arran	United Kingdom	2014	Nature Conservation Marine Protected Area
625	South Cape Mendocino	United States of America	2012	State Marine Reserve
626	South Dorset	United Kingdom	2013	Marine Conservation Zone
627	South Humboldt Bay	United States of America	2012	State Marine Recreational Management Area
628	South La Jolla	United States of America	2012	State Marine Conservation Area
629	South La Jolla	United States of America	2012	State Marine Reserve
630	South Point (Santa Rosa Island)	United States of America	2003	State and Federal Marine Reserve
631	South Tasman Rise	Australia	2007	Commonwealth Marine Reserve
632	South Uist Machair	United Kingdom	2005	Special Areas of Conservation
633	South Uist Machair and Lochs	United Kingdom	1997	Special Protection Areas
634	South Wight Maritime	United Kingdom	2005	Special Areas of Conservation
635	Southeast Farallon Island	United States of America	2010	State Marine Conservation Area
636	Southeast Farallon Island	United States of America	2010	State Marine Reserve
637	Southeast Farallon Island	United States of America	2010	Special Closure
638	South-East Islay Skerries	United Kingdom	2005	Special Areas of Conservation
639	Southern Kangaroo Island	Australia	2009	Marine Park

#	Name	Country	Year of designation	Category of MPA
640	Southern Kangaroo Island Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
641	Southern Spencer Gulf	Australia	2009	Marine Park
642	South-west Corner Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
643	South-West Deeps (West)	United Kingdom	2013	Marine Conservation Zone
644	Southwest Seal Rock	United States of America	2012	Special Closure
645	St Abb`s Head to Fast Castle	United Kingdom	1997	Special Protection Areas
646	St Kilda	United Kingdom	1992	Special Protection Areas
647	St Kilda	United Kingdom	2005	Special Areas of Conservation
648	St Kilda-Chapman Creek	Australia	2007	Aquatic Reserve
649	St. Anns Bank	Canada	2017	Marine Protected Area
650	St. Lawrence Estuary	Canada	1998	Area of Interest
651	Stanton Banks	United Kingdom	2015	Special Areas of Conservation
652	Steamboat Rock	United States of America	2012	Special Closure
653	Stewart Peninsula - Newry Island - Ball Bay	Australia	1983	Dugong Protection Area A
654	Stewarts Point	United States of America	2010	State Marine Conservation Area
655	Stewarts Point	United States of America	2010	State Marine Reserve
656	Stour and Orwell Estuaries	United Kingdom	1994	Special Protection Areas
657	Strangford Lough	United Kingdom	2005	Special Areas of Conservation
658	Strangford Lough	United Kingdom	1998	Special Protection Areas
659	Sugarloaf Island	United States of America	2012	Special Closure
660	Sule Skerry and Sule Stack	United Kingdom	1994	Special Protection Areas

#	Name	Country	Year of designation	Category of MPA
661	Sullom Voe	United Kingdom	2005	Special Areas of Conservation
662	Sumburgh Head	United Kingdom	1996	Special Protection Areas
663	Sunart	United Kingdom	2005	Special Areas of Conservation
664	Swallow Sand	United Kingdom	2013	Marine Conservation Zone
665	Swami's	United States of America	2012	State Marine Conservation Area
666	Swan Estuary	Australia	1990	Marine Park
667	Tamar Estuaries Complex	United Kingdom	1997	Special Protection Areas
668	Tamar Estuary Sites	United Kingdom	2013	Marine Conservation Zone
669	Tarium Niryutait	Canada	2010	Marine Protected Area
670	Tasman Fracture	Australia	2007	Commonwealth Marine Reserve
671	Tatihou - Saint-Vaast-la-Hougue	France	2015	Site of Community Importance (Habitats Directive)
672	Teesmouth and Cleveland Coast	United Kingdom	1995	Special Protection Areas
673	Ten Mile	United States of America	2012	State Marine Reserve
674	Ten Mile Beach	United States of America	2012	State Marine Conservation Area
675	Ten Mile Estuary	United States of America	2012	State Marine Conservation Area
676	Thames Estuary and Marshes	United Kingdom	2000	Special Protection Areas
677	Thanet Coast	United Kingdom	2013	Marine Conservation Zone
678	Thanet Coast	United Kingdom	2005	Special Areas of Conservation
679	Thanet Coast and Sandwich Bay	United Kingdom	1994	Special Protection Areas
680	The Arches	Australia	2002	Marine Sanctuary
681	The Barra Fan and Hebrides Terrace Seamount	United Kingdom	2014	Nature Conservation

#	Name	Country	Year of designation	Category of MPA
				Marine Protected Area
682	The Blue Coast Marine Park	France	2015	Parc Naturel Régional Marin
683	The Canyons	United Kingdom	2013	Marine Conservation Zone
684	The Dee Estuary	United Kingdom	1985	Special Protection Areas
685	The Gully	Canada	2004	Marine Protected Area
686	The Manacles	United Kingdom	2013	Marine Conservation Zone
687	The Needles	United Kingdom	2016	Marine Conservation Zone
688	The Swale	United Kingdom	1982	Special Protection Areas
689	The Swale Estuary	United Kingdom	2016	Marine Conservation Zone
690	The Vadills	United Kingdom	2005	Special Areas of Conservation
691	The Wash	United Kingdom	1988	Special Protection Areas
692	The Wash and North Norfolk Coast	United Kingdom	2005	Special Areas of Conservation
693	Thorny Passage	Australia	2009	Marine Park
694	Tijuana River Mouth	United States of America	2012	State Marine Conservation Area
695	Tinderbox	Australia	1991	Marine Reserve
696	Torbay	United Kingdom	2013	Marine Conservation Zone
697	Towra Point	Australia	1987	Aquatic Reserve
698	Traeth Lafan/ Lavan Sands, Conway Bay	United Kingdom	1992	Special Protection Areas
699	Tregor Goëlo	France	2007	Site of Community Importance (Habitats Directive)
700	Treshnish Isles	United Kingdom	2005	Special Areas of Conservation
701	Troup, Pennan and Lion`s Heads	United Kingdom	1997	Special Protection Areas
702	Turbot Bank	United Kingdom	2014	Nature Conservation

#	Name	Country	Year of designation	Category of MPA
				Marine Protected Area
703	Tweed Estuary	United Kingdom	2005	Special Areas of Conservation
704	Twelve Apostles	Australia	2002	Marine National Park
705	Twilight Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
706	Two Rocks Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
707	Upper Fowey and Pont Pill	United Kingdom	2014	Marine Conservation Zone
708	Upper Gulf St Vincent	Australia	2009	Marine Park
709	Upper Loch Fyne and Loch Goil	United Kingdom	2014	Nature Conservation Marine Protected Area
710	Upper Newport Bay	United States of America	2012	State Marine Conservation Area
711	Upper Solway Flats and Marshes	United Kingdom	1992	Special Protection Areas
712	Upper South East	Australia	2009	Marine Park
713	Upper Spencer Gulf	Australia	2009	Marine Park
714	Upstart Bay	Australia	1983	Dugong Protection Area A
715	Utopia	United Kingdom	2016	Marine Conservation Zone
716	Van Damme	United States of America	2012	State Marine Conservation Area
717	Vandenberg	United States of America	2007	State Marine Reserve
718	Vizcaino Rock	United States of America	2012	Special Closure
719	Waialea Bay	United States of America	1985	Marine Life Conservation District
720	Waikiki	United States of America	1988	Marine Life Conservation District

#	Name	Country	Year of designation	Category of MPA
721	Wai'opae Tidepools	United States of America	2003	Marine Life Conservation District
722	Walpole-Nornalup Inlets	Australia	2009	Marine Park
723	Waterfall-Fortescue	Australia	2009	Marine Conservation Area
724	Waterfoot	United Kingdom	2016	Marine Conservation Zone
725	Wessel Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
726	West Cape York Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
727	West Coast Bays	Australia	2009	Marine Park
728	West of Walney	United Kingdom	2016	Marine Conservation Zone
729	West Shetland Shelf	United Kingdom	2014	Nature Conservation Marine Protected Area
730	West Westray	United Kingdom	1996	Special Protection Areas
731	Wester Ross	United Kingdom	2014	Nature Conservation Marine Protected Area
732	Western Channel	United Kingdom	2016	Marine Conservation Zone
733	Western Eyre Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
734	Western Kangaroo Island	Australia	2009	Marine Park
735	Western Kangaroo Island Commonwealth Marine Reserve	Australia	2013	Commonwealth Marine Reserve
736	White Rock (Cambria)	United States of America	2007	State Marine Conservation Area
737	Whitsand and Looe Bay	United Kingdom	2013	Marine Conservation Zone
738	Wilsons Promontory	Australia	2002	Marine National Park

#	Name	Country	Year of designation	Category of MPA
739	Wilsons Promontory	Australia	1986	Marine Park
740	Wilsons Promontory	Australia	1986	Marine Reserve
741	Wyre and Rousay Sounds	United Kingdom	2014	Nature Conservation Marine Protected Area
742	Y Fenai a Bae Conwy/ Menai Strait and Conwy Bay	United Kingdom	2004	Special Areas of Conservation
743	Yaringa	Australia	2002	Marine National Park
744	Yell Sound Coast	United Kingdom	2005	Special Areas of Conservation
745	Ythan Estuary, Sands of Forvie and Meikle Loch	United Kingdom	1998	Special Protection Areas
746	Zeehan	Australia	2007	Commonwealth Marine Reserve

APPENDIX B

CHAPTER 3

Table B.1: Substrate class suitability for kelp habitat. Substrate types are from (Greenlaw et al. 2013).

Substrate class	**Suitable habitat for kelp (1 = yes, 0 = no)**
Boulders	1
Continuous bedrock	1
Discontinuous bedrock	1
Other	0
Mixed sediment	0
Sand & gravel	0
Gravel	0
Mud	0
Sand	0
Sand & mud	0

Table B.2: Release locations for propagules.

Species	**Longitude**	**Latitude**
Laminarian kelps, *Membranipora membranacea*	-62.963	44.664
	-62.904	44.666
	-62.908	44.639
	-62.744	44.708
	-62.782	44.653
	-62.631	44.747
	-62.532	44.774
	-62.426	44.800
	-62.257	44.864
	-62.279	44.892
	-62.142	44.880
	-62.174	44.920
	-62.045	44.927
Stronglyocentrotus droebachiensis	-61.989	44.868
	-61.977	44.845
	-61.964	44.816
	-61.954	44.797
	-62.453	44.729
	-62.461	44.738
	-62.431	44.704
	-62.405	44.674
	-62.647	44.703
	-62.613	44.669
	-62.586	44.643
	-62.562	44.620
	-62.222	44.826
	-62.213	44.813
	-62.187	44.771
	-62.182	44.763

Table B.3: Acoustic Doppler Current Profiler deployment information.

Location	**Longitude (dd)**	**Latitude (dd)**	**Depth (m)**	**Sampling frequency (h)**	**ADCP data date range (mm/dd/yyyy)**	**Species**
Liscomb	-62.0709	44.8523	53	0.5	02/07/2019 – 09/29/2019	*M. membranacea,* *S. droebachiensis*
Ship Harbour	-62.7651	44.7025	32.2	2	12/7/2018 – 09/24/2019	Laminarian kelps

Table B.4: Summary of runs for particle tracking simulations. Number below species refers to interval at which particle locations were extracted from the model (e.g. every 96 hours for *S. droebachiensis*).

Run number	**Species**	**Release date**	**End simulation**
1	*Stronglyocentrotus droebachiensis* (96 hours)	2019-02-01 12:00	2019-04-02 12:00
2		2019-02-05 12:00	2019-04-06 12:00
3		2019-02-10 12:00	2019-04-11 12:00
4		2019-02-15 12:00	2019-04-16 12:00
5		2019-02-20 12:00	2019-04-21 12:00
6		2019-03-01 12:00	2019-04-30 12:00
7		2019-03-05 12:00	2019-05-04 12:00
8		2019-03-10 12:00	2019-05-09 12:00
9		2019-03-15 12:00	2019-05-14 12:00
10		2019-03-20 12:00	2019-05-19 12:00
11	*Membranipora membranacea* (84 hours)	2019-07-01 12:00	2019-07-29 12:00
12		2019-07-05 12:00	2019-08-02 12:00
13		2019-07-10 12:00	2019-08-07 12:00
14		2019-07-15 12:00	2019-08-12 12:00
15		2019-07-20 12:00	2019-08-17 12:00
16		2019-08-01 12:00	2019-08-29 12:00
17		2019-08-05 12:00	2019-09-02 12:00
18		2019-08-10 12:00	2019-09-07 12:00
19		2019-08-15 12:00	2019-09-12 12:00
20		2019-08-20 12:00	2019-09-17 12:00
21	Laminarian kelps (12 hours)	2019-10-15 12:00	2019-10-17 12:00
22		2019-10-20 12:00	2019-10-22 12:00
23		2019-10-25 12:00	2019-10-27 12:00
24		2019-10-30 12:00	2019-11-01 12:00
25		2019-11-04 12:00	2019-11-06 12:00
26		2019-11-15 12:00	2019-11-17 12:00
27		2019-11-20 12:00	2019-11-22 12:00
28		2019-11-25 12:00	2019-11-27 12:00
29		2019-11-30 12:00	2019-12-02 12:00
30		2019-12-04 12:00	2019-12-06 12:00

Table B.5: Accuracy results for random forest model used to predict the distribution of suitable habitat for kelp in the Eastern Shore Islands Area of Interest. Observational data were divided into training and validation sets by 2/3 and 1/3, respectively.

			Confusion matrix			
			Predicted			
Data usage			Absent	Present	**Class error (%)**	**Total error (%)**
Training (n = 330)	Observed	Absent	173	30	14.78	20.7
		Present	41	99	29.29	
Validation (n = 162)		Absent	84	22	20.75	21.7
		Present	14	46	23.3	

Table B.6: Cost breakdown for applying the 3D approach including the development of a fine-scale regional physical ocean model and applying outputs to calculate dispersal trajectories for target species.

Model stage	Item	Details of cost	Cost (CAD$)
Development	Post-doctoral researcher	2-year model development	120 000
	Base model	Code and expertise from physical oceanographer	5 000
	Computation	256 CPUs utilized for 3 days week^{-1} for 15 months at $7.155 per instance hour^{-1} ((“AWS pricing calculator” 2023)	184 000
Validation	In-situ measurements	4 ADCPs, moorings, tide gauges, TS profiles	100 000
Operation	PhD student	2 months to run particle tracking simulations and process outputs	4 400
	Total		**413 400**

Table B.7: Cost breakdown for applying the 2D approach to calculate dispersal area for a target species.

Item	Details of cost	Cost (CAD)
ADCP	Purchase price for instrument	20 000
Instrument deployment	Boat time and divers (2 days)	2000
Data analysis	Clean and process current data. Assemble input data for 2D approach and apply.	1 000
Total		**23 000**

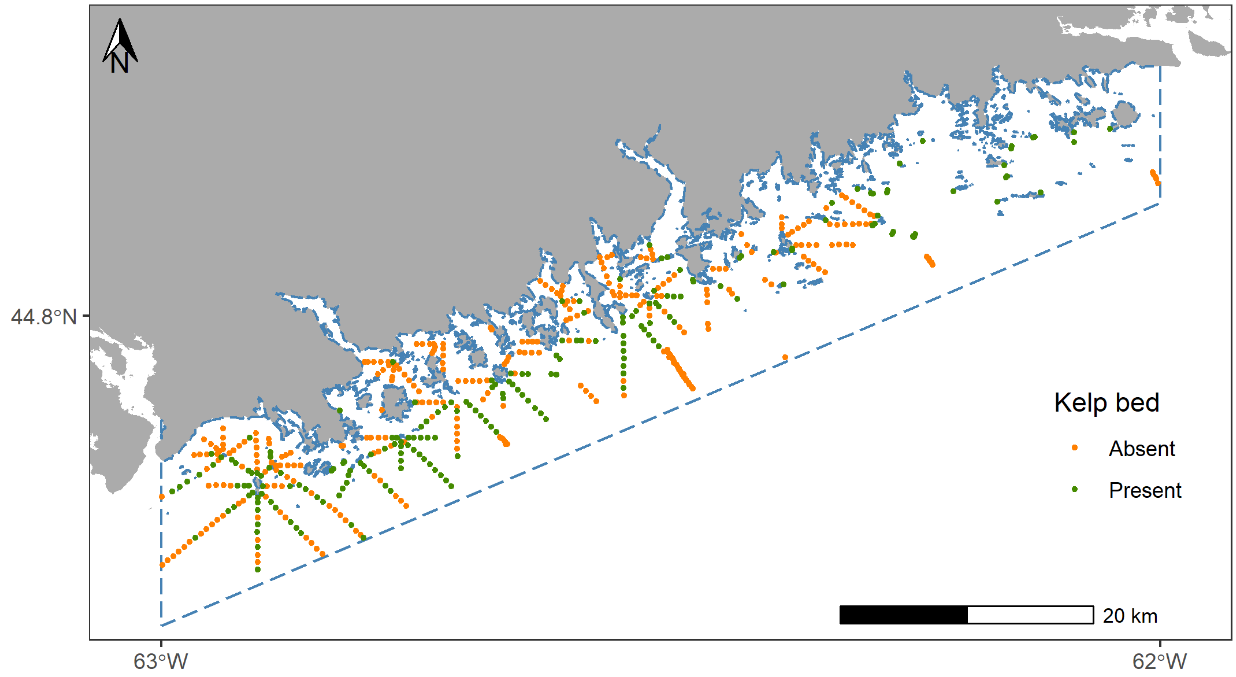


Figure B.1: Map of point location data used to train a random forest model to predict the distribution of suitable habitat for kelp within the Eastern Shore Islands (ESI) proposed Marine Protected Area (between 62° W and 63° W). The model domain is indicated by the blue outline and is bound by the 40-m isobath and longitudinal boundaries of the ESI.

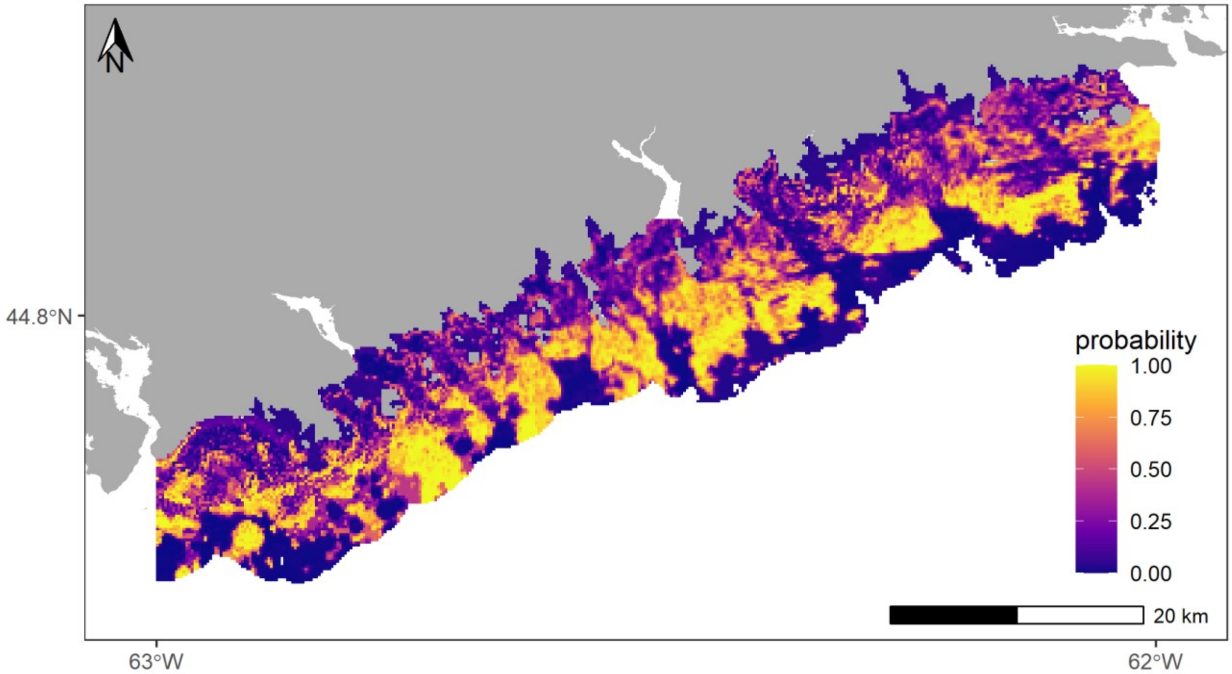


Figure B.2: Map of raw probabilities from random forest model predicting the distribution of suitable habitat for kelp in the Eastern Shore Islands Area of Interest (between 62° W and 63° W).

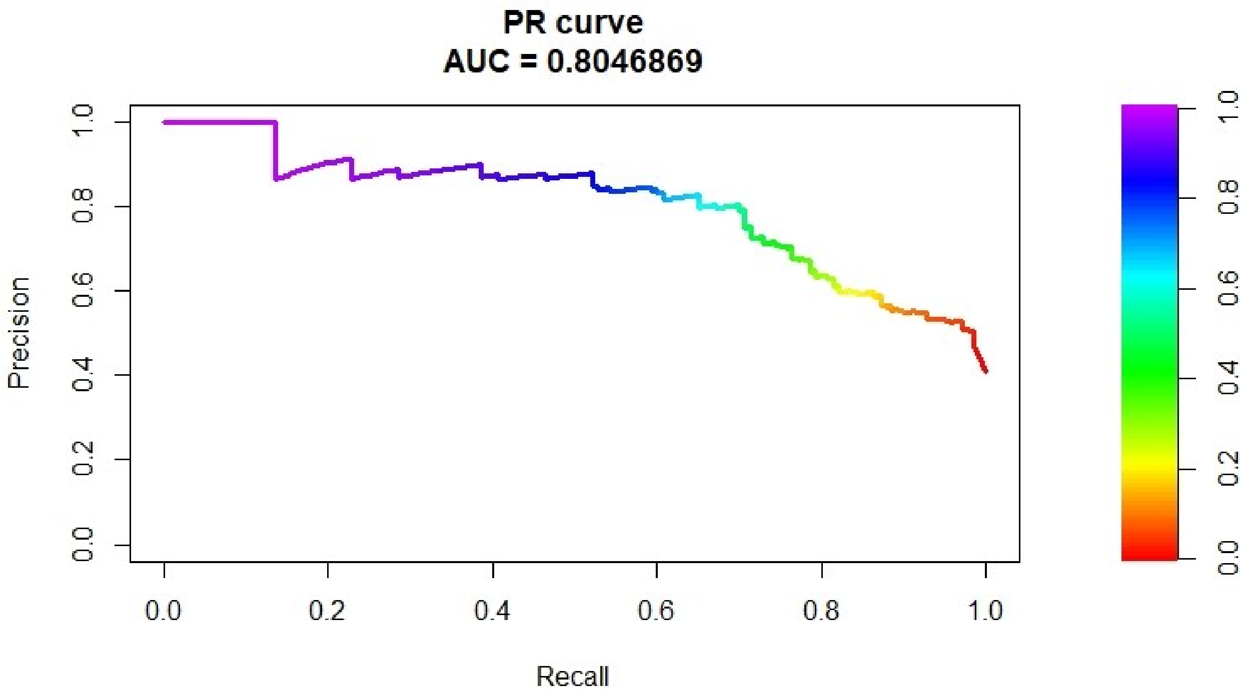


Figure B.3: Precision-recall curve for random forest model used to predict suitable habitat for kelp in the Eastern Shore Islands Area of Interest.

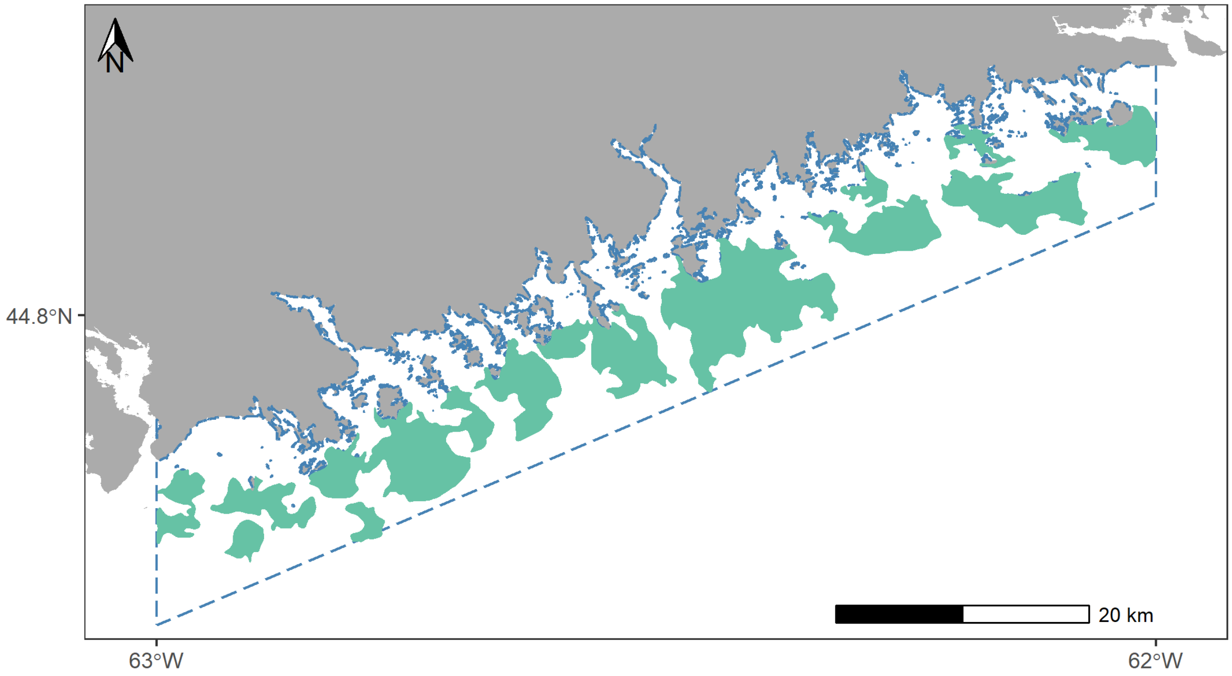


Figure B.4: Map of kelp patches (green polygons) predicted from the random forest model within the Eastern Shore Islands (ESI) proposed Marine Protected Area (between 62° W and 63° W). The dashed line indicates the model domain and is bound by the 40-m isobath and longitudinal boundaries of the ESI.

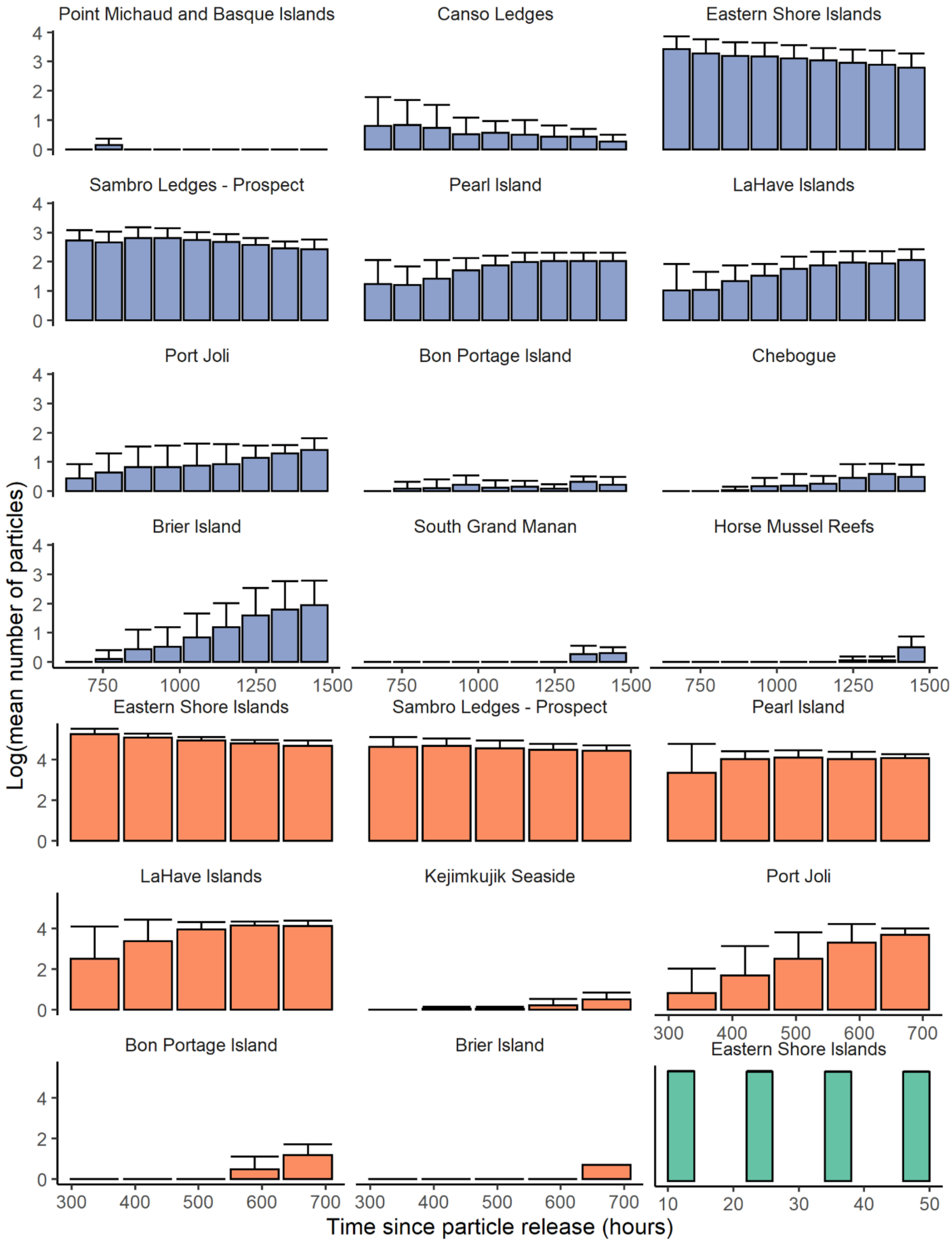

Point Michaud and Basque Islands
Canso Ledges
Eastern Shore Islands
Sambro Ledges - Prospect
Pearl Island
LaHave Islands
Port Joli
Bon Portage Island
Chebogue
Brier Island
South Grand Manan
Horse Mussel Reefs
Eastern Shore Islands
Sambro Ledges - Prospect
Pearl Island
LaHave Islands
Kejimkujik Seaside
Port Joli
Bon Portage Island
Brier Island
Eastern Shore Islands
Log(mean number of particles)
Time since particle release (hours)
0
1
2
3
4
750
1000
1250
1500
300
400
500
600
700
10
20
30
40
50

Figure B.5: Mean number of particles (+ standard deviation) crossing the boundaries into each coastal proposed marine protected area (MPA) during the 3D simulations for laminarian kelps (green), *Membranipora membranacea* (orange), and *Strongylocentrotus droebachiensis* (purple) during their competent propagule duration (CPD). The label at the top of each plot indicates the name of the proposed coastal MPA. MPAs not reached by any particles during any simulation are not shown.

B.1 Details of random forest modelling

B.1.1 Kelp habitat mapping

In the drop camera surveys in 2017, 3-minute video clips (spanning 5 – 50 m in distance because of vessel drift) were collected at 10 cm – 2 m above the seafloor at a series of locations in a radial pattern from selected islands using a SV-HD-SVI camera (Shark Marine Technologies Inc., St. Catharines, Ontario; (Vandermeulen 2017); *n* = 445) [for details see Vandermeulen (2018)]. In 2019, four 15 – 20 km-long video transects were sampled from inshore (~35 m depth) to offshore (~130 m depth), with the drop-camera Campod at ~1 m above the seafloor. From the Campod video, image framegrabs were extracted in ArcMap at 200-m intervals (Metaxas, Murillo-Perez, unpublished data; *n* = 339). Presence or absence of kelp habitat was recorded for each drop video or extracted image. We filtered the data to only include sample locations from within our model domain for training and validating the species distribution model (see below).

At 17 additional locations, we completed 100-120-meter transects with SCUBA using hand-held GoPro 2 or GoPro 5 cameras set to 1080 HD, at 6 and 9 m depth, between 4 and 9 August 2018. The camera was attached to a 1.5-m plumb line, allowing divers to swim at a constant height above the seafloor and providing a scale for post-processing images. We extracted frame-grabs from the video footage at 10-s intervals and evaluated every 3rd non-overlapping image (30-s interval) for percent cover of kelp habitat. We replaced images of poor quality by the preceding or ensuing one. Before analysis, we enhanced images by modifying the contrast, highlight and saturation settings using Photos for Windows. We extracted percent cover of kelp using the points method in ImageJ, where 100 points were overlaid on each image, and the feature directly behind each point recorded. In 2020, we conducted 17 150-m long transect surveys during which two snorkelers swam in parallel trajectories 2 m apart and recorded the presence/absence of kelp habitat.

B.1.2 Species distribution modelling

A digital elevation model and spatial layer of relative wave exposure at 35-m resolution were obtained from DFO (O’Brien et al. 2022). A physiographic coastline classification map was based on (Greenlaw et al. 2013). The coastline classification map was processed to create a binary variable for presence of hard substrate (1 = true, 0 = false) as suitable substrate for kelp (Table B.1). The relative wave exposure index is calculated as the product of fetch (*f*; in km), average wind speed (*s*; km h^{-1}), and wind frequency (*k*; percentage of time the wind blows in a particular direction), summed over 32 compass headings (Keddy 1984):

$$Relative\ Wave\ Exposure\ Index = \sum_{i=1}^{32} f_i\, s_i\, k_i\,.\,(1)$$

Wind velocity data for the relative wave exposure index calculations were obtained from the Copernicus Climate Data Store at 0.25 ° resolution (Hersbach et al. 2018). All predictors were upscaled to a resolution of 210 m in raster format for the entire study domain. This spatial resolution represents an intermediate value between the spatial extent of observations at each point location (~ 50 m) and the distance between observation locations (~ 650 m).

We selected to use a random forest model because correlated predictor variables do not introduce bias. Additionally, a random forest model can be validated using "out-of-bag" data that is inherent in the model design due to bootstrap sampling. A random forest model is a type of classification and regression tree machine learning algorithm that 'grows' a forest of trees with bootstrap sampled data. Each tree is successively split into two groups based on a single random predictor (Breiman 2001). The trees are then ensembled by majority vote. We divided our dataset into training and validation sets, using ⅔ and ⅓ of the full dataset, respectively. Model calculations were completed in R 4.0.2 using the *randomForest* package (Liaw and Wiener 2002, R Core Team 2020). We assessed the error of the final model using out of bag error, validation error, and the area under the precision-recall curve. Raw probabilities were converted to a binary "presence/absence" classification based on the precision-recall curve.

We defined kelp patches from the raw raster prediction by making assumptions about patch size and contiguity using the '*smoothr'* package in R (Strimas-Mackey 2020). First, to remove noise introduced by the fine resolution raster grid, all cells classified as "absent", but contiguous to cells classified as "present" on all sides, were converted to "present". Next, we smoothed the edges of kelp patches, using Gaussian kernel regression. Since we aimed to release > 100,000 propagules per patch (see below), we only retained the largest kelp patches (threshold = 3 km^2) that encompassed the full spatial range across the ESI and resulted in a computationally feasible number of patches. The centroids of each of the resulting patches were used as the release point for propagules to calculate dispersal for kelps (*S. latissma* and *L. digitata*) and *M. membranacea*.

The current distribution of the sea urchin *S. droebachiensis* is limited because of mass mortality due to disease outbreaks caused by the amoeba *Paramoeba invadens* (Feehan and Scheibling 2014). Based on a recent survey with the drop-camera Campod (see details in Kelp habitat mapping), the present depth range of *S. droebachiensis* in the ESI extends from 45 m to 100 m. We selected 16 locations in the survey transects (four per transect) of the drop-camera as release points for *S. droebachiensis* larvae along the depth range in which they were observed (45, 60, 75, and 90 m).

To determine the distribution of kelp in the ESI, we trained a random forest model that accounts for the main physical and geomorphic factors but were unable to represent the full complexity of the ecosystem. Ocean properties including temperature, salinity and nitrate concentration were not included in the model due to a mismatch in resolution of available data. Biotic controls on kelp, such as distributions of the grazer *S. droebachiensis* and the invasive species *M. membranacea*, were also not included in the model. *S. droebachiensis* have experienced mass mortality events in recent years (Feehan and Scheibling 2014) and are not currently present in kelp beds at ESI (personal observations). The invasive bryozoan *M. membranacea* can cause defoliation of kelp beds (Denley and Metaxas 2017) but data resolution was not sufficient to include it as a predictor in the random forest model. However, we are confident that our random forest model provides a realistic distribution of kelp habitat in the ESI because of the accuracy of the validation set (79.3 %) combined with empirical validation of the model output in situ.

The random forest model produced a mosaic distribution of kelp patches in the Eastern Shore Islands (Figure B.2, Figure B.4). The depth range of predicted kelp patches was 0 – 41 m (mean: 17.75 m ± 8.74), and kelp beds were more often predicted in areas with a higher relative wave exposure. We optimized the random forest model with 500 trees and 2 variables randomly sampled for each split. The final model had an out of bag error of 20.7% and validation set error of 21.7% (Table B.5). Depth was the most important predictor variable, followed by relative wave exposure index and suitable habitat, with mean decreases in Gini index of 59.54, 53.43, and 31.14, respectively. The threshold from the precision-recall curve to convert estimated probabilities to presence/absence of kelp patches was 0.44 with associated recall and precision values of 0.729 and 0.723, respectively (Figure B.2). After post-processing of the distribution layer, there were 13 kelp patches occupying 329.4 km^2 or 31.6 % of the model domain area (depth < 40 m). The average patch size (after removing patches smaller than 3 km^2) was 25.3 km^2.

B.2 Calculation of rates of propagule release

B.2.1 *Strongylocentrotus droebachiensis*

We calculated the number of oocytes released per unit area following methods described in (Meidel and Scheibling 2001). In the Eastern Shore Islands (ESI), urchins are found between 40 and 100 m at low densities (1.47 ± 1.55 ind m^{-2}). We measured test diameter of urchins and calculated adult density in 5-mm size classes from image framegrabs extracted from four 15 – 20 km-long video transects. These video transects, conducted in 2019, sampled from inshore (~35 m depth) to offshore (~130 m depth), with the drop-camera Campod at ~1 m above the seafloor (Metaxas, Murillo-Perez, unpublished data; n = 339). Based on these data, we used fecundity parameters for post-transitional barrens from Scheibling and Meidel (2001).

We calculated total wet body mass (B_j) for urchins in 5-mm size classes using a regression relationship developed by Meidel and Scheibling (2001).

$$B_j = e^{2.81\,lnj-7.0} \text{ (1)}$$

In equation 1, j is the median test diameter (mm) for each size class.

We calculated fecundity (E_j), in units of spawned dry mass (g), for urchins in 5-mm size classes. This relationship, developed by Meidel and Scheibling (2001), converts the proportion of wet to dry gonad weight spawned.

$$E_j = 0.249\, I_j R B_j \text{ (2)}$$

In equation 2, I_i is the proportion of total body weight that is gonad, R is the proportion of gonad weight spawned, and B_j is total wet body weight (g), derived from equation 1.

We calculated the number of eggs spawned per unit area (O; oocytes m^{-2}), as the product of the number of eggs spawned for each adult female, summed across size classes.

$$O = Daf\ \sum_j p_j \frac{E_j}{5.56\times10^{-7}} \text{ (3)}$$

In equation 3, D is the average density of urchins (ind m^{-2}), a is the proportion of adults (test diameter greater than 25 mm), f is the proportion of females, p_j is the proportion of urchins in each size class, and 5.56 x 10^{-7} is the dry weight per egg (g).

For our calculations, we used values of I_j and R from Meidel and Scheibling (2001). We assumed a 1:1 sex ratio ($f = 0.5$) (Meidel and Scheibling 1998, 2001; (Meidel and Scheibling 1998, 2001, Filbee-Dexter and Scheibling 2014). We used empirical estimates of D, a, and p_j from the ESI. Lastly, we assumed a maximum fertilization rate of 18 %, based on calculations from a comparable density of urchins from (Wahle and Peckham 1999) to convert number of eggs to zygotes.

Based on these calculations, sea urchins produce 4116 zygotes m^{-2}. We used the value of 5000 zygotes m^{-2} in the 3D model.

B.2.2 *Membranipora membranacea*

We calculated the number of oocytes released per unit area combined for the two dominant kelp substrates (*Saccharina latissima* and *Laminaria digitata*). We measured colonies of *M. membranacea* on each species of kelp in the ESI in 2019 (Attridge et al. in review, Pratt et al. 2021 and in review). Colonies were divided into five size classes (< 1 mm, 1 – 3 mm, 3 – 5 mm, 5 – 8 mm, and > 8 mm) following (Denley et al. 2019a). We obtained average fecundity of *M. membranacea* colonies of each size class per kelp substrate from Denley et al. (2019).

$$O = \sum_{s} D_s \sum_{j} C_{js} F_{js} \quad (4)$$

In equation 4, O is the number of oocytes spawned per unit area (oocytes m^{-2}), s refers to each of the two numerically dominant kelp substrates (*S. latissima and L. digitata*), j refers to five size classes, D_s is average density of kelp (ind m^{-2}), C_{js} is the number of *M. membranacea* colonies on each kelp plant, and F_{js} is the average number of oocytes released per colony.

Fertilization rates for oocytes are extremely high (at least 98 % fertilization success observed by (Temkin 1994)) because fertilization occurs in the intertentacular organ after spermatozeugmata (an aggregate of 32 or 64 sperm) are drawn into the lophophore by feeding currents of *M. membranacea* colonies. We therefore assumed a fertilization rate of 100 %.

Based on these calculations, *M. membranacea* produce 135 055 zygotes m^{-2}. We used the value of 1 x 10^5 zygotes m^{-2} in the 3D model.

B.2.3 Laminarian kelps

We calculated the number of spores released per unit area (spores m^{-2}) for each of the two numerically dominant kelp species (*Laminaria digitata* and *Saccharina latissima*) using data from the field and literature.

$$P_s = a_s D_s A_s G_s H_s \times 2 \quad (5)$$

In equation 5, P is the number of spores per unit area (spores m^{-2}), s represents each of the two dominant kelp species (*Saccharina latissima* and *Laminaria digitata*), a is the proportion of fecund plants, D is the average density of kelp (ind m^{-2}), A is the total sorus area per plant (cm^2), G is the average sporangial density (spores cm^{-2}), and H is the number of spores per sporangium. The calculated value of P_s using equation (5) is multiplied by two to account for both sides of the kelp blade.

For our calculations, we used G values for each kelp species from (Chapman 1984). We empirically measured the proportion of fecund plants (a) in the ESI in October 2021 using data from ten quadrats at each of three sites and each of two depths (6 m and 9 m) per site (Savard-Drouin & Metaxas, unpublished data). Data were pooled from all recorded kelps (n = 222 for *L. digitata* and n = 172 for *S. latissima*). We also collected reproductively mature kelps (10 per species for three sites at two time periods) to determine for sorus area (A_s) (Savard-Drouin, Metaxas unpublished data). We traced sorus area onto acetate sheets and then processed images in ImageJ (n = 59 for *L. digitata* and n = 59 for *S. latissima*). All empirical measurements were collected in October and November of 2021 and data were pooled across the two sampling periods. We assumed that each sporangium contained 32 spores, with a 1:1 sex ratio (Schreiber 1930, Lüning 1980). Therefore, we used a H_s value of 16. Based on our calculations, *L. digitata* and *S. latissima* will release 1.2 x 10^{10} and 1.1 x 10^{10} spores over one spawning season, respectively; however, only a small proportion differentiate into gametophytes (Gaylord et al. 2006). We divided the calculated number of released propagules by the ratio of spores to microscopic recruits measured by Chapman (1984), as 10^4 spores: 1 gametophyte. This approach allowed us to model an ecologically relevant number of propagules within our logistical capabilities.

Based on these calculations, kelps produce 1.2 x 10^6 spores of *Laminaria digitata* m^{-2} and 1.1 x 10^6 spores of *Saccharina latissima* m^{-2}. We used the value of 1 x 10^6 spores m^{-2} to represent spore production for both species combined in the 3D model.

APPENDIX C

CHAPTER 4

Table C.1: Confusion matrices summarizing random forest model accuracy for training and validation sets.

Data use	**Confusion matrix**				**Class error (%)**	**Total error (%)**
			Predicted			
			Absent	Present		
Training (n = 682)	Observed	Absent	309	82	20.97	27.13
		Present	103	188	35.40	
Validation (n = 319)		Absent	134	39	22.54	23.82
		Present	37	109	25.34	

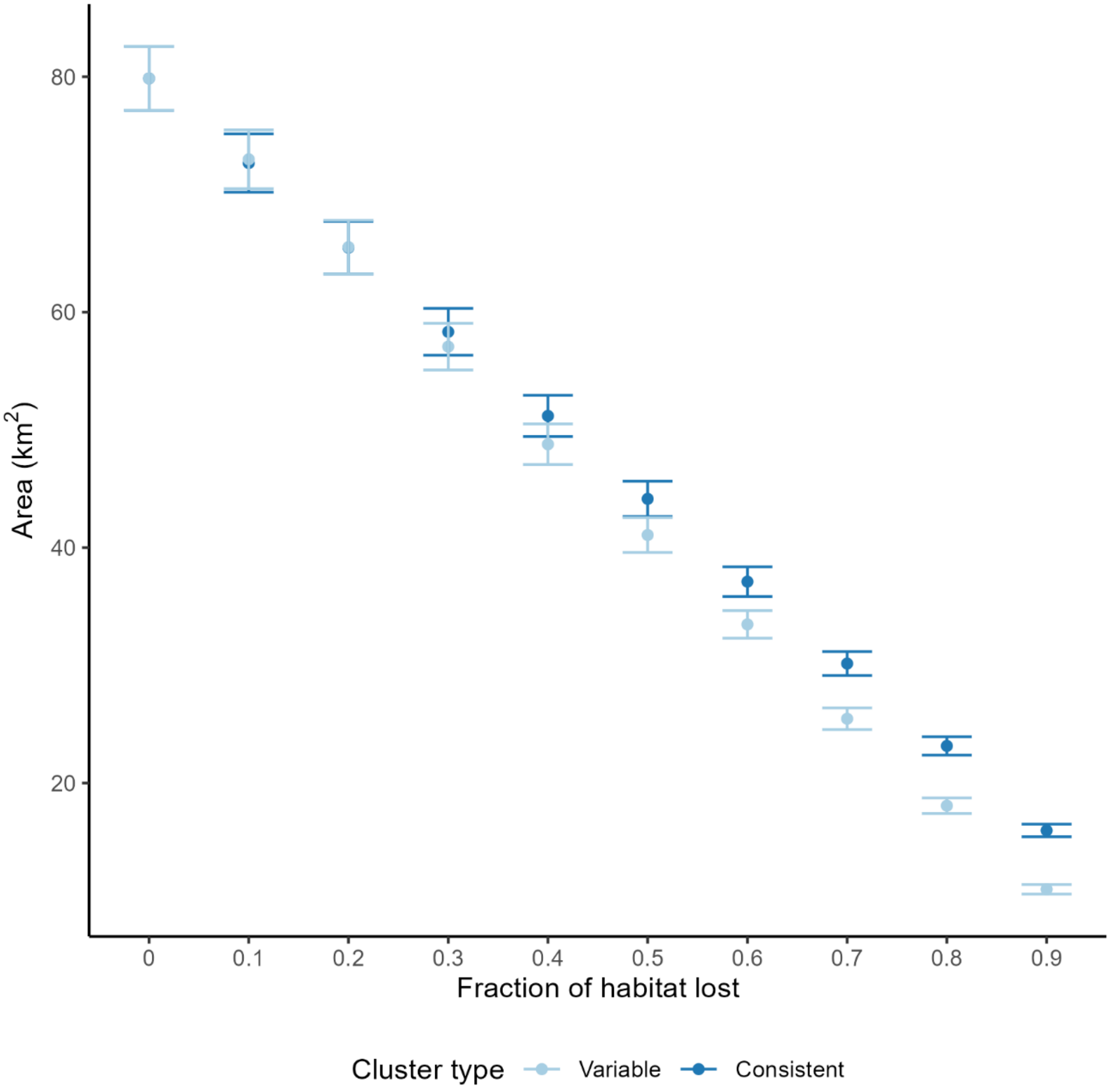


Figure C.1: Mean cluster area (km^2) across clusters for each habitat loss treatment in each of the two *in silico* habitat loss experiments, where clusters are either re-clustered (variable; light blue) or held constant (consistent; dark blue) after each habitat loss increment. Error bars represent the 95 % confidence intervals for each habitat loss treatment across 100 random seeds.

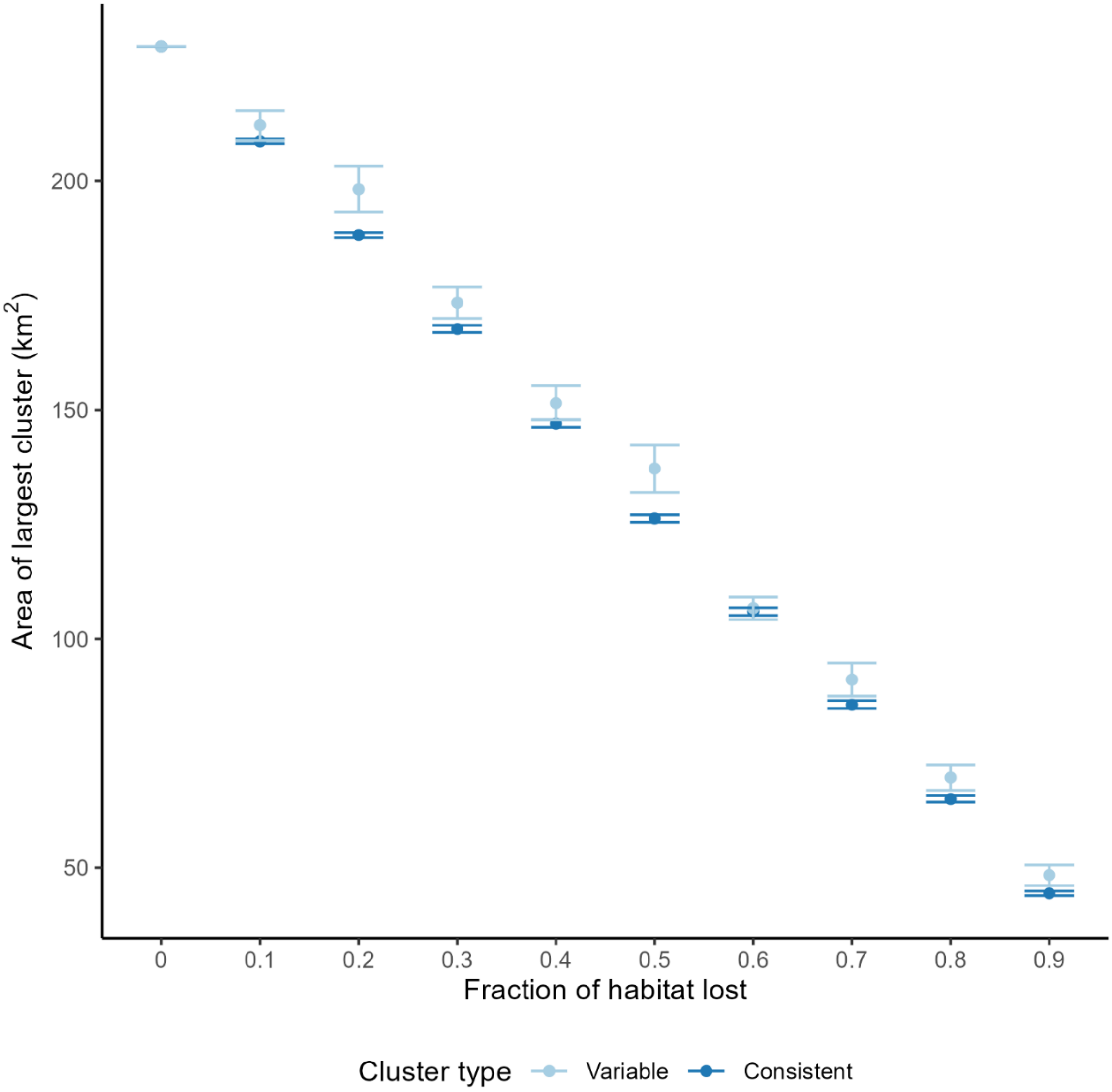


Figure C.2: Mean area of the largest cluster (km^2) across clusters for each habitat loss treatment in each of the two *in silico* habitat loss experiments, where clusters are either re-clustered (variable; light blue) or held constant (consistent; dark blue) after each habitat loss increment. Error bars represent the 95 % confidence intervals for each habitat loss treatment across 100 random seeds.

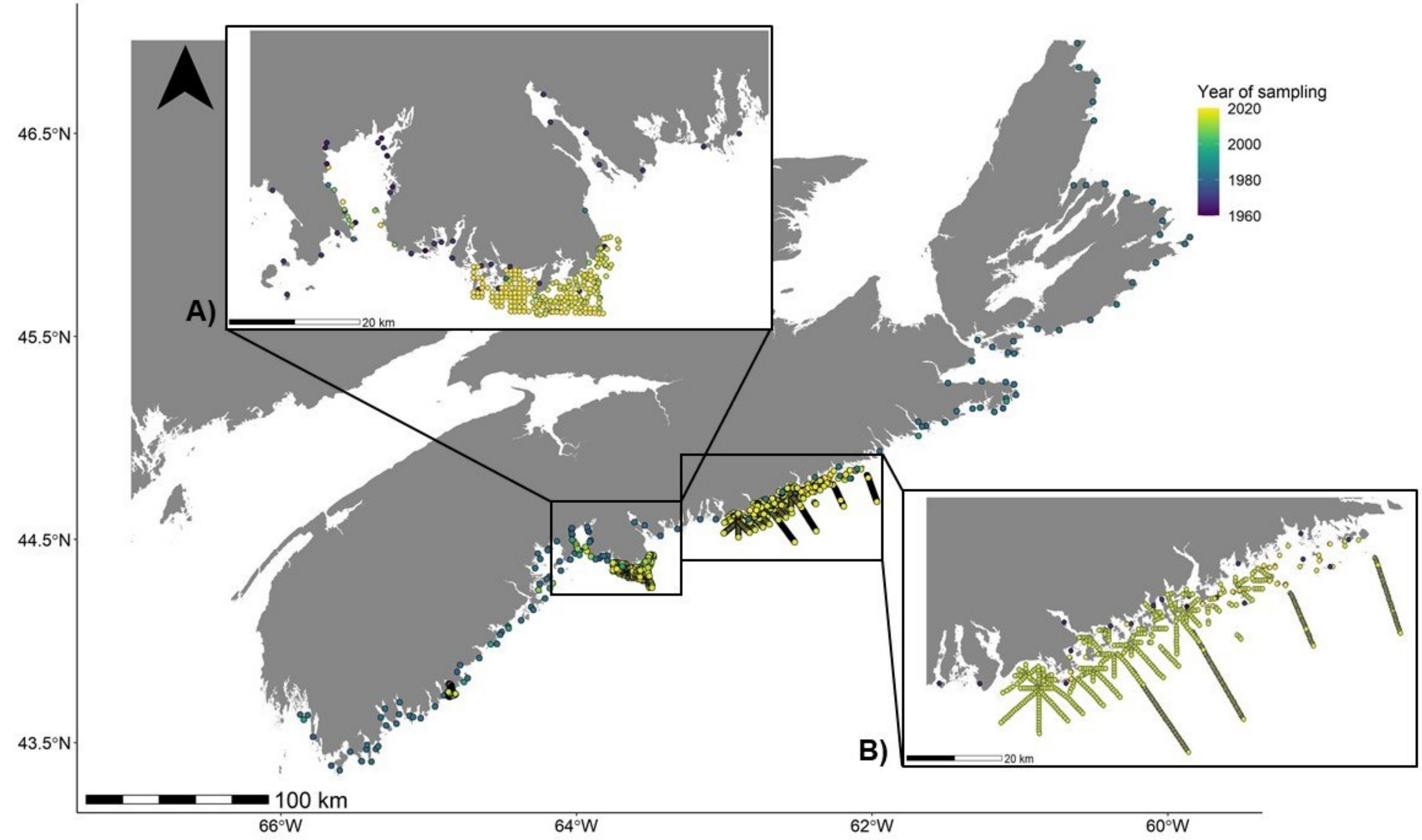


Figure C.3: Survey sites for kelp abundance within the study domain, extracted from a literature search (1980 to 2021) with year of sampling ranging from 1977 to 2021 (n = 1383). Subset ‘A’ is St. Margaret’s Bay and subset ‘B’ is Eastern Shore Islands, Nova Scotia.

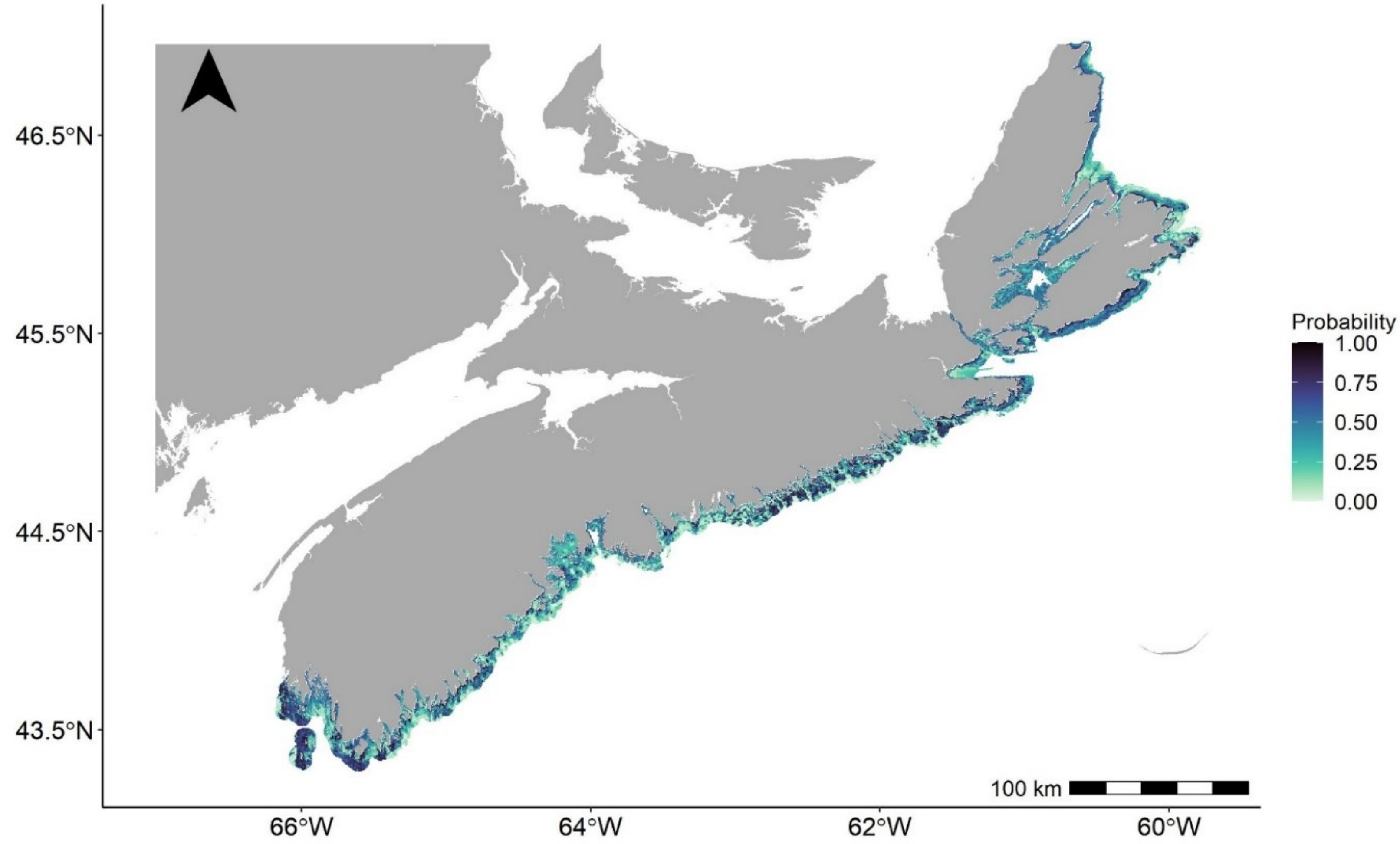


Figure C.4: SDM predicted probabilities of kelp suitable habitat within the model domain.

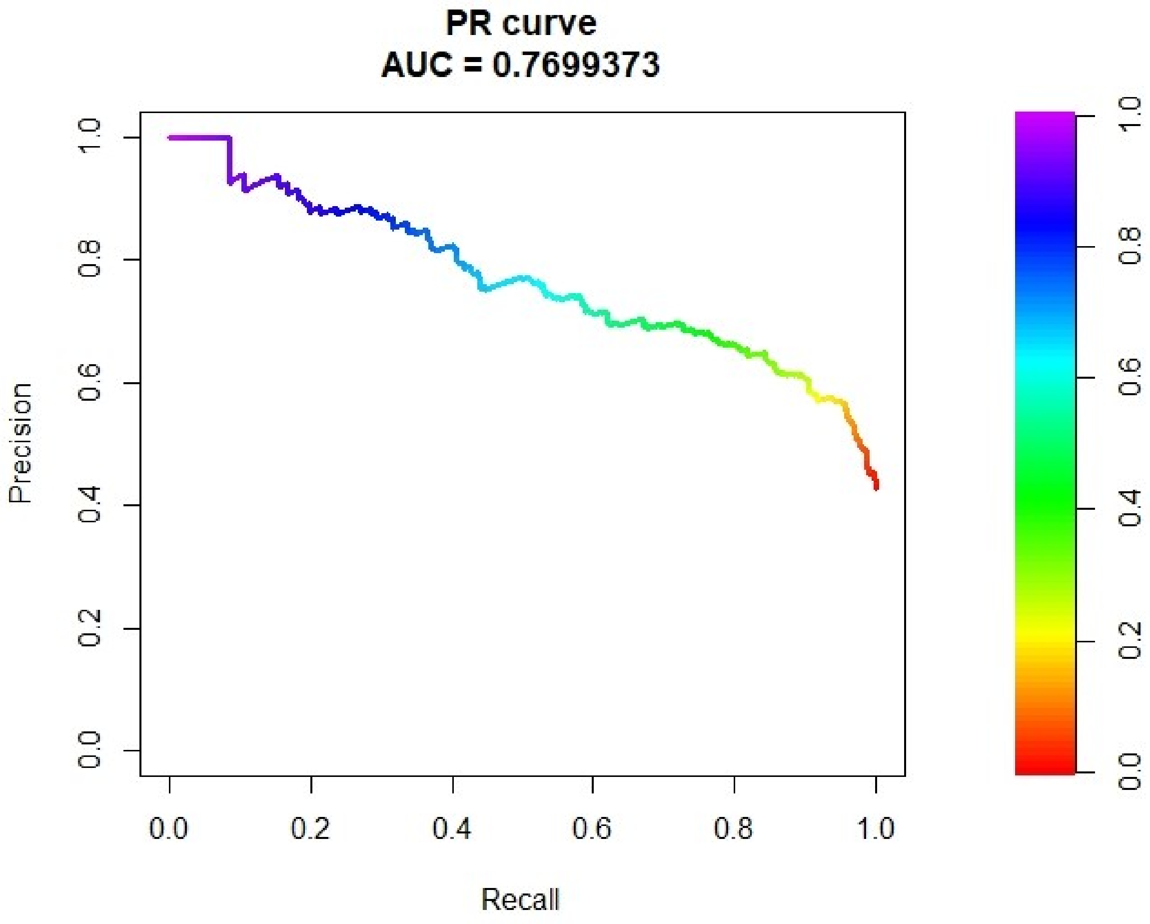


Figure C.5: Precision-Recall curve used to determine the threshold to convert probability of kelp presence to a binary response. The colour ramp to the right of the plot corresponds to thresholds between 0 and 1 for converting probabilities to presence/absence categories. The optimal decision threshold occurs at 0.454, with associated recall (0.715) and precision (0.696) values.

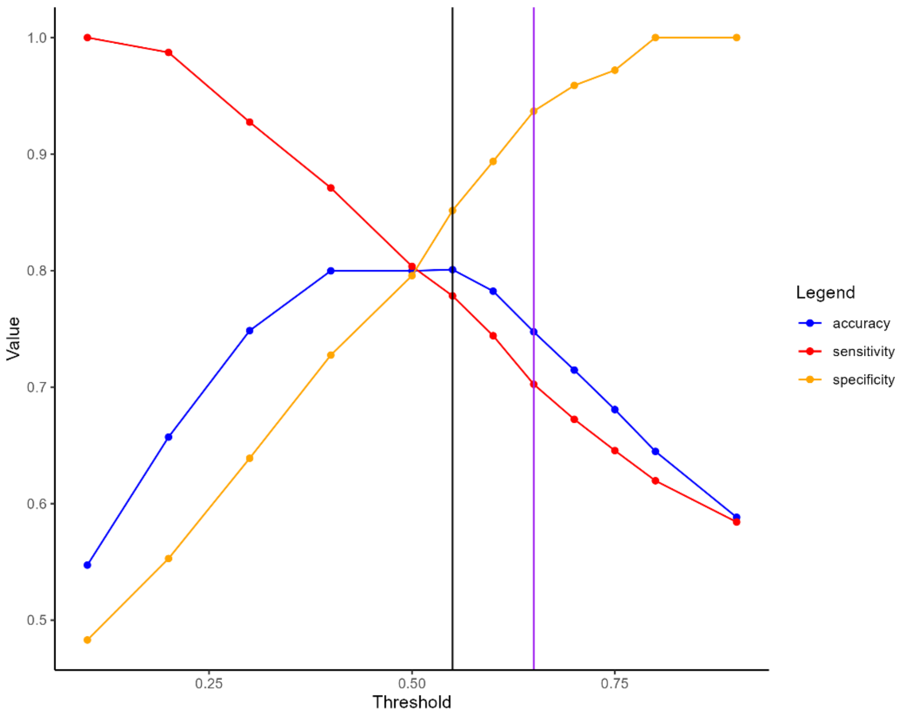


Figure C.6: Performance metrics of random forest model at upscaled model resolution of 630 m.

C.1 Details random forest model for the Atlantic Coast of Nova Scotia

C.1.1 Literature review

We conducted a primary and grey literature search to collate available data on kelp abundance. We focused on the Atlantic coast of Nova Scotia, from Cape Breton (Meat Cove) (N 47.028°, W -60.558°) to Cape Forchu in the southwestern shore (N 43.823°, W -66.126°) (hereafter "the study domain") with a depth limit of 50 m. We sourced peer-reviewed papers from 1980 to 2021 using Google Scholar (https://scholar.google.ca) and Novanet (https://novanet.ca) to search for publications that observed or measured any kelp species found in the study domain. We converted all measures of abundance (density, percent cover, biomass etc.) to a binary measure of presence/absence. Our compiled dataset included site name, latitude, longitude, year of sampling, and presence or absence of kelp. We extracted a total of 1383 unique observations within the study domain (Figure C.3). In some cases, multiple observations existed for the same location which reflected alternative states of the community (kelp bed, urchin barrens, turf dominance). In this case, a location was scored as "kelp presence" if kelp was present for any one of the records, indicating that the habitat was suitable for kelp even though biological factors may have led to temporary defoliation.

C.1.2 Species distribution model

We created a species distribution model (SDM) for kelp suitable habitat using five ecological predictor variables: depth, slope, bathymetric position index (BPI), substrate type, and relative exposure index (REI).

DFO provided a Digital Elevation Model (DEM) at 35-m resolution. We derived slope and BPI from the DEM using R and ArcMap, respectively. Slope was calculated in degrees as per Horn's method (Horn 1981) using an 8-cell averaging neighborhood. Fine-scale BPI was calculated using the Benthic Terrain Modeler (BTM) 3.0 toolkit at a 1-cell inner radius and 9-cell outer radius averaging neighborhood. This neighborhood scale identifies local scale (315 m) bathymetric peaks and troughs. To minimize loss of BPI values in cells with proximity to land (closer than 315 m), we acquired a 20-m resolution terrestrial DEM of Nova Scotia (Service Nova Scotia 2000) and upscaled to 35 m to match the coastal DEM. A substrate classification shapefile for the Coastal Maritimes Region was obtained from (Greenlaw et al. 2013). Suitable (boulders, continuous bedrock, discontinuous bedrock) and unsuitable (gravel, mixed sediment, sand, mud) substrate types for kelp were converted to a binary layer (1 = TRUE, 0 = FALSE; Figure 5). REI is a measure of relative-wave exposure calculated from wind speed, wind frequency, and fetch (km) (Keddy 1982). We obtained a raster layer of calculated REI values for the study domain from (O’Brien et al. 2022). The data layer provided to us was calculated to the 50-m depth contour and 5-km distance offshore.

All predictor layers were scaled up to a 210-m cell resolution in raster format and cropped at the extent of the study domain. Values from the predictor layers were extracted at the coordinates of each unique site from the literature search. Only observations with values available for all predictor layers were retained for use in the species distribution model.

We used a classification Random Forest Model (RFM) to predict the distribution of kelp suitable habitat in the study domain. A RFM is a supervised learning algorithm that constructs an ensemble of ‘decision trees’ and combines their predictions by majority vote (Breiman 2001). The algorithm builds decision trees from a ‘bootstrapped’ dataset using a random subset of predictor variables at each split of the tree. We selected to use this type of model because it has high performance accuracy with little variable tuning and has demonstrated effectiveness for the purpose of species distribution modeling (Li and Wang 2013).

The RFM was optimized and run using the ‘randomForest’ package in R Studio, with 500 decision trees (n) and 2 predictors (mtry) sampled at each split. Data were split into training (2/3) and validation (1/3) sets. We evaluated model performance using out-of-bag (OOB) error, area under the receiver-operator characteristic curve (AUC ROC), and area under the precision-recall curve (AUC PRC). We used the Gini index and Boruta algorithm to rate variable importance and ensure each predictor was significantly improving model performance, respectively.

The RFM produces probability values (for the presence of kelp and thus suitable habitat) for each grid cell in the study domain (Figure C.4). We converted probabilities of kelp occurrence to a binary response variable using the PRC curve. A PRC curve plots recall on the x-axis and precision on the y-axis. Recall (also called sensitivity) is equal to the number of true positives divided by the sum of true positives and false negatives from the confusion matrix. Precision is equal to the number of true positives divided by the sum of true positives and false positives from the confusion matrix. We opted to use a PRC curve instead of the more commonly use receiver-operator characteristic (ROC) curve because our data was imbalanced with more absences than presences (Saito and Rehmsmeier 2015). Since our focus was to correctly identify suitable kelp habitat (kelp presence), using the PRC curve was advantageous because true positives are incorporated in both measures. Each point on the curve refers to the precision and recall associated with a specific threshold (above which probabilities are converted to 1 and vice versa). The location on the curve with the shortest distance to the top-right corner (1,1) is the point of optimized classification and was used as the threshold value (Liu et al. 2005).

The most important predictor in the RFM, according to the Gini index, was depth (101.7), followed by REI (75.9), slope (67.2), BPI (66.5), and substrate type (19.3). The Out-of-bag (OOB) error for the training and validation sets were 27.13% and 23.83%, respectively (Table C.1). We obtained a similar OOB error rate (24.48%) when training the RFM with 9/10 of the data, demonstrating that the training set was sufficiently large for accurate model predictions with the predictor variables. The RFM exhibited a high area under the PRC (0.770) (Figure C.5). From the PRC plot, optimal model recall (0.715) and precision (0.696) resulted in a decision threshold of 0.454. However, we upscaled our spatial resolution from 210 m to 630 m grid cells using the mean, Additionally, we clipped the domain of the model to only include the Atlantic Coast of Nova Scotia from Canso Ledges to Yarmouth for further analysis. We tested the accuracy, sensitivity, and specificity of the model with training and test data at the upscaled resolution to determine the threshold to convert probabilities to a binary classification (present/absent; Figure C.6). At the upscaled resolution (630 m), we selected a threshold of 0.55. We opted for a higher threshold because we wanted to minimize false positives whist maintaining the highest overall model accuracy.

Kelp presence was predicted across most of the entire extent of coastal Nova Scotia (Figure 4.2). High probabilities of kelp were predicted in Lobster Bay and Barrington Passage on the Southwestern shore, as well the Eastern shore, and the exposed Atlantic coast of Cape Breton. Large clusters of offshore patches were observed along Eastern Shore Islands (ESI), while smaller, more fragmented patches were predicted in embayments along the Southern shore such as Mahone Bay and the LaHave Islands. Larger kelp patches occurred farther towards the Southwestern shore, nearshore to locations such as Port Mouton, Western Head, and Yarmouth. We note that the predictions of kelp patch locations are based on data that account for habitat suitability but may not account for current state of the kelp beds.

APPENDIX D

CHAPTER 5

Table D.1: Modelling parameters for Lagrangian particle tracking simulations.

Species	**Laminarian kelps**	***Membranipora membranacea***
Time step for advection (s)	120	300
Time step for model output (m)	1	5
Time step for particle location output (h)	0.5	6
Length of particle tracking simulation (h)	48	672

Table D.2: Release times for kelp propagules.

Run number	Month	Day	Year
1	10	01	2018
2	10	06	2018
3	10	11	2018
4	10	16	2018
5	10	21	2018
6	10	26	2018
7	10	31	2018
8	11	05	2018
9	11	10	2018
10	11	15	2018
11	11	20	2018
12	11	25	2018
13	11	30	2018
14	12	05	2018
15	10	01	2019
16	10	06	2019
17	10	11	2019
18	10	16	2019
19	10	21	2019
20	10	26	2019
21	10	31	2019
22	11	05	2019
23	11	10	2019
24	11	15	2019
25	11	20	2019
26	11	25	2019
27	11	30	2019
28	12	05	2019

Table D.3: Release times for *Membranipora membranacea* propagules.

Run number	**Month**	**Day**	**Year**
1	07	01	2018
2	07	06	2018
3	07	11	2018
4	07	16	2018
5	07	21	2018
6	07	26	2018
7	07	31	2018
8	08	05	2018
9	08	10	2018
10	08	15	2018
11	08	20	2018
12	08	25	2018
13	08	30	2018
14	09	05	2018
15	07	01	2019
16	07	06	2019
17	07	11	2019
18	07	16	2019
19	07	21	2019
20	07	26	2019
21	07	31	2019
22	08	05	2019
23	08	10	2019
24	08	15	2019
25	08	20	2019
26	08	25	2019
27	08	30	2019
28	09	05	2019

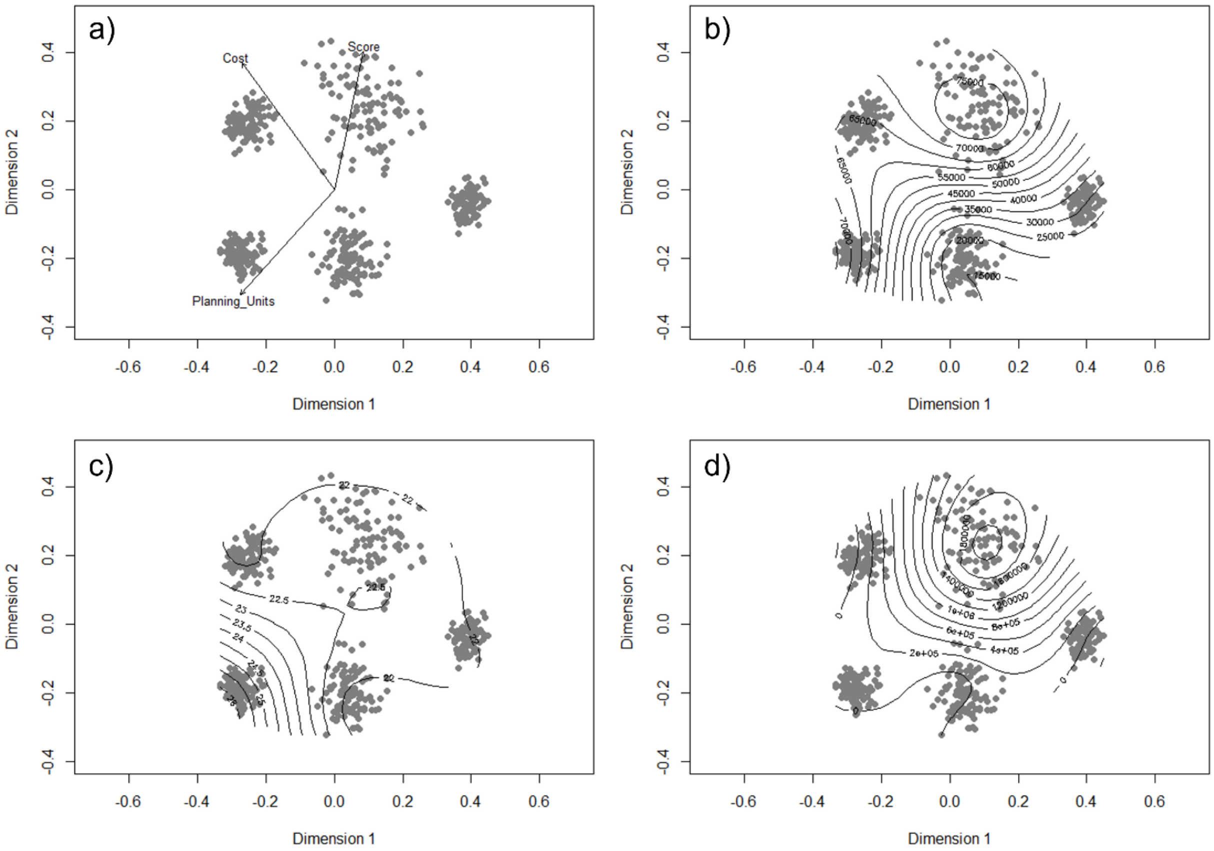


Figure D.1: Significantly correlated vectors and isopleth plots from a principal coordinates analysis (PCoA) based on the Jaccard similarity matrix. (a) Select explanatory variables significantly correlated with the PCoA surface ($p < 0.05$). Arrows reflect the direction of the relationship in non-dimensional space, and the length of the arrow reflects the relative importance of the variable. Isopleth plots for significantly correlated explanatory variables: (b) cost ($r^2 = 0.51$, $p < 0.001$), (c) number of planning units ($r^2 = 0.41$, $p < 0.001$), (d) score ($r^2 = 0.41$, $p < 0.001$).

APPENDIX E

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